International
Whaling
Commission

Report of the Special Meeting
of the Scientific Committee
on Sei and Bryde's Whales

La Jolla, California, December, 1974

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Preface

The Scientific Committee of the International Whaling Commission held a special meeting in December 1974 to discuss problems of sei and Bryde's whales, to develop the new management procedure adopted by the Commission in the previous June, and to consolidate the research plans for the proposed International Decade of Cetacean Research.

The report of this meeting was published in *Rep. int. Whal. Commn* 25, together with some of the background papers concerned with management questions. It was intended that the documents submitted to the sei and Bryde's whale part of the meeting should be published separately, with some additional papers prepared for the June 1975 meeting of the Committee. Various delays prevented the publication of this material until now.

Dr. P. B. Best acted as rapporteur for the sei and Bryde's whale meeting, arranged for the refereeing of the papers and carried out the first and major part of the editorial work involved.

The original report of the sei and Bryde's whale meeting is reproduced here (slightly edited) to put the following papers into perspective.

Contents

Report of the Special Meeting of the Scientific Committee on Sei and Bryde's Whales

La Jolla, 3–13 December, 1974

R. Gambell

Secretary to the Commission

The Committee met at 10 a.m. on 3 December 1974 and on subsequent days in the laboratory of the Southwest Fisheries Centre, by courtesy of the Director, Dr Brian J. Rothschild, under the chairmanship of K. R. Allen.

Present were:

Australia	K. R. Allen	
	J. L. Bannister	
	W. H. Dawbin	
Canada	E. D. Mitchell	
	V. M. Kozicki	
Iceland	J. Jonsson	
Japan	Y. Fukuda	
	F. Nagasaki	
	S. Ohsumi	
	H. Omura	
Norway	A. Jonsgard	
S. Africa	P. B. Best	
United Kingdom	R. Gambell	
USA	W. Aron	
	D. G. Chapman	
	L. Talbot	
	M. F. Tillman	
	D. W. Rice	
	R. Gilmore	Observers
	J. G. Mead	
	W. F. Perrin	
	W. E. Schevill	
	T. Smith	
USSR	R. G. Borodin	
	M. V. Ivashin	
	Y. B. Riazantsev	
	V. A. Zemsky	
	A. V. Yablokov	Observer
FAO	L. K. Boerema	
	S. J. Holt	Observers

1. THE AGENDA ADOPTED IS SHOWN IN ANNEX A.

2. A LIST OF THE RELEVANT DOCUMENTS AVAILABLE TO THE MEETING IS APPENDED AS ANNEX B.

The following basic data were available:

Catch and effort by 10° square for sei whales–
- Antarctic 1964/65–1973/74
- North Pacific 1947–1973

Size composition by Area–
- North Pacific 1947–73

Size composition by 10° square–
- Antarctic 1964/65–1973/74
- North Pacific 1970–1973

Age length keys–
- Durban sei, 1962–65 (UK)
- Antarctic Area II sei, 1960/61, 1962/63–1964/65 (UK)
- Antarctic sei, 1966–73 (Japan)
- North Atlantic sei, 1966–72 (Canada)
- North Pacific Bryde's whales, 1959–65, 1971–74 (Japan)

3. DISTRIBUTION AND STOCK IDENTITY

(a) Sei whales

Biochemical studies on whale stock identification are now progressing in Japan (Doc. 31). So far, certain enzyme systems in the liver appear the most promising, though further study is needed before it is known whether these can be used as genetic markers.

North Pacific

Evidence from mark recoveries, the distribution of catches, and baleen plate dimensions indicate that there may be three stocks in the North Pacific, one west of 175°W, one between 175°W and 155°W and one east of 155°W (Doc. 19). It was pointed out by Omura that the distribution of sei whales in the western North Pacific as shown in Doc. 22 was incorrect, those animals found west of 140°E being chiefly Bryde's whales.

Two marks recovered suggest that sei whales off California migrate to off Vancouver Island, while the separation of this population from that off the Japanese coast is demonstrated by specific parasite differences (Doc. 26).

North Atlantic

It can be inferred from a review of the Norwegian literature (Doc. 15) that in the past sei whales in the eastern North Atlantic migrated from their winter grounds off Spain, Portugal and Northwest Africa to Finmark, Bear Island and Novaya Zemlya in summer, rarely reaching Spitzbergen. Jonsgard stated that sei whales appear to have changed their migratory habits in more recent times.

In the Northwest Atlantic the evidence from catches, mark recoveries and the timing of migration suggests that sei whales found off North-east Newfoundland and Labrador are a separate stock from those off the southern end of Nova Scotia, the former migrating to Greenland or possibly to the Denmark Strait region and the latter migrating to the eastern seaboard of the USA (Docs. 32, 36, 40).

Southern Hemisphere

The movements of sei whales within the Antarctic as determined by mark recoveries do not appear very different from those of fin whales although there is a possibility that they are more restricted in extent (Doc. 6). Movements have frequently been recorded between Areas II and III in both directions, and to a lesser extent between Areas IV and V and between Areas I and II. No movements have been recorded between any other Areas.

There are mark returns linking sei whales off the coast of Brazil with the western half of Area II, sei whales off the Natal coast of South Africa with the eastern half of Area III and western half of Area IV, and sei whales off western Australia and southeast Australia with Area IV.

The relative position of the Jacobson's organ in southern sei whales has been found to be sexually dimorphic and possibly of use as a stock indicator (Doc. 35).

(b) Bryde's whales

North Pacific

Two forms of Bryde's whale seem to exist in the North Pacific, an offshore form and a smaller inshore form (Doc. 25). Bryde's whales from the Bonin Islands, belonging to the offshore form, have been linked by mark returns with those of Sanriku and Oshima on the coast of Japan, while Ohsumi stated that recent pelagic catches of Bryde's whales in the central Pacific (Doc. 23) can also apparently be referred to the offshore form. The inshore form has so far only been recorded from the west coast of Kyushu, Japan (Doc. 25), though evidence of a limited offshore distribution (Doc. 26) and from the shape of one baleen plate examined suggest that the same form may be present off Baja California.

Stock units amongst the offshore form are unknown.

Tentative identifications from sightings suggest the presence of the species in the equatorial Pacific (Doc. 3).

North Atlantic

Little is known of the distribution of Bryde's whales in this region. From the evidence of strandings, there appears to be a resident population in the Caribbean and Gulf of Mexico that may extend to the Atlantic coast of the USA as far as Chesapeake Bay (Doc. 36). Sightings of the species have also been recorded from off northern Venezuela in winter (Doc. 32).

Southern Hemisphere

Evidence given in Doc. 4 indicates the presence of two forms of Bryde's whale off the west coast of South Africa, a larger offshore form with relatively broader baleen plates than sei whales and a smaller inshore form with baleen plates resembling those of sei whales in shape. Two similar forms probably exist off the Brazilian coast, while Bryde's whales of the offshore form have also been recorded from Chile and the Natal coast of South Africa. Animals from western Australia seem anomalous. The species may be polymorphic, with some small localized coastal populations (Doc. 10). The year-round tropical and temperate distribution of Bryde's whales of the offshore form would suggest that an initial approximation of stock identity would be to consider the populations in the South Atlantic, South Pacific, and Indian Oceans as separate.

However, the tropical and temperate distribution of Bryde's whales raises the question of whether it is valid to consider northern and southern populations of this species as separate stocks. Evidence from foetal length data indicates that although breeding may take place over a wide time span, there is a peak season (Omura, 1962), which from inspection of the data in Doc. 23, may fall in autumn in the Northern Hemisphere. The offshore form in the Southern Hemisphere also seems to have a peak in the breeding season in autumn (Doc. 4). This, taken in conjunction with the differences in L_∞ between the two hemispheres (see below), suggests that it is reasonable to consider the northern and southern populations as separate.

4. TRENDS IN AVAILABILITY

(a) Sei whales

North Pacific

Although catch per unit effort values and sightings indices are available for this area, the CPUE values are considered to be less reliable due to the shifting area of exploitation, while the research area for sightings has remained more constant (Doc. 29). Downward trends in availability occurred from 1967 for the Asian side of the North Pacific (west of 180°) and from 1969 for the American side. These trends were used for calculations of population size.

Discussion of the possibility that some of the sightings data included Bryde's whales as well as sei whales revealed that although no distinction has been made between the two species, Bryde's whales are mainly found south of 35°N (depending on prevailing oceanographic conditions). The data used in the analysis in Doc. 29 mainly came from the area north of 35°N.

A decline of about 75% in the CPUE of sei whales off California apparently occurred between 1960 and 1970 (Doc. 26).

North Atlantic

Catch per unit effort figures for the Canadian fishery are complicated by interrelationships with the availability of fin whales, and there is no simple way of distinguishing sei whale effort separately at present (Doc. 32). Sightings from catching vessels also apparently contain an "interest" factor on the part of catcher personnel. There also appears to be some natural variability in the availability of sei whales to the coastal operations, possibly related to oceanographic conditions although these have not been successfully correlated as yet.

Southern Hemisphere

Three sets of estimates of stock abundance have been used in an analysis of the Antarctic sei whale stocks, total CPUE, CPUE for Japanese fleets only and sightings indices from scouting vessels. To minimize the possible effects of shifting emphasis from one species to another, CPUE values for sector D only have been used (Doc. 30). Because of certain inconsistencies between different presentations of the sightings data, greater confidence is placed in calculations based on CPUE changes. The sightings data also contain observations for the sector between 30° and 40°S, where sightings of Bryde's whales may be recorded as sei whales, no distinction being made between the two species by the scouting vessels.

All three indices of abundance, however, showed major declines in all four areas investigated from the onset of heavy exploitation, and provided the basis for modified DeLury estimates of population size.

(b) Bryde's whales

North Pacific

Data on the availability of Bryde's whales using CPUE or sightings indices are difficult to separate from those for sei whales. CPUE values have been calculated separately for waters warmer than 16.9°C for the seasons 1970 to 1974 (Doc. 23), but lack of data on the known USSR catches from these data make their evaluation difficult.

North Atlantic

The species is not known to feature in commercial catches in this area and no data on abundance from sightings are available.

Southern Hemisphere

The species is only being caught in significant numbers by a Somali-registered operation off the west coast of Africa. Effort figures for this operation are only available for a limited period so far. No estimates of abundance from sightings are possible because of the failure to date to distinguish the species from sei whales.

5. BIOLOGICAL PARAMETERS

5.1 Age and growth

(a) Sei whales

Gambell stated that ear plug readability problems previously experienced for this species now seem to have been solved by bleaching techiques so that there is no longer any bias with the size of the whale for males. Identification of the neo-natal line however can be difficult in this species.

Most derivations of age from growth layers for this species have assumed one growth layer per year throughout life (Doc. 17), though two layers for the first year of life are proposed by analogy with the gray whale (Doc. 26).

Some estimates of growth parameters for sei whales were available from several sources, as shown in Table 1.

The figures for L_∞ used in Doc. 14, 60 ft for males and 65 ft for females are clearly not supported by this evidence. An analysis presented in Doc. 18 showed that Antarctic sei whales in a particular aggregation have a more similar age structure than would be expected from a random age composition, as well as a tendency to be composed of animals of a particular sex or reproductive condition. This segregation appears to be limited so that all sex and age configurations frequenting the area seem to be randomly represented in samples taken over the whole Antarctic season. A short whaling season and very small catches could yield biased age and sex frequency distributions.

Best and Mitchell reported that segregation of migrating sei whales by length, sex and reproductive condition was also apparent for the west coast of South Africa and for the western North Atlantic, respectively.

In the latter area segregation is more by size than age. Using Japanese age/length keys applied to the total Antarctic catch for the seasons 1966/67 to 1972/73, Allen was able to calculate that the age at full recruitment to the fishery was approximately 18 years. Mean ages at recruitment for males ranged from 11.1 to 11.6 years (1969/70–1972/73) and for females from 10.8 to 11.4 years (1966–1973). There appeared to be no trend to the mean age at recruitment with time over these periods.

Unpublished data from Masaki (presented by Ohsumi) indicated that the mean age at recruitment had decreased in some areas of the North Pacific, e.g. in Area V, male t_r had decreased from about 7 years in 1965 to 6 in 1972, and female t_r from 8 to 5 or 6 years over the same period. It was thought that the shift in whaling grounds in recent seasons may have been responsible for this change.

(b) Bryde's Whales

The readability of Bryde's whale ear plugs (given as about 61–65% in Doc. 4, and stated by Ohsumi at about 50%) was considered to be higher than for untreated sei whale plugs and was not biased by length for either sex (Doc. 4).

Growth curves for the species were presented, with the values for L_∞ shown in Table 2.

5.2 Length/Weight relationships

(a) Sei whales

The length/weight formula for sei whales given by Omura (1950) has been recalculated to account for 6% loss of

Table 1

Sei whale growth parameter estimates

	Males			Females			
Area	t_0	K	L_∞ (ft)	t_0	K	L_∞ (ft)	Source
Northern Hemisphere							
Californian coast	–	–	44.9	–	–	49.3	Doc. 26[1]
N.W. Atlantic	–	–	44–45	–	–	46–47	Doc. 32[2]
Southern Hemisphere							
Durban	9.36	0.1454	48.5	10.0	0.1337	50.0	Doc. 17
South Georgia	–	–	50.7	–	–	54.2	Doc. 17[1]
Antarctic	–	–	48.5	–	–	52.0	Allen[3]

[1] Average length of animals over 25 years

[2] Length at physical maturity

[3] Average length of animals 30 years or more, from Japanese data, as presented at meeting.

Table 2

Estimates of L_∞ for Bryde's whales

Area	Males (ft)	Females (ft)	Source
Northern Hemisphere			
N. Pacific (pelagic)	42.0	43.8	Doc. 23
Southern Hemisphere			
South Africa			
(inshore form)	42–43	45–46	Doc. 4
(offshore form)	45	47–48	Doc. 4

Age at full recruitment to the North Pacific pelagic fishery was 15–18 years, with an average age calculated as 9.7–9.9 years (Doc. 23).

body fluids when cutting up the whale (Doc. 17). The amended aquation is:

$$W = 0.001436\ L^{2.43}$$

where W = weight in m tons

and L = length in feet

(b) Bryde's whales

The length/wieght formula for this species given by Fujino (1955) is:

$$W = 0.00047\ L^{2.74}$$

where W = weight in m tons

and L = length in feet.

This formula does not account for loss of body fluids during weighing.

A corrected formula (using a 6% loss factor) would be:

$$W = 0.00050\ L^{2.74}$$

5.3 Mortality Rates

(a) Sei Whales

Previous estimates of the adult natural mortality rate have been 0.059–0.079, with a mean of 0.065 (Doi *et al.*, 1967).

Additional estimates shown in Table 3 are now available for total mortality rates (Z), using the slope of the right-hand limb of an age distribution.

Table 3

Sei whale total mortality (Z) estimates

Area	Males	Females	Source
Northern Hemisphere			
N. Pacific Area II	0.050	0.057	Masaki Unpublished MS
N. Pacific Area III	0.057	0.078	
N. Pacific Area IV	0.054	0.062	
N. Pacific Area V	0.053	0.058	
Total (1965–72)	0.054	0.062	
California Coast	0.103	0.088	Doc. 26
Southern Hemisphere			
Durban, 1962–65	0.047–0.066 (both sexes)		Doc. 16
South Georgia, 1960/61, 1963/64, 1964/65	0.073–0.094	0.064–0.101	Doc. 16

If a single overall adult natural mortality rate is to be chosen, the meeting decided that 0.06 would be a reasonable approximation.

The somewhat higher figures for sei whales off the California coast might reflect the unique disease that causes progressive shedding of the baleen plates in 7% of this population (Doc. 26).

No direct measurement of a juvenile mortality rate has been made for sei whales. An estimated range of values of 0.065–0.138 with a mean of 0.10 has been used for the pre-sexual maturity stage of life (Doi *et al.*, 1967).

(b) Bryde's whales

The range of values for total mortality rates (Z) now available are given in Table 4.

Table 4

Bryde's whale total mortality (Z) estimates

Area	Combined sexes	Source
N. Pacific, pelagic	0.091	Doc. 23[1]
”	0.080	Doc. 23[2]
Bonin Islands	0.059–0.085	Doi *et al.* (1967)

[1] Based on age distribution between years 15 and 38.

[2] Based on corpora count distribution in whales with between 2 and 14 corpora.

A figure of 0.080 was considered to be the best approximation to date (Doc. 23). Calculations of the probable natural mortality rate in the sexually immature stage ranged from 0.12 to 0.20 (Doc. 23).

5.4 Reproductive rates

5.4.1 Age at sexual maturity

(a) Sei whales In the Southern Hemisphere the age at sexual maturity in both sexes has declined from 10–11 years prior to 1930 to 9.5 years in 1945, and in 1963 was calculated as 8.0 (Doc. 9). This is assumed to represent a response to exploitation of competing species. Ohsumi stated that more recent data on the age at sexual maturity have been collected by Japanese scientists but are not yet available.

In the North Pacific a tendency for the mean age at sexual maturity of both sexes to decrease with time has been noted, from about 10 years prior to 1930 to 6 (females) or 7½ (males) in the early 1960s (Masaki, unpublished MS). The age at sexual maturity of both sexes in the comparatively lightly-exploited Californian stock of sei whales (1959–70) was 10 years, or 11 growth layers (Doc. 26).

In the North Atlantic the age at sexual maturity in the sei whale stock has been calculated as 12.0 growth layers for males and 18.0 growth layers for females (Doc. 32). Both samples however, contained only a small number of immature animals (8 males, 13 females).

(b) Bryde's whales Table 5 shows the ages at sexual maturity which have been estimated for this species.

5.4.2. Pregnancy rate

(a) Sei whales The apparent pregnancy rate (based on BIWS records) for the species in the Antarctic was around

Table 5

Estimated age at sexual maturity in Bryde's whales

Area	Males	Females	Source
Northern Hemisphere			
N. Pacific, pelagic	8–10	7–8	Doc. 23
Japanese coast	9–13	9–10	Omura (1962)
Southern Hemisphere			
South Africa			
(inshore form)	9–10	10	Doc. 4
(offshore form)	10–11	8–9	Doc. 4

25% in 1946 but has increased subsequently to reach over 50% in the 1970s (Doc. 9). The high recent values have been confirmed by biologists' collections at South Georgia and in Antarctic Area II in 1960/61–1965/66 (69%), at Durban (1962–65) (60%), and in the Antarctic from 1959/60–1963/64 (61%).

In the North Pacific, however, there has been a slight tendency for the pregnancy rate to decrease. At present it is estimated to be 60–65%. This change could be due to the shift southwards of the whaling grounds, if pregnant females tended to go farther north (Masaki, unpublished MS as presented by Ohsumi). A gradation also seems to be observed across the North Pacific from west to east, pregnancy rates on the Japanese coast being high (75%) and those in the eastern pelagic area being low (50%). This is based on unpublished data for the period 1965–72 (Masaki, unpublished MS).

The observed pregnancy rate for sei whales off the California coast (1959–70) was 40% (Doc. 26). In the Northwest Atlantic, the observed preganacy rate (1966–72) was 30% (Doc. 32).

All the above estimates do not allow for selection against lactating females, which would tend to make observed preganacy rates higher than the true rates. The estimate for the Californian coast has been adjusted to allow for this bias, giving a figure of 36% (Doc. 26).

Ovulation rates may provide a more accurate representation of the possible fecundity of the population, being free from the above bias.

The ovulation rates recorded for sei whales are given in Table 6.

Table 6

Sei whale ovulation rate estimates

Area	Rate (per growth layer)	Source
Northern Hemisphere		
California coast (1959–70)	0.70	Doc. 26
N.W. Atlantic (1966–72)	0.26	Doc. 32
N. Pacific, Average[1] (1965–72)	0.56	Masaki (unpublished MS)
Southern Hemisphere		
Durban/Antarctic	0.61	Gambell (1973)

[1] Masaki (unpublished MS) has also found a decline in ovulation rate with age, from 1.00 in newly mature animals to less than 0.50 in animals over 30 years of age.

(b) Brydes whales Observed preganacy rates and calculated ovulation rates now available for this species are shown in Table 7.

Table 7

Observed pregnancy rates and estimated ovulation rates in Bryde's whales

Area	Pregnancy Rate %	Ovulation Rate (per year)	Source
Northern Hemisphere			
N. Pacific, pelagic	41.7	0.455	Doc. 23
Southern Hemisphere			
South Africa			
(Inshore form)	44.0	2.35	Doc. 4
(Offshore form)	22.6	0.42	Doc. 4

The apparent differences in preganacy rates between the two forms of Bryde's whales off South Africa are not confirmed by larger samples examined by inspectors only. Apparent differences in the ovulation rate, however, are supported by an analysis of the size frequency of ovarian corpora, the mean number of ovulations per year being estimated as 1.88 for inshore and 0.50 for offshore whales (Doc. 4). Such a difference was considered highly unlikely on biological grounds by some members present at the meeting.

6. POPULATIONS

6.1 Population models

(a) Sei whales

Four new stock assessments were available to the meeting (Docs. 5, 14, 29, 30).

The virtual population technique was applied to Antarctic sei whale catches using a Japanese age/length key with 1961/62 as the base year (Doc. 5). The initial population size so calculated may be considered as a minimum value as no allowance was made for natural mortality. The present (1974/75) stock size estimated was obtained by extrapolation from the initial size using a net recruitment rate of 0.05.

Borodin stated that calculations using a mortality rate of 0.04 gave an initial population of 110,000 animals. The value of 0.06 generally adopted as the best estimate of M by the meeting would give a higher value still.

The model presented in Doc. 14 for Antarctic sei whales was based largely on a misconception that the shape of the right-hand limb of the size frequency in the commercial catch was related to M, whereas in fact, its shape depends almost entirely on the size distribution of sei whales at their asymptotic length, the size at full recruitment to the fishery being close to the maximum size for the species. Hence, the results obtained must be considered erroneous.

The model for North Pacific sei whales used the modified DeLury method as applied to trends in abundance from sightings indices, essentially extrapolating the model of Ohsumi and Fukuda (1975a) backwards to obtain the initial population size and forwards to obtain the present population size (Doc. 29). It was pointed out that the possible observed change in the mean age at recruitment during the period concerned would not materially affect calculations of initial or present stock size, but might affect estimates of their proportionality one to the other.

A similar model was applied to the Antarctic sei whale catch per unit of effort (CPUE) and sightings indices (Doc. 30). This assumes that recruitment to the exploitable phase of the stock is constant, being based on the recruitment from the unexploited stock throughout the period under consideration. New estimates of the mean age at recruitment to the Antarctic fishery produced at this meeting, however, suggested a value of about 11 years, while significant exploitation of the stock has now been in progress for 13 years. However, because of the observed changes in biological parameters during the period when ultimate recruits to the DeLury time-series were being born, there may have been increasing recruitment during the DeLury time-series, and this might counter-balance some of the possible reduction in the mature female stock at the end of the time-series.

A review of previously published assessments for Antarctic sei whales (Doc. 8) illustrated how tentative estimates of the original stock size were, and pointed out that the arbitrary yield figure of 10–15% used from analogy with blue and fin whales would now be considered unrealistic. The use of corrected (r-M) values would probably raise estimates of population size but lower estimates of yield.

It was also pointed out at the meeting that since these original assessments had been made, a great deal more data from mark recoveries, sightings and ratio of fin to sei population sizes had become available and should be utilized.

(b) Bryde's whales

Estimates of exploitable population size based on mark recoveries in the Northwest Pacific suggest that the population size has declined consistently since 1955. This trend is inconsistent with the observed degree of change in the CPUE (Doc. 23). In addition, the calculated decrease in population size over 11,000 animals is inconsistent with the catches over the same period which have totalled about 3,670 animals.

An estimate of Bryde's whale population size based on a comparison of relative abundance with sei whales in sightings records in the central Pacific gave figures of 8–9,000 whales. This is considered an underestimate as the entire distribution area of Bryde's whales was not covered (Doc. 23).

6.2 Population numbers

(a) Sei whales

North Pacific The estimates of exploitable population size available are shown in Table 8.

North Atlantic An analysis of mark recapture and sightings data in Doc. 40 gave the population estimates shown in Table 9.

Southern Hemisphere The estimates of exploitable population size available are given in Table 10.

The unexploited component of the mature stock is normally considered to be about 38.4% of the initial size of the exploited component. However in view of the revised age at mean recruitment (about 11 years), and taking the age at sexual maturity as 8 years, the unexploited component of the mature stock can be recalculated as 25%.

The total mature stocks in the unexploited and present conditions have therefore been calculated for Areas II to V in Table 11, using Chapman's (1974) estimates of population size.

Estimates for Areas I and VI require re-examination.

The apparent reduction in abundance in some Areas of the component of the population between 30° and 40°S from sightings data, may mean that estimates of present total mature stock size are too high in those Areas.

Table 8

North Pacific sei whale population size estimates (000s)

Area	1963	1967	1974	Source
Total	49.6–49.9	37.0–38.2	20.6–23.7	Doc. 29
	–	35.0	–	Ohsumi and Fukuda (1975a)[1]
"	–	37.2	–	" [2]
"	–	36.7	–	" [3]
"	–	22.0	–	" [4]
"	–	–	19.0–20.0	Doc. 23[5]
Asian side (west of 180°)	–	18.4–19.8	–	Doc. 29
American side (east of 180°)	–	(1969) 7.7–8.1	–	Doc. 29

[1] Modified DeLury method
[2] Relative abundance *cf* fin from sightings.
[3] Mortality rate and fishing effort
[4] Doi's (1971) sightings method
[5] Refers to 1972/73

Table 9

North Atlantic sei whale population size estimates

Nova Scotia stock	1393–2248	(mark recoveries)
" " "	870	(sightings)
Labrador stock	965	(sightings)
Total Northwest Atlantic	2078	(sightings)

Table 10

Southern Hemisphere sei whale exploitable population size estimates (000s)

Area	1961/62	1973/74	Source
II	43.0–47.4	19.9–24.2	Doc. 30
	40	17.0	Chapman (1974)
III	20.3–21.9	5.4–7.0	Doc. 30
	25	6.4	Chapman (1974)
IV	20.3–35.9	5.8–21.5	Doc. 30
	27	12.9	Chapman (1974)
V	21.8–22.3	11.8–12.3	Doc. 30
	22	12.0	Chapman (1974)
II–V	110.1–122.6	47.5–60.2	Doc. 30
	114	48.3	Chapman (1974)
Total	98.0 +	57.3	Doc. 5
	121.1–134.9	52.3–66.2	Doc. 30[1]
	131.8–134.5	51.9–54.0	Ohsumi and Fukuda 1975b
	125	53	Chapman (1974)[1]

[1] Adding 10% for Areas I and VI

Table 11

Southern Hemisphere sei whale mature population size estimates (000s)

Area	1961/62	MSY Level 50%	 60%	1973/74
II	50	25	30	27
III	31.4	15.7	18.8	12.8
IV	33.8	16.9	20.3	19.7
V	27.5	13.8	16.5	17.5

(b) Bryde's whales

The estimates of Bryde's whale population sizes available are given in Table 12.

Table 12

North Pacific Bryde's whale population size estimates (000s)

Area	Year	Total	Exploitable	Source
West of 150°E	1955–74	–	10.0	Doc. 23
East of 150°E	1972–73	8.0–9.0+	–	Doc. 23

6.3 Population yields

(a) Sei whales

No new estimates of the population level giving maximum sustainable yield (MSY) were available. This had been calculated as 50% or 60% of the initial stock of mature animals, depending on whether a linear or convex relationship respectively between the rate of reproduction and the stock size is adopted (Doi and Ohsumi, 1970). This level as a percentage of the exploitable population size varies with the age at recruitment; for the Antarctic with an age at first entry of 17 years as used by Doi and Ohsumi, it is 33% of the initial exploitable stock.

However, in view of the observed changes in reproductive parameters for this species prior to the onset of heavy exploitation in the Antarctic (Doc. 9), it was considered necessary to re-examine the model and the population level that should be the ultimate aim of management.

Estimates of 1974 replacement yield for the North Pacific were given as 1,869–2,251, depending on the value of M used (Doc. 29). In view of the meeting's adoption of 0.06 as the best value for this parameter, the most reasonable estimate of present sustainable yield appeared to be 1,869.

Due to uncertainties in the calculations of population size in the Antarctic, no new estimates of sustainable yield were available. The most recent figure available for the replacement yield was around 5,200 (Ohsumi and Fukuda, 1975b). Recruitment rates for total Antarctic catches calculated at the meeting fluctuated widely, possibly due to shifts in location of the pelagic fleets in relation to the 40°S limit and/or shifts in catching effort from one species to another.

The fact that the mean age at recruitment to the Antarctic fishery is considerably less than previously estimated, so that a much smaller proportion of the unexploited stock is probably mature, infers that previous estimates of the sustainable yield may have to be revised downwards.

(b) Bryde's whales

Although no model has yet been developed for this species, it has been assumed that the maximum sustainable yield will be attained at around half the initial population size, and that the rate of exploitation at that level will be equivalent to the value of M or natural mortality prevailing (Doc. 23). Under these assumptions, the MSY of the North Pacific stock has been estimated as

$$0.05\text{–}0.07 \times \frac{20{,}000\text{–}30{,}000}{2}$$

or

500–1,050 whales

7. TROPHIC RELATIONSHIPS

7.1 Feeding behaviour

(a) Sei whales

Sei whales appear to be one of the most versatile of the baleen whales in their feeding habits, being able to use both the 'skimming' and 'swallowing' techniques for feeding. Data on stomach contents show that fin and sei whales cover broader trophic levels than other species of baleen whale, although the trophic levels of their main food are different in the North Pacific and the Antarctic. Sei whales cover on average higher levels in the North Pacific than in the Antarctic, but this apparently reflects the fact that the two regions are not trophically equivalent in structure, the Antarctic being characterized by a relatively greater biomass at a lower trophic level than the North Pacific (Doc. 21).

The question of food selection and preferences was discussed. As pointed out in Doc. 21, if a baleen whale is able to cover the distribution or swarming condition of another food organism on a higher trophic level, they will accept that in preference to their normal food. The apparent order of food selection as determined from stomach contents does not therefore necessarily correspond to an order of preference, but rather of availability.

(b) Bryde's whales

Bryde's whales seem to feed on a more restricted diet and at a generally higher trophic level than sei whales (Doc. 21). Evidence from the west coast of South Africa suggests that the inshore form may actively select fish in preference to euphausids, while the offshore form feeds to a great extent on euphausids. Mitchell raised the question of pigmentation patterns and the nature of food organisms taken, those species of baleen whales with conspicuous disruptive patterns around the eye being considered as adapted to prey on fast-moving organisms such as euphausids, fish and squid. It was not clear how Bryde's whales fitted in to this hypothesis. Evidence from the North Pacific (Doc. 23) indicated considerable seasonal fluctuations in the amount and nature of feeding despite the species being considered as less migratory than other baleen whales.

7.2 Interspecific competition

The question of the apparent response of the sei whale stocks in the Antarctic to reductions in the level of blue and fin whales was discussed. Because of the apparent lack of direct competition with these species based on comparisons of stomach contents (Doc. 21), it was suggested that this response might have been to the historical reduction in right whale stocks, a species which appears to be in direct competition with sei whales. The time lag involved, however, was considered too great. Never-the-less, Doc. 9 refers to evidence from South Georgia of direct competition between blue, fin and sei whales.

The question of a change in the migratory habits of sei whales as a result of blue and fin whale reduction was also discussed. It was thought that inspection of logbooks from pelagic whaling fleets in the earlier years of the Antarctic fishery might provide some data on the historical distribution of sei whales. Gambell stated that evidence of a progressively earlier migration into the Antarctic in more recent seasons following the decline of blue and fin whales came from catch data at South Georgia.

The suggestion was made that the reduction of blue and fin whales may have created a greater availability of euphausids to the sei whales which had therefore shifted their preference from copepods to euphausids.

It was concluded that before the question of interspecific competition could be quantitatively assessed, more information was needed on the relative biomass of the different food species and their fluctuations. Until such data are available, however, the modelling approach used in Doc. 27 would provide an initial approximation.

8. FURTHER RESEARCH

8.1–2 Re-examination or re-analysis of data and matters that can be accommodated within existing programmes

The following projects would seem of immediate importance.

(1) The construction of a sei whale population model that allows for the sort of biological parameter changes that seem to have occurred as a result of changes in other baleen whale stocks rather than in the sei whale population.

(2) A re-examination of recruitment rates for Antarctic sei whales, possibly stratifying by geographical zones to allow for possible segregation of age classes.

(3) Recalculations of the modified DeLury method estimates of population size for sei whales incorporating known parameter changes and possibly using sightings data for zone D (40°–50°S) of the Antarctic instead of for the whole region south of 30°S.

(4) Subject to the availability of suitable data, an analysis of mark recovery information for Southern Hemisphere sei whales, for calculations of population size.

(5) An examination of logbooks or other records from supply ships, factory ships, catchers, etc., for the Antarctic fleets prior to 1961/62 to determine the distribution and abundance of sei whales at that time.

(6) The organization of trials by each whaling nation to measure the efficiency of recovery of Discovery marks on its factory ships or land stations.

(7) The sampling of different populations of Bryde's whales, particularly coastal stocks off Western Australia and the west coast of Kyushu, Japan, for futher examination of their systematic status and biology.

(8) The collection of more quantitative information on the food and feeding behaviour of all baleen whale species, in particular with regard to possible food preferences or selection.

(9) The investigation of possible means of distinguishing sei from Bryde's whales at sea through differences in behaviour as well as in morphology.

(10) An analysis of sei whale catches in the Antarctic in smaller divisions than 10° of latitude to determine the degree of segregation by size, age and sexual class.

(11) More data on baleen whales weighed whole and then in parts are required to obtain a factor to account for loss of body fluids in previous calculations of length/weight relationships.

8.3 New areas of research

Two main lines of study into the problem of stock identity were suggested in Doc. 38. The first of these, population morphology, has proved useful in determining the family organization of white whales and sperm whales, and such a technique might prove possible for stock separation of baleen whales.

The second approach, through the study of DNA variation using biochemical methods, could provide information on real genetic differences between different populations of sei and Bryde's whales. There may be problems with obtaining material of sufficient freshness, but several members of the Committee expressed an interest in co-operating in such a study.

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Annex A

Sei and Bryde's Whale Agenda (revised)

1. Adoption of agenda
2. Review of data
3. Distribution and population identity
4. Trends in availability
5. Biological parameters
    5.1. Age and growth
    5.2. Length-weight relationships
    5.3. Mortality rates
    5.4. Reproductive rates
        5.4.1. Age at sexual maturity
        5.4.2. Pregnancy rate
6. Populations
    6.1. Models
    6.2. Population numbers
    6.3. Yields
7. Trophic relationships
    7.1. Feeding behaviour
    7.2. Interspecific competition
8. Further research
    8.1. Re-examination or re-analysis of data
    8.2. Research that can be accommodated within existing programmes
    8.3. New areas of research

Annex B

LIST OF RELEVANT DOCUMENTS SUBMITTED

SC/SP 74/Doc
3 BALCOMB, K. C. Observations on Bryde's Whale in the Central Pacific Ocean.
4 BEST, P. B. Two Allopatric Forms of Bryde's Whale off South Africa.
5 BORODIN, R. G. Application of the Method of Virtual Population for Assessment of Sei Whale Stocks in the Antarctic.
6 BROWN, S. G. Some Results of Sei Whale Marking in the Southern Hemisphere.
8 GAMBELL, RAY. A Review of Population Assessments of Antarctic Sei Whales.
9 GAMBELL, RAY. A Review of Reproduction Parameters and Their Density Dependent Relationship in Southern Hemisphere Sei Whales.
10 GASKIN, D. E. Sei and Bryde's Whales in Waters Around New Zealand.
14 JONES, R. Further Assessments of the Numbers of Antarctic Sei Whales.
15 JONSGARD, AGE and DARLING, KATE. Sei Whales (*B. borealis*) in the Eastern North Atlantic.
16 LOCKYER, C. Mortality Rates for Mature Southern Sei Whales.
17 LOCKYER, C. Some Estimates of Growth Rates in the Sei Whale, *Balaenoptera borealis.*
18 LOCKYER, C. Some Possible Factors Affecting Age Distribution of the Catch of Sei Whales.
19 MASAKI, YASUAKI. The Separation of the Stock Units of Sei Whales in the North Pacific.
21 NEMOTO, T. and KAWAMURA, A. Characteristics of Baleen Whales in Feeding and Distribution Especially of Sei Whales.
22 NISHIWAKI, M. Systematic Relationship Between Sei (*Balaenoptera borealis*) and Bryde's Whales (*Balaenoptera edeni*)
23 OHSUMI, S. Bryde's Whales in the Palagic Whaling Ground of the North Pacific.
25 OMURA, H. Review of the Bryde's Whale Stock in the Northwest Pacific
26 RICE, DALE W. Synopsis of Biological Data on the Sei Whale and the Bryde's Whale in the Eastern North Pacific.
27 SMITH, TIM D. An Example of a Dynamic Matrix Model of Competing Populations.
28 SMITH, TIM D. Researches in Comparative Population Dynamics.
29 TILLMAN, M. F. Re-examination of Population Estimates for the North Pacific Sei Whale.
30 TILLMAN, M. F. and BREIWICK, J. M. Estimates of Stock Size for the Antarctic Sei Whale.
31 WADA, S. Status of Biochemical Studies on Whale Stock Identification in Japan.
32 MITCHELL, E. D. and KOZICKI, V. M. The Sei Whale (*Balaenoptera borealis*) in the Northwest Atlantic Ocean.
34 MOREJOHN, G. V. and RICE, D. W. First Record of Bryde's Whale (*Balaenoptera Edeni*) off California.
35 MIKHALEV, Y. A. SHEVCHENKO, V. I. and NEIZHKO, V. I. The Position of the Organ of Jakobson as Population Pattern of Sei Whales.
36 MEAD, J. G. Records of Sei and Bryde's Whales from the Atlantic Coast of the United States, The Gulf of Mexico, and the Caribbean.
38 YABLAKOV, A. V. Proposals for Sei Whale Research.
40 MITCHELL, E. D. and CHAPMAN, D. G. Preliminary Assessment of Stocks of Northwest Atlantic Sei Whale (*Balaenoptera Borealis*)

SC/SP 74/Doc 4

Two Allopatric Forms of Bryde's Whale off South Africa

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Abstract

Two forms of Bryde's whale are described, mainly from the west coast of the Cape Province of South Africa. These forms differ in their distribution, one being found close inshore and the other offshore. The inshore form is smaller, less scarred and has narrower baleen plates than the offshore form. It also feeds mostly on epipelagic fish, while the offshore form takes euphausiids and more mesopelagic fish. The inshore form appears to have an unrestricted breeding season and a relatively high ovulation rate, while the offshore form has a more restricted breeding season and a lower ovulation rate. Both forms are discussed in relation to the taxonomic identity of *Balaenoptera edeni* and *brydei*.

INTRODUCTION

In an earlier report, attention was drawn to the possibility of there being two races or types (here called 'forms') of Bryde's whale off the west coast of South Africa (Best, 1967). At the time discussion was limited to differences in distribution and feeding. The present report makes a fuller comparison of the two forms, including data on external appearance, growth and reproduction, gathered chiefly from the examination of animals landed at Donkergat whaling station, Saldanha Bay (33°S, 18°E). The distinctness of the two forms is confirmed.

Comparisons are also made with published and unpublished information for Bryde's whales from other parts of the world, in an effort to establish the incidence of these two forms elsewhere.

MATERIAL AND METHODS

A total of 128 Bryde's whales (68 males and 60 females) was personally examined by the author at Donkergat from 1962 to 1965. Ovaries from an additional 10 whales were collected by the whaling inspector, Mr D. Hansen, in 1964 and 1965. Certain data for two male and four female Bryde's whales examined at Durban whaling station by members of the Whale Research Unit, United Kingdom, were provided by Dr. R. Gambell, and ovaries and baleen plates from an additional five whales at Durban became available through collections of the Sea Fisheries Branch in 1968 and 1969. Biological material was therefore available from a total of 149 whales.

The procedure used in collecting and examining reproductive material was exactly the same as that used for sperm whales (Best, 1968; 1969). The processes of stomach content examination and evaluation have also been described previously (Best, 1967), and the method of examination and classifying for physical maturity was identical to that used for sperm whales (Best, 1970).

At least one ear plug was collected where possible from each whale. These were generally so small that it was unnecessary for any special cuts to be made with the bone saw. After the lower jaw had been removed and the head cut from the spinal column, the fatty tissue anatomically ventral to the tympanic bulla was cut away with a flensing knife to expose the bulla and the proximal part of the external auditory meatus lying in the squamo mastoid groove. The meatus was then slit open with a small knife and first the glove finger then the ear plug removed. This method proved both simple and rapid once mastered, though for plugs larger than the normal sei whale's it was usually necessary to remove the bulla first. Ear plugs collected were fixed in 5% formalin and eventually bisected longitudinally with a scalpel and polished on waterproof carborundum paper under running water before reading.

DISTRIBUTION AND MOVEMENTS

Omura (1959) summarized and illustrated the known global distribution of Bryde's whale, but there have been subsequent records from Curacao Island in the Caribbean (Soot-Ryen, 1961), Brazil (Omura, 1962a), Chile (Clarke and Aguayo, 1965), the Gulf of Mexico (Rice, 1965), Formosa (Nasu, 1966), the Arab (Persian) Gulf (Mahdi, 1967; Al-Robbae, 1969), New Zealand (Gaskin, 1968), the south-eastern coast of Australia (Dixon, 1970), California (Morejohn and Rice, 1973), and Malaysia (Berry, Wells and Ng, 1973). Clarke and Aguayo (1965) also revealed earlier records from Ecuador and Colombia. A photograph of a Bryde's whale published by Cousteau and Diolé (1972, p. 48) was apparently taken about 700 miles SSE of Cape Guardafui in the north-west Indian Ocean (Cousteau and Diolé, p. 259) on 12 May 1967 (Diolé, in litt.). As stated by Scheffer and Rice (1963), the species is probably found in all tropical and sub-tropical seas.

Around Southern Africa Bryde's whale seems to be concentrated mainly on the west coast, substantial catches being made from Donkergat and in earlier years off Angola, the Congo and French Equatorial Africa (Ruud, 1952). East coast records are much less common. The number caught from the whaling station at Durban has varied annually from zero to nine in the seasons from 1962 to 1974 since a research programme was initiated at the station (Table 1), and this seems to be a true reflection of their actual abundance, the whale gunners making no discrimination between sei and Bryde's whales at sea. According to Ruud (1952), the northern limit of catches on the east African coast was Linga Linga (23° 30'S).

From the monthly distribution of catch positions of Bryde's whales off the Cape Province, it was suggested in an earlier paper that the species either participated in a seasonal onshore-offshore or in a limited North-South migration (Best, 1960). More recent observations, however, have thrown new light on this interpretation. Accurate catch positions are now available for 578 Bryde's whales caught from July 1962 to October 1966, and these have been analysed as the number killed each month in ten mile intervals from the coastline (Fig. 1). At first sight this figure seems to be very similar to that previously published, in that large numbers of animals were caught over 50 miles from the coast from March to May and in October, while substantial catches were made less than 20 miles from the coast from May to September. The more extensive data here presented, however, clearly shows that there are two separate groups of animals involved, one inshore and one offshore, and that at no time from March to October does an intermediary group occur. This is most obvious from the total distribution of all animals killed, but the simultaneous occurrence of a group offshore and one inshore is best seen in May.

As the offshore group occurs in the centre of the main whaling area (see Best, 1967), its relative rarity during June, July, August and September is probably a valid reflection of its abundance, and hence it must indulge in marked seasonal movements. The inshore group occupies an area that is not normally fished unless the weather farther offshore is inclement, and hence its actual seasonal abundance may not be truly reflected in Fig. 1. It is clear nonetheless, that this group is present in some numbers during the months from May through September, and it has in fact been taken in every month of the whaling season. Seasonality of movement is thus less obvious in this group.

Unfortunately there are very few direct observations on the direction of movement of Bryde's whales from the Donkergat spotter aircraft, due in part to the difficulty of distinguishing them from sei whales. It is perhaps worth noting that seven out of ten sightings made within 30 miles of the coast (and so presumably of inshore Bryde's whales) during June and July involved whales moving south, south-west or south-east, suggesting that there is a southward movement at this time of year. As far as offshore whales are concerned, it might be expected from the similarity with

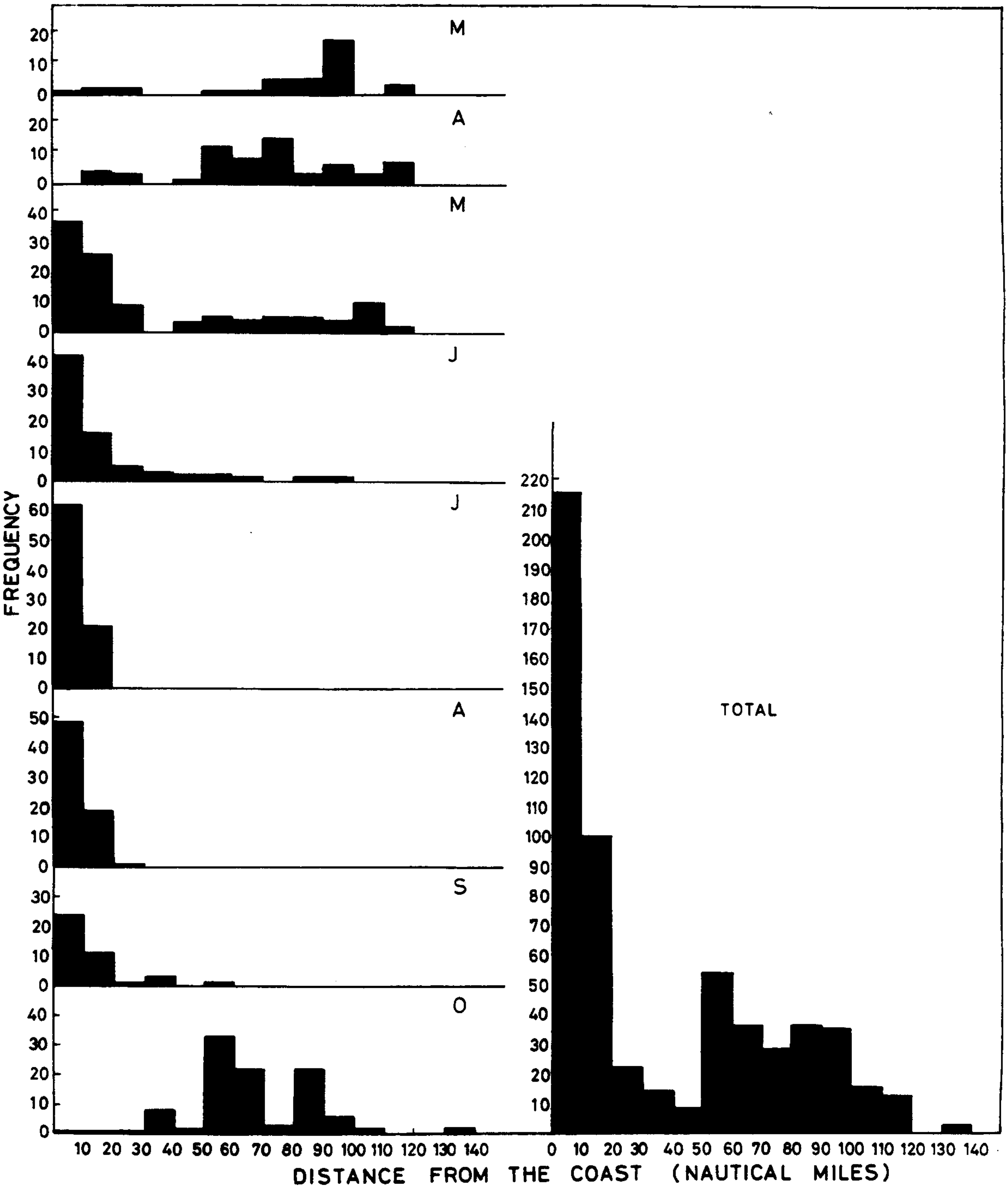

Fig. 1. Distance offshore of Bryde's whale catches from Donkergat, by month and in total.

Table 1

Annual catch of Bryde's whales off Durban

				Month				
Year	April	May	June	July	Aug.	Sept.	Oct.	Total
1962	–	–	–	2	1	–	–	3
1963	–	–	–	–	–	–	2	2
1964	–	–	–	–	–	–	–	0
1965	–	–	–	–	–	–	–	0
1966	–	–	3	1	–	–	–	4
1967	–	1	3	–	2	–	–	6
1968	1	1	1	1	–	–	–	4
1969	3	–	–	–	–	1	–	4
1970	–	1	–	–	–	–	–	1
1971	–	–	1	–	–	–	–	1
1972	1	2	–	–	–	–	–	3
1973	2	1	3	–	–	–	–	6
1974	3	2	–	–	3	1	–	9
Total	10	8	11	4	6	2	2	43

the pattern of sei whale abundance (Best, 1967) that the autumn peak represents northward-moving animals and the spring peak southward-moving animals. If this is the case, the lack of records of Bryde's whales from the Antarctic (Symons, 1955) must mean that the southward migration in summer fails to go beyond about 40°S.

The possibility of the offshore whales making extensive migrations between subtropical and tropical waters is shown by a whale marked 94 miles offshore in 33°16′S, 16°02′E on 22 February 1963 and recovered 10 years and about five months later in 00°32′S, 05°10′E on 15 July 1973. Although this whale was recorded as a sei whale both at marking and on recovery, a later cable from the factory ship on which it was recovered (M.V. 'Sierra') stated that it might have been a Bryde's whale. Judging from cine film and photographs taken on board the 'Sierra', the majority of her catch consists of the offshore form of Bryde's whale. The author was present at the time this whale was marked but failed to record whether or not the animal had the ridges on the rostrum characteristic of Bryde's whale, and relied on the gunner's identification as a sei whale. There is therefore a distinct possibility that this animal was actually an offshore form of Bryde's whale.

Off Durban, Bryde's whales have been taken in every month from April to October (Table 1). Despite the regular occurrence of an annual migration of pilchards to Natal waters in midwinter (Davies, 1956), there is no sign of a great increase in the abundance of Bryde's whales at this time of year, as might be expected from the feeding habits of the species on the west coast (see below). An analysis of the monthly catch positions for the 43 whales taken from 1962 to 1974 suggests that Bryde's whales are on average farther offshore in April and May than in any other month of the whaling season (Fig. 2). While this trend is reminiscent of that seen on the west coast, the data are too limited to show a clear separation of the population into inshore and offshore groups. Bryde's whales are frequently seen in Algoa Bay, apparently year-round, and eight have been identified and marked on marking cruises. This may represent the easternmost limit of the inshore population, for none of the marked whales was recovered off Durban, and oceanographic conditions farther east along the coast appear unsuitable. On the west coast the most northerly record of a Bryde's whale seen close inshore is a sighting of three animals at Hondeklipbaai (30°18′S, 17°16′E) from a whale catcher on 13 August 1963. The inshore population may well extend farther north on this coast, however, as oceanographic and feeding conditions appear suitable.

EXTERNAL CHARACTERS

All the 128 Bryde's whales examined by the author at Donkergat from 1962 to 1965 had the usual diagnostic external characters of the species, namely, ventral grooves extending back at least as far as the umbilicus, and baleen with very coarse bristles forming a 'bush' at the top of each plate. Six whales (including two inshore and three offshore) and one foetus 2.35 m long were examined for ridges either side of the rostrum (Omura, 1962a) and all were found to possess them. In addition, 53 whales (including seven inshore and 44 offshore) examined had a median groove extending from the umbilicus to the genital aperture, while one offshore animal had an incomplete groove and one no groove at all. Hence in these characters no differences could be found between whales belonging to the inshore and offshore groups.

However, although detailed notes of the colour pattern were not included as part of the routine examination of whales on the flensing platform, it was clear that certain features of pigmentation, or rather of scarring, were peculiar to either the inshore or offshore whales. These are discussed below.

Body scarring

The first type of scarring concerned the number of oval pits or scars scattered over the body, which have been described for most other species of *Balaenopteridae* and attributed to a number of external agents (Mackintosh and Wheeler, 1929), the most probable of which now appears to be a small shark, *Isistius brasiliensis* (Jones, 1971).

In offshore whales these pits and scars were exceedingly numerous, more so than in any other baleen whale examined at Donkergat. In adult animals the old scars became so concentrated, particularly in the posterior half of the whale, that the skin in these regions bore an appearance like new galvanised iron, and even turned completely white on occasions. This feature has been particularly well illustrated for Bryde's whales off the Bonin Islands, North Pacific, by Omura, Nishimoto and Fujino (1952), and is visible in Fig. 13a. By contrast Bryde's whales caught inshore off South Africa bore few if any oval scars (Fig. 13b).

During the examination of animals on the flensing platform, the degree of scarring was recorded as none, few, moderate or many. In Table 2 the number of whales in each of these categories has been compared for those animals killed within 20 miles of the coast and those killed outside 50 miles, and this analysis clearly shows the difference in scarring between the two groups. As this scarring is almost certainly permanent, its absence on inshore Bryde's whales suggests that this group is constantly restricted to coastal waters where the agent responsible for the pits must be very scarce.

Table 2

Degree of scarring in Bryde's whales off Donkergat

	Inshore form		Offshore form	
Oval scars	No.	%	No.	%
None	21	58.3	0	0
Few	13	36.1	1	1.6
Moderate	0	0	0	0
Many	2	5.6	62	98.4
Total	36	100.0	63	100.0
Scratches on tail/peduncle				
Present	9	81.8	0	0
Absent	2	18.2	6	100
Total	11	100.0	6	100

A second, less obvious type of scarring was only noticed late in the field programme so that relatively few observations were made on its occurrence. On the undersurface of the tail flukes and along the keel of the ventral peduncle of several whales belonging to the inshore group there were found long, thin scratches, usually healed, running in the same direction as the long axis of the whale. Such scratches strongly suggest that the animal had been swimming close to the sea floor and had acquired the injuries when the tail region had come into contact with the substratum on a down-stroke. While 81.8% of inshore Bryde's whales bore these scars, they were not observed in whales killed more than 50 miles offshore (Table 2). Consequently it appears that the distribution of the offshore group of Bryde's whales is also limited and that they rarely if ever enter coastal waters.

Morphometrics

Total length

Bryde's whales killed close inshore were generally smaller than those killed farther out. The size frequency distributions of male and female whales from within 20 miles and outside 50 miles of the coast are shown in Fig. 3. Males inshore had a modal length of 43 feet compared with a mode of 45 feet offshore, and females inshore had a modal length of 45 feet as opposed to 48 feet offshore. These differences in size might be attributed to differences in the age composition, younger animals being found closer inshore. However evidence given below confirms that inshore Bryde's whales have a slower overall rate of growth and reach a smaller maximum size than offshore whales.

The probability of there being local races of Bryde's whales differing in size has been suggested by Omura (1959), when comparing animals off the Bonin Islands with individuals from Western Australia, Pulu Sugi and the coast of Japan.

Body proportions

Besides the total length, a series of 13 body measurements was taken on 108 Bryde's whales landed at Donkergat in

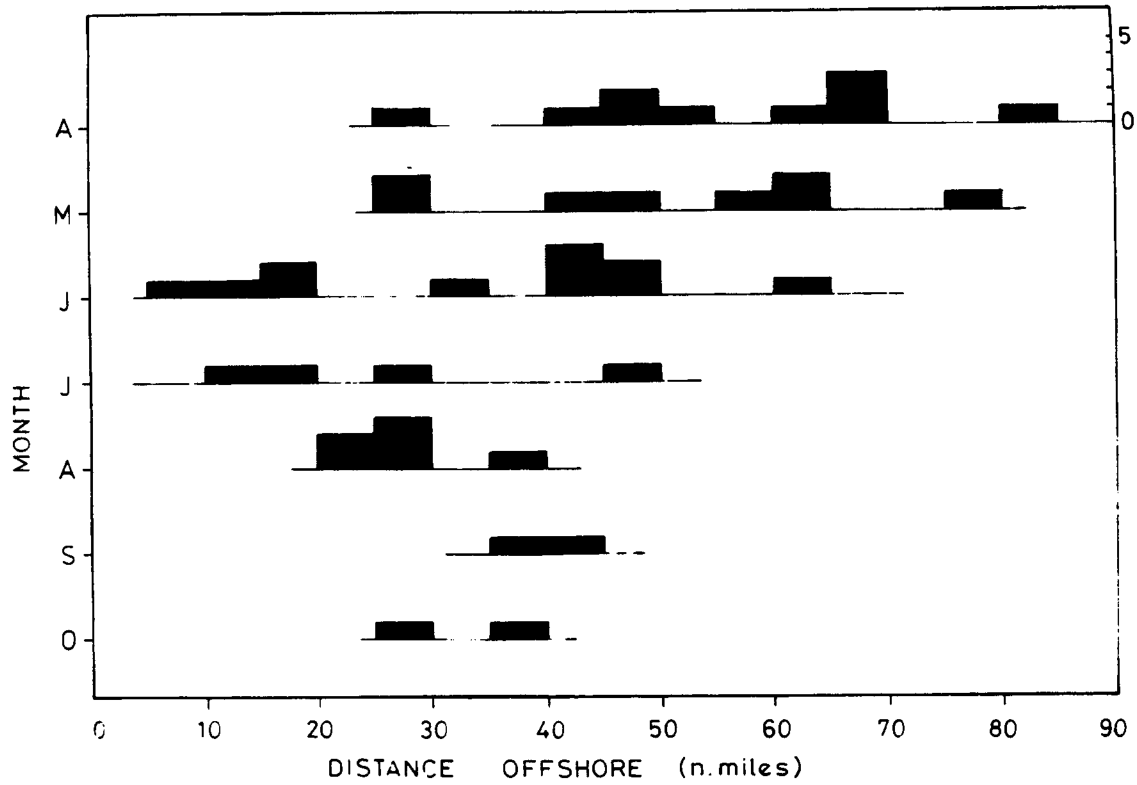

Fig. 2. Distance offshore of Bryde's whale catches from Durban, by month.

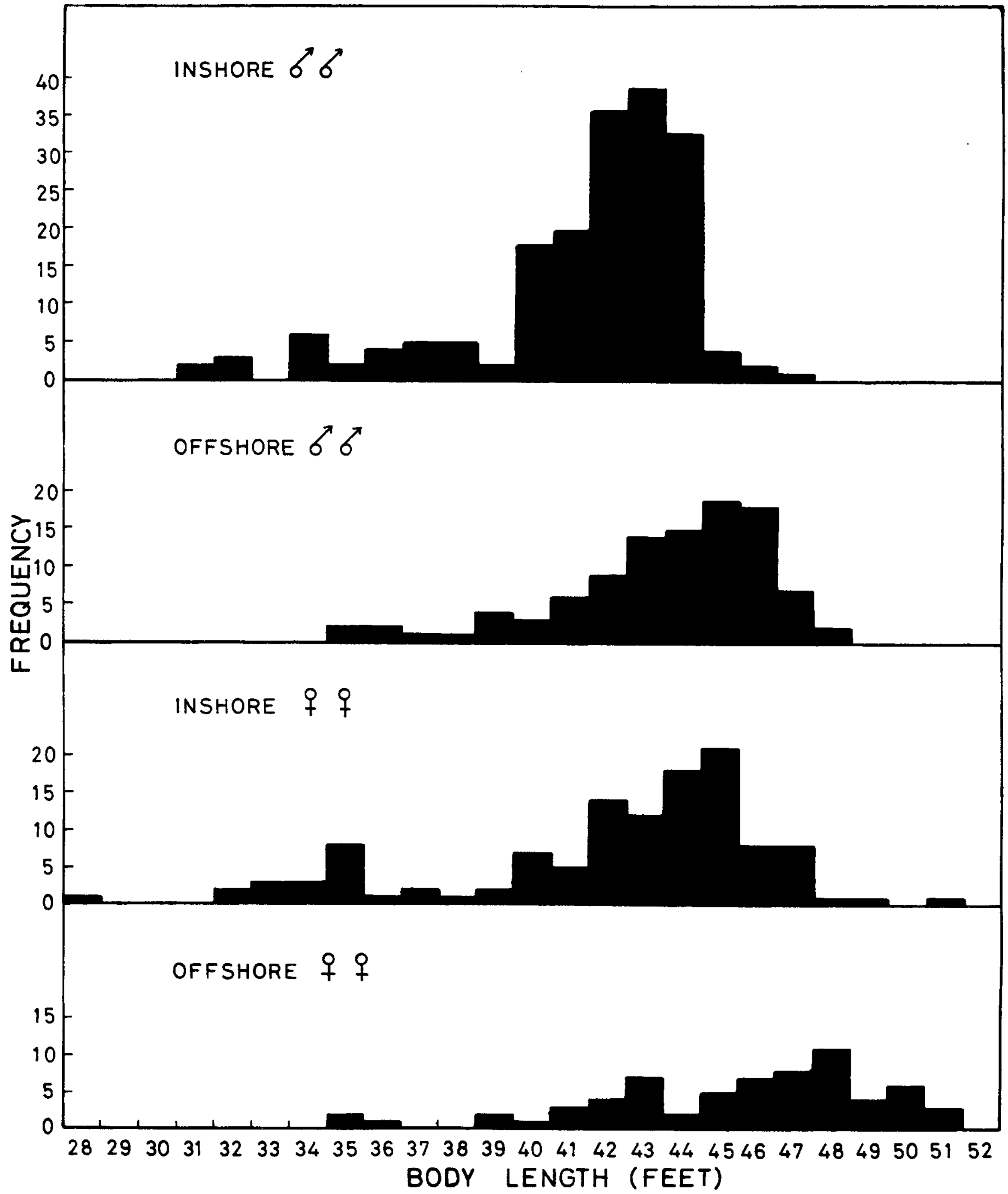

Fig. 3. Size distribution of Bryde's whales landed at Donkergat, 1962–1966.

the 1962, 1963 and 1964 seasons. These measurements were as follows:

1. Length, tip of upper jaw to tip of dorsal fin
2. Length, tip of upper jaw to centre of anus
3. Length, tip of upper jaw to centre of eye
4. Length, tip of upper jaw to centre of blowhole along midline
5. Length, tip of upper jaw to angle of gape
6. Length, tip of upper jaw to anterior insertion of flipper
7. Length, tip of upper jaw to centre of umbilicus
8. Girth, at umbilicus
9. Flipper, length, anterior insertion to tip
10. Flipper, length, axilla to tip
11. Flipper, maximum width
12. Dorsal fin, vertical height from fin tip to base
13. Dorsal fin, length of base

Measurements 1 to 7 and the total length were all taken with a flexible metal tape-measure in a straight line parallel to the longitudinal axis of the whale, whereas the girth was measured from the umbilicus round the curve of the body to the mid-dorsal line just anterior to the dorsal fin, and the measurement doubled. Other measurements were taken from point to point, and all were measured in feet and inches (see Appendix 1 where these measurements, including the total length, are set out for each whale and expressed as inches).

Using a combination of differences in scarring, body size and distribution, 116 of the 128 Bryde's whales examined at Donkergat could be classified as either 'inshore' or 'offshore' forms. Body measurements are available for 101 of these animals. From a preliminary inspection of the data there is some suggestion that inshore animals may have a shorter distance from the tip of the snout to the centre of the eye (measurement 3) and a greater girth (measurement 8). However this hypothesis is not supported by a statistical comparison of the regressions of each measurement against total length for inshore and offshore whales.

The pattern of growth for each measurement seems to be approximately linear except in the largest animals (those over 570 inches in length), where the rate of relative growth decreases. Consequently a straight line has been fitted by the method of least squares to the observations for each population group, combining the data for both sexes, and omitting animals 570 inches or more in length. The slopes and intercepts of the regressions for each population group have then been compared by an analysis of covariance test (Bennett and Franklin, 1961, pp. 442–444, with the formula for T_a corrected), but in none of the 13 measurements was there any significant difference in either coefficient (Table 3). The data therefore fail to show any morphometric differences between inshore and offshore Bryde's whales, and in the subsequent analysis they have been combined as a single group.

The allometry of body proportions has been studied by expressing each measurement as a percentage of body length and then calculating its correlation with increasing body length (Table 3). In nine of the measurements (1, 2, 5, 6, 7, 9, 10, 11 and 13) the correlation coefficients were not significantly different from zero, indicating that these proportions changed isometrically with body length. In measurements 3 and 4, however (the distances from the tip of the snout to the centre of the eye and to the centre of the blowhole, respectively), there was a significant positive correlation, indicating positive allometry or an increase in proportion with growth. Significant negative correlations, indicating negative allometry, were recorded for measurements 8 and 12, or the girth at the umbilicus and the height of the dorsal fin.

Among baleen whales, an increase in the relative size of the head region with growth has already been recorded for the humpback whale (Matthews, 1937), the fin whale (Mackintosh and Wheeler, 1929; Fujino, 1954; Ohsumi, 1960), and the sei whale (Matthews, 1938). In Bryde's whale the positive allometry of the head region is confined to measurements concerning the length of the rostrum, and in this respect the species resembles the sei whale rather than the other balaenopterids. Negative allometry of the dorsal fin has so far only been recorded for the fin whale (Ohsumi, 1960), while to date there have been insufficient measurements of the girths of other species to compare with the present findings.

A series of body measurements for 85 male and 113 female Bryde's whales from the Bonin Islands in the North Pacific was compiled by Omura *et al.* (1952). This has been compared with the results of similar measurements made at Donkergat in Table 3. The whales from the Bonin Islands seem to differ from those off Donkergat only in measurements 3, 4, 5 and possibly 13, suggesting that the North Pacific animals have a proportionately longer rostrum and longer base to the dorsal fin. The latter dimension is very prone to subjective interpretation in measurement, so that the observed difference may not be significant. Although the length of the rostrum is partly dependent on body size (see above), the modal length of the Bonin Islands whales was 40 feet for males and 43 feet for females, both of which are slightly less than at Donkergat. Consequently the greater size of the rostrum in North Pacific Bryde's whales cannot be due to ontogenetic changes alone, and may reflect an actual racial separation of the stocks.

Dr Chittleborough (of the Western Australian Marine Research Laboratories) has kindly sent me data from nine Bryde's whales landed at Australian whaling stations from 1961 to 1963, two from the east coast and seven from the west coast. These were all examined and measured by whaling inspectors. The distance from the posterior end of the throat grooves to the umbilicus can be obtained from eight of these animals by subtracting two of the recorded body measurements i.e. 'notch of flukes to end of throat grooves' minus 'notch of flukes to centre of navel'. Expressed as a percentage of body length the values for each whale were

East coast – 1.6%, 2.4%
West coast – 4.0%, 5.1%, 6.5%, 7.0%, 7.8%, 8.3%.

These proportions indicate that the ventral grooves did not extend back as far as the umbilicus in any whale. According to data for 196 Bryde's whales given by Omura *et al.* (1952), in only 1.5% of animals did the gap between the posterior end of their throat grooves and the centre of their navel exceed 3% of the body length, while in only 1.3% of 150 sei whales (Matthews, 1938 – omitting obvious errors) was this distance less than 3% of the body length. It therefore seems that either the east coast animals were Bryde's whales and the west coast animals sei whales, or that there are two forms of Bryde's whales off Australia, one of which is atypical in the relative positions of its navel and the posterior end of the throat grooves. Dr Chittleborough has said that 'in most cases I was sent a sample of baleen' and that 'as far as I can tell they are all of the same species, at least the baleen was the same as the first three, (*in litt.* 10 Nov. 1970). Unfortunately these baleen samples are no longer available, so that it is not possible to establish whether they were all indeed Bryde's whales. A photograph of one of the east coast animals sent me by Dr Chittleborough is certainly of a Bryde's whale.

Baleen

Number of plates

The total number of baleen plates (including the anterior, rudimentary ones) was counted in one inshore and one offshore whale at Donkergat. The inshore whale had 278 plates on its right hand side and 289 on the left, and the offshore whale 276 plates on the right and 278 on the left: from these figures there would appear to be little difference between them in the number of baleen plates.

These counts also fall within the range recorded for 126 Bryde's whales from the Bonin Islands (255 to 365, Omura *et al.*, 1952), and Clarke and Aguayo (1965) found 275 plates on the left and 307 plates on the right side of a Bryde's whale from Chile. Olsen's (1913) counts of 250 to 280 plates in 12 specimens from Saldanha Bay apparently did not include rudimentary plates at the front of the mouth.

Baleen shape

One of the largest baleen plates was collected from each of 26 Bryde's whales landed at Donkergat in 1962, for age

Table 3

Summary of body measurements of Bryde's whales.

Meas.	Inshore form South Africa			Offshore form South Africa			Diff. (values of p)		All Bryde's whales examined, S. Africa (Meas. as % of body length)						Bonin Islands (Omura *et al.* 1952) Males (as % body length)				Bonin Islands (Omura *et al.* 1952) Females (as % body length)			
No.	n[1]	a[2]	b[3]	n	a	b	a	b	n	r[4]	p	Range	Ave.	±SD	n	Range	Ave.	±SD	n	Range	Ave.	±SD
1	31	−2.55	0.78	52	−0.58	0.73	>0.9	>0.1	101	0.0889	>0.3	66.5–74.9	71.7	2.8	–	–	–	–	–	–	–	–
2	32	−0.39	0.75	52	−0.67	0.75	>0.9	>0.8	101	0.1393	>0.1	68.0–77.2	73.8	1.1	84[5]	70.9–78.4	75.0	–	113[5]	70.0–76.8	74.2	–
3	33	−1.02	0.20	53	−0.74	0.20	>0.4	>0.7	104	0.3757	<0.001	15.0–20.7	18.0	1.5	83	17.5–23.8	20.4	1.0	112	19.1–22.9	21.0	0.9
4	33	−2.10	0.20	53	−1.25	0.19	>0.7	>0.6	104	0.4166	<0.001	12.4–18.7	15.8	0.7	84	15.5–19.9	17.2	0.9	113	14.9–20.1	17.8	1.1
5	31	0.90	0.15	52	−0.45	0.19	>0.7	>0.1	101	0.1021	>0.3	15.0–19.9	17.6	1.2	25	18.0–22.3	20.3	1.2	18	18.5–22.4	20.3	1.2
6	32	−2.01	0.33	50	0.48	0.28	>0.7	>0.3	100	0.1825	>0.05	25.1–32.3	28.9	1.6	–	–	–	–	–	–	–	–
7	21	−2.55	0.61	9	1.92	0.52	>0.9	>0.4	32	−0.0729	>0.6	46.5–58.8	54.7	3.3	84[5]	50.8–63.5	56.8	–	113[5]	51.4–62.8	56.7	–
8	30	4.25	0.30	48	7.78	0.20	>0.8	>0.3	95	−0.3059	<0.005	30.9–46.6	39.0	3.1	–	–	–	–	–	–	–	–
9	30	−0.96	0.14	49	−0.11	0.12	>0.7	>0.5	95	0.0792	>0.4	9.8–12.9	11.7	0.6	79	9.6–14.0	12.0	0.8	105	8.5–13.8	12.0	0.9
10	19	−0.92	0.11	47	−0.28	0.10	>0.7	>0.6	78	0.1919	>0.05	8.0–10.2	9.0	0.6	79	7.8–11.3	9.3	0.7	105	6.2–10.5	9.3	0.7
11	30	−0.31	0.03	49	−0.02	0.03	>0.7	>0.2	95	0.1098	>0.25	2.2–2.9	2.6	<0.1	77	2.3–3.1	2.7	0.2	105	2.4–3.0	2.7	0.2
12	27	0.45	0.02	44	0.47	0.02	>0.9	>0.9	83	−0.2659	<0.02	1.8–3.6	2.7	<0.1	70	1.4–2.9	2.5	0.3	100	1.6–3.6	2.5	0.3
13	18	1.14	0.02	35	0.56	0.03	>0.7	>0.6	60	−0.1616	>0.2	2.6–5.0	3.9	0.8	81	3.6–6.7	4.6	0.6	110	3.2–8.4	4.7	0.7

[1] = sample size

[2] = intercept of regression of measurement on body length

[3] = slope of same regression

[4] = correlation coefficient

[5] = originally measured from notch in flukes.

determination purposes, but these were incorrectly fixed and had partially decomposed by the time they were required for examination. Only 12 of the plates were still sufficiently intact for certain measurements to be made, and although in most cases it was difficult to recognise the gum line, the length and breadth of each was measured as described by Omura and Fujino (1953). Six of the plates came from whales belonging to the inshore group and six from whales belonging to the offshore group (Table 4). The length: breadth quotient of plates from inshore whales was generally greater than that of offshore whales, only one of their plates having a quotient less than 2.25 while none of the plates from offshore whales had a quotient more than 2.24. The mean quotient for inshore whales was 2.32 and for offshore whales, 1.99. As there was little difference in the absolute lengths of the plates, the greater values for inshore whales infer that they must have narrower plates.

Table 4

Measurements of baleen plates from Bryde's whales off South Africa

Platform number	Form	Length (mm)	Breadth (mm)	Length/ breadth
Donkergat				
152	Inshore	274	115	2.38
153	„	320	139	2.30
154	„	295	129	2.29
159	„	351	158	2.22
233	„	370	152	2.43
334	„	378	165	2.29
677	Offshore	333	181	1.84
678	„	340	163	2.09
719	„	392	175	2.24
721	„	378	206	1.83
812	„	385	183	2.10
918	„	335	180	1.86
Durban				
U68/741	–	356	191	1.86
U69/582*	–	325	162	2.01
U69/652	–	236	178	1.33
U69/683	–	351	172	2.04
U69/2138	–	380	188	2.02

*labelled as sei whale

This conclusion is of considerable interest. Omura and Fujino (1954) have compared the baleen plate shape of 236 sei whales (228 from the coast of Japan and 8 from the North Pacific, pelagic) with that of 272 Bryde's whales (265 from the Bonin Islands and 7 from the coast of Japan). Sei whales generally had relatively longer baleen plates, up to 60 cm in length, whereas Bryde's whales' plates hardly ever exceeded 40 cm. Sei whale baleen length:breadth quotients were (in 95% of instances) greater than 2.20, whereas all the plates from Bryde's whales had a quotient less than 2.20. The lower limit for Bryde's whales was a quotient of 1.20. These limits, and the approximate extent of Omura and Fujino's data, have been entered in Fig. 4, which compares the actual length and breadth values for each baleen plate. (It is important to note at this stage that the shape of the baleen plate depends in part on its position in the baleen series, so that comparisons between whales should really only be based on plates from the same part of the series).

Offshore Bryde's whales from the Cape Province have baleen plates with a similar shape to those of Bryde's whales from the North Pacific, their length:breadth quotient being generally less than 2.24. Baleen plates are also available for five Bryde's whales landed at Durban, the measurements of which are shown in Table 4 and Fig. 4. All four had length:breadth quotients less than 2.20, and so are similar in this respect to offshore whales from Donkergat. These animals were killed between 39 and 65 miles from the coast. A Bryde's whale from Chile also had baleen plates with a similar length:breadth quotient (Clarke and Aguayo, 1965), as did three whales from Western Australia described by Chittleborough (1959a), though the latter seem to have had very small baleen plates altogether (Fig. 4). Dr Omura (Whales Research Institute, Tokyo), in a letter dated 28 July 1970, sent me the measurements of a baleen plate from a 43 feet male Bryde's whale caught in 1961 off the coast of Brazil in the position 23°13'S, 41°53'W. This plate measured 30 cm in length with a width of 19 cm, or a length:breadth quotient of 1.58, and is clearly referable to a whale of the offshore type.

Dr Omura, however, has already described a baleen plate from a Bryde's whale killed off Brazil that has a length: breadth quotient of 2.68, and is very similar to that of a sei whale in shape (Omura, 1962a). All six inshore Bryde's whales from the Cape Province had baleen length:breadth quotients of more than 2.20 and so resembled sei whales from the North Pacific (cf Omura and Fujino's 1954 data in Fig. 4), though in this case the similarity is due to the narrower rather than longer plate. In the whaling grounds off both Brazil and the Cape Province, therefore, there appear to be two forms of Bryde's whales differing in their baleen shape. This difference very probably accounts for the high length:breadth quotients for Bryde's whales from the Cape Province reported by Olsen (1913), which have previously been considered to be atypical for the species (Omura, 1966).

I am indebted to Dr Omura for sending me additional evidence of the existence of Bryde's whales with narrow baleen plates. In a letter dated 28 July 1970 he enclosed details of a baleen plate collected by Robert L. Brownell (Jr.) from a Bryde's whale stranded near Calamajue, Baja California. The carcase of this whale had already decayed so that it was a skeleton when found (in January 1967), but identification was confirmed from the baleen. The plate sent to Dr Omura measured 31 cm by 11 cm, or a length: breadth quotient of 2.82, equivalent to that of a sei whale (Fig. 4). Bob Brownell kindly gave me permission to publish details of this specimen.

In a further letter dated 14 January 1971, Dr Omura enclosed data concerning a Bryde's whale baleen plate that he fortuitously found in December 1970 hanging on the wall of a Japanese restaurant in Katsuura, a city near Taiji. According to the restaurant-owner, this plate came from Kyushu, where whaling had stopped several years previously. It measured 35 cm by 14.5 cm, or a length: breadth quotient of 2.41, similar to that of a sei whale or a Bryde's whale of the inshore form off the Cape Province (see Omura, 1977).

Diameter of baleen bristles

Only two of the baleen plates collected at Donkergat were intact enough for representative samples to be taken of their baleen fringes, one being from an inshore and the other from an offshore whale. The diameters of 50 baleen bristles at their base varied from 0.19 to 0.84 with a mean of 0.46 mm and a mode at 0.27 mm in the inshore whale, and from 0.22 to 1.11 with a mean of 0.49 mm and a mode at 0.32 mm in the offshore whale. As the accuracy of measurement was ± 0.03 mm, there seemed to be no significant difference between the bristle diameters of the two whales. The ranges recorded were also similar to those figured by Nemoto (1959) for Bryde's whales from the Bonin Islands and Saldanha Bay, and to those recorded by Clarke and Aguayo (1965) for a Bryde's whale from Chile.

FEEDING

Comparison between inshore and offshore forms

The diet of Bryde's whales off the Cape Province was studied in a previous report (Best, 1967), where the composition of their food, the amounts eaten and seasonal trends in feeding were analysed. A difference was also described between the diet of inshore and offshore whales, and the food organisms consumed by each form are listed separately in Table 5.

Inshore whales subsist almost entirely on the epipelagic shoaling fish anchovies, pilchards and maasbankers, and euphausiids were only eaten once (in conjunction with maasbankers) despite the presence of large swarms in

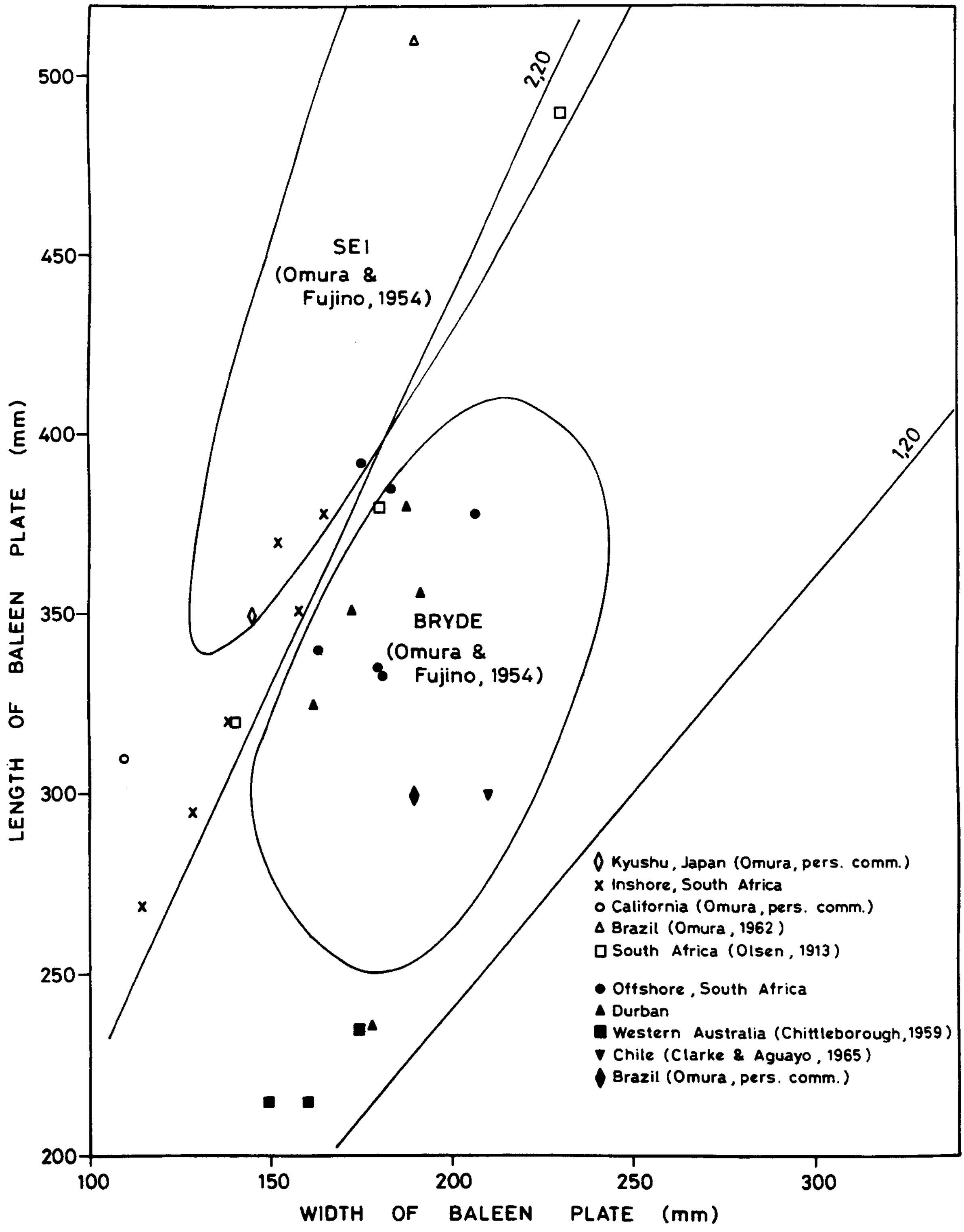

Fig. 4. Baleen plate dimensions for sei and Bryde's whales.

Table 5

Species composition of diet of Bryde's whales off Donkergat

Species	Inshore form (number of stomachs)	Offshore form (number of stomachs)
Fish		
Engraulis capensis	25	0
Trachurus trachurus	11	0
Sardinops ocellata	10	0
Maurolicus muelleri	0	3
Lestidium sp.	0	3
Scomberesox saurus	0	1
Scombrid sp.	0	1
Euphausiids		
Euphausia lucens	0	18
E. recurva	0	5
Nyctiphanes capensis	1	1
Thysanoessa gregaria	0	1

coastal waters (Nepgen, 1957). As there is no difference between the number of baleen plates or the thickness of the bristles in inshore and offshore whales, it seems the scarcity of euphausiids in the diet of the inshore animals must reflect an actual food preference rather than an inability to collect plankton.

The fish consumed by offshore whales are more mesopelagic in nature, and were considerably less important to their diet in this region than euphausiids. On occasion, however, large amounts of fish were eaten, 67 kg of *Lestidium* being found in the forestomach of one animal, for instance.

Bryde's whales off the Bonin Islands, North Pacific, which have been shown above to be similar to offshore Bryde's whales from the Cape Province in scarring and baleen shape, are also recorded as having a similar diet, their principal food item being euphausiids with small mesopelagic fish (*Yarrella* sp., *Myctophum aspersum*) as a supplement (Nishimoto, Tozawa and Kawakami, 1952). Bryde's whales off the west coast of Kyushu, Japan, where animals with a baleen shape similar to inshore animals from the Cape Province have been found (see above), have been recorded as feeding only on sardines and anchovies (Nemoto, 1959). Bryde's whales found elsewhere in Japanese waters apparently vary their diet between euphausiids and small fish (Omura, 1962b). At Sanriku for instance, anchovies were the dominant food, being found in 13 of the 21 stomachs containing food, while 'krill' was only found twice. At Oshima the proportion of 'krill' was higher (17 out of 30 stomachs containing food) and that of anchovies lower (12 out of 30).

The three Bryde's whales from Western Australia described by Chittleborough (1959a) were feeding on anchovies and possibly young mackerel: these whales had baleen plates similar in shape to the offshore Bryde's whales from the Cape Province, though very much smaller in size. A female 31 feet 3 inches long killed on 11 July 1961 in the same locality as the previous three also had small fish of an anchovy type in the stomach (data forwarded by Dr Chittleborough). These whales are somewhat anomalous to Bryde's whales so far described elsewhere in the world.

Of 23 Bryde's whale stomachs examined at Durban from 1962 to 1970, two were recorded as damaged by the harpoon and 16 as empty or 'nil'. The stomachs of three animals contained fish. One (killed 9/7/62) was full of 'sardines' (none preserved), a second (killed 22/8/62) contained fish remains, mostly bones and scales, and the third (killed 26/4/69) contained fish remains, identified as *Carangid* sp. (by M. J. Penrith of the Oceanography Department, University of Cape Town). A fourth animal (killed 1/10/63) was full of 'shrimp remains', presumably euphausiids. A fifth animal, killed 18/4/69, was 'full of baby squid', one of which was preserved and identified as *Lycoteuthis diadema* (by Miss M. A. Roeleveld of the South African Museum). As far as can be ascertained, this last record is the first time Bryde's whale has been recorded as feeding on cephalopods.

Feeding behaviour

Compared to other baleen whale species off the Cape Province, Bryde's whales are voracious feeders (Best, 1967). Full or partially-filled stomachs were encountered on several occasions, and by weighing and measuring the volume of the wet contents it was possible to estimate the capacity of the stomach. Besides the 67 kg of *Lestidium* mentioned above (and found in a 48 feet female), the following amounts of food were found in forestomachs intact and judged to be full: 72 kg (64 litres) of *Trachurus trachurus* in a 41 feet male, 92 kg (86 litres) of *Trachurus trachurus* in a 43 feet male and 120 kg (114 litres) of euphausiids in a 45 feet male. These figures show that the forestomach can be dilated considerably beyond what Gambell (1968) apparently considered to be a fully distended sei whale stomach of 60 litres in volume. Bryde's whales off the Bonin Islands, North Pacific, feed even more intensively, for Nishimoto *et al.* (1952) recorded five first stomachs containing from 121 to 203.9 kg of euphausiids.

According to Sergeant's (1969) calculations, large rorquals should eat about 4% of their body weight daily. Assuming an average body weight of 14 metric tons for a 43 feet long Bryde's whale (Fujino, 1955) the daily food intake should average about 560 kg. If a full stomach contains 120 to 200 kg, then the species must feed three to five times daily. This contrasts with a twice-daily feeding rate proposed for blue, fin and sei whales (Sergeant, 1969). The figures for stomach capacity given, however, were based on forestomachs only. Judging from the frequent similarity in the freshness of the contents of first and second stomachs, it is possible that an overflow of food into the second stomach occurs when the first is full. This would effectively reduce the number of daily feeds necessary.

The feeding habits of inshore Bryde's whales off the Cape Province are of particular interest, as they concern predation of commercial species of fish on the actual fishing grounds. Anchovies were the most frequently consumed species, being found in 25 of the 30 stomachs containing food. Maasbankers were found in 11 stomachs, in six of which they were mixed with anchovies. Pilchards were never eaten unless mixed with anchovies, and then in very small quantities, forming only 0.7 to 15.7% (mean 5.3%) by number of the fish in six stomachs. Whether this species composition represents active selection or not is difficult to judge, as little is known of the relative abundance of these species on the fishing grounds at that time (1962 to 1965). Data from blanket-net catches presented by Stander and Le Roux (1968) suggest that juvenile anchovies have greatly outnumbered juvenile pilchards since 1962–63, and hence the predominance of anchovies in stomach contents may simply reflect their greater abundance on the fishing grounds.

Random samples of fish were taken from stomach contents in August and September 1963, and their standard lengths measured to the nearest 0.5 cm (Table 6). The size composition of the anchovies eaten differed little from that of the commercial catch: anchovies landed in St Helena Bay in September 1964 varied from 7.0 to 13.9 cm in length with a mode from 9.0 to 9.9 cm (Robinson, 1966). The South African commercial anchovy fishery employs a purse seine net with a mesh size of 3/8 inch, so that the size composition of the commercial catch cannot be the result of gear selection, and is more likely to be due to the schooling behaviour of the fish (D. Pollock, personal comm.). It is suggested that juvenile anchovies form separate schools that are distributed much closer inshore than those of the adult, outside the limits of the normal fishing grounds, and only join adult schools when they attain a certain size. Similar behaviour has been reported for the northern anchovy *Engraulis mordax* (Miller, 1955). The size composition of anchovies from Bryde's whale stomach contents tends to confirm this hypothesis, for their baleen apparatus is undoubtedly fine enough to catch fish much smaller than those actually eaten.

Table 6

Size composition of fish eaten by Bryde's whales of the inshore form off Donkergat.

Standard length (cm)	Number of fish measured						
	Anchovies (*Engraulis capensis*)					Maasbankers (*Trachurus trachurus*)	Pilchards (*Sardinops ocellata*)
	Early Aug.	Late Aug.	Early Sept.	Late Sept.	Total		
7	10	–	–	–	10	–	–
7.5	20	18	–	–	38	–	1
8	26	44	3	–	73	–	2
8.5	23	64	11	1	99	–	5
9	14	97	24	5	140	–	7
9.5	7	109	51	38	205	–	3
10	4	74	74	47	199	–	4
10.5	2	52	58	23	135	6	–
11	2	26	42	15	85	18	3
11.5	2	18	19	18	57	15	3
12	2	15	8	24	49	29	2
12.5	–	7	4	9	20	33	1
13	–	3	–	3	6	20	4
13.5	–	2	–	2	4	10	2
14	–	–	–	1	1	6	–
14.5	–	–	–	–	–	3	1
15	–	–	–	–	–	4	–
15.5	–	–	–	–	–	10	–
16	–	–	–	–	–	8	–
16.5	–	–	–	–	–	5	–
17	–	–	–	–	–	1	–
22	–	–	–	–	–	1	–
Total	112	529	294	186	1,121	169	38

The size composition of the pilchards eaten was very similar to that of anchovies, presumably because they were always consumed together with anchovies. Robinson (1966) found that commercial anchovy catches contained an average of 6.3% of other fish species, including pilchards, which is similar to the proportion of pilchards amongst anchovies in whale stomach contents. Anchovy schools at sea must therefore contain a small number of other fish species in association with them.

The absence of maasbankers smaller than 10.5 cm standard length from Bryde's whale stomach contents may also reflect a change in the schooling behaviour of the fish, for smaller fish could undoubtedly be consumed by the whale. Unfortunately confirmatory evidence from commercial catches is not available, as the mesh size for pilchard and maasbanker nets is 1¼ inches.

There was a marked increase in the size of anchovies eaten during August and September 1963. Their size distribution is plotted by half-monthly intervals in Table 6. The modal length increased from 8 cm in early August to 10 cm in September, but this rate of increase seems too rapid to be due to growth alone, and may possibly reflect patterns of anchovy migration with age.

MALE REPRODUCTION

Both testes were collected from each male Bryde's whale landed at Donkergat and weighed fresh minus the epididymis. A sample of about 1 cubic centimetre was taken from the same place in each testis, namely, from the side distal to the attachment of the cauda epididymis at its midlength, and at a depth of about 1 cm below the tunica albuginea. Only the larger testis was sampled. These samples were examined histologically and classified as immature, maturing or mature, using the same criteria as for the sperm whale (Best, 1969). In this instance, however, maturing testis tissue did not contain mature and immature tubules clearly separated in adjacent lobules, but rather a series of tubules in various stages of maturation throughout the testis sample.

Using the microprojection apparatus described previously (Best, 1969), the diameters of 20 seminiferous tubules approximately circular in outline were measured in each animal. The mean tubule diameter in immature males varied from 49 to 89 μ with an average of 71 μ, and in mature males from 121 to 209 μ with an average of 152 μ. In maturing whales mean tubule diameter increased with body length ($r = 0.8688$, $p<0.005$), indicating a gradual increase in maturation: diameters ranged from 78 to 147 μ.

The testes of 19 inshore and 39 offshore Bryde's whales were classified in this way as either immature, maturing or mature. The combined testis weights of these whales are plotted against body length in Fig. 5.

Although both sets of data show a rapid increase in testis weight at a certain body length, with immature and mature testes characteristically different in weight, the acceleration in testis growth seems to occur at a distinctly smaller body length in inshore animals. If the proportions of immature, maturing and mature males are calculated for each foot of body length and smoothed by threes (Fig. 6), the stage at which immature and mature animals are present in equal proportions occurs at 39 to 40 feet in inshore whales and 42 to 43 feet in offshore whales. Male Bryde's whales of the inshore form therefore seem to attain sexual maturity at a smaller size than the offshore form.

Male Bryde's whales from the Bonin Islands reach sexual maturity at 40.4 feet (Nishiwaki, Hibiya and Kimura, 1954). Despite their similarity in scarring, baleen shape and diet, therefore, males from the Bonin Islands seem to reach sexual maturity at a smaller size than offshore Bryde's whales from the Cape Province. The data presented by Nishiwaki *et al.* (1954) show that 50% of Bonin Island whales were mature at a single testis weight of 0.6 to 0.7 kg, whereas from the Donkergat data the distinction between immature and mature testes arises at a combined testis weight of about 3 kg. However the amount of variation in testis weight at any body length from Nishiwaki *et al.*'s data seems sufficient to cover both estimates, so that this slight difference in the criterion of maturity used will not

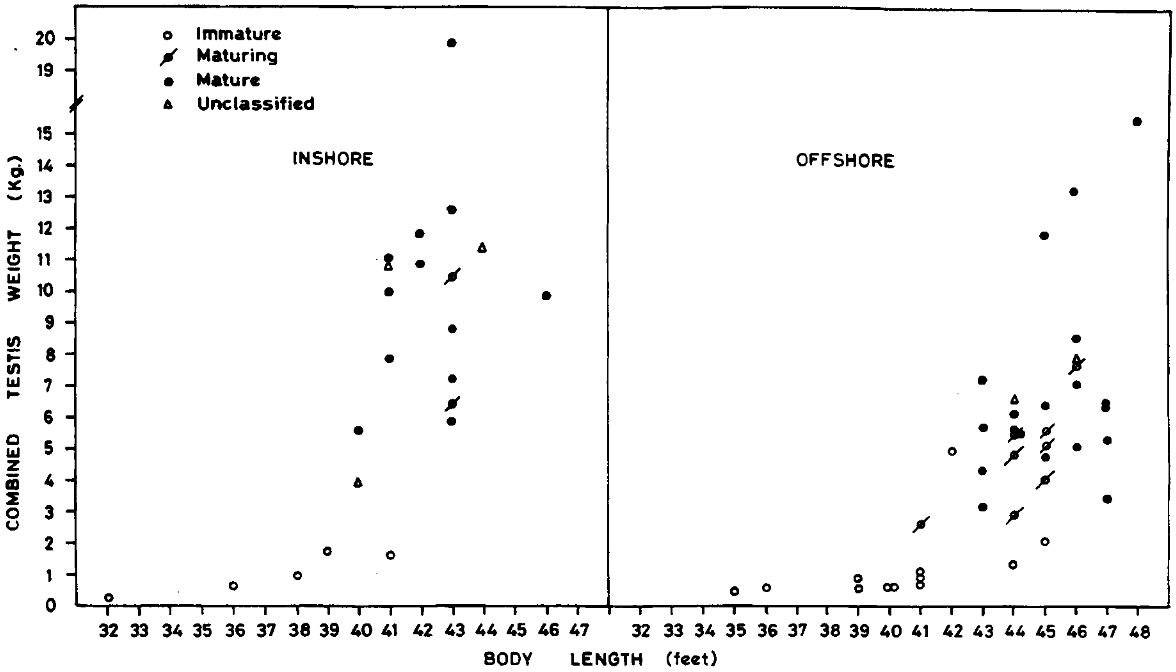

Fig. 5. Testes weights for Bryde's whales landed at Donkergat, 1962 and 1963.

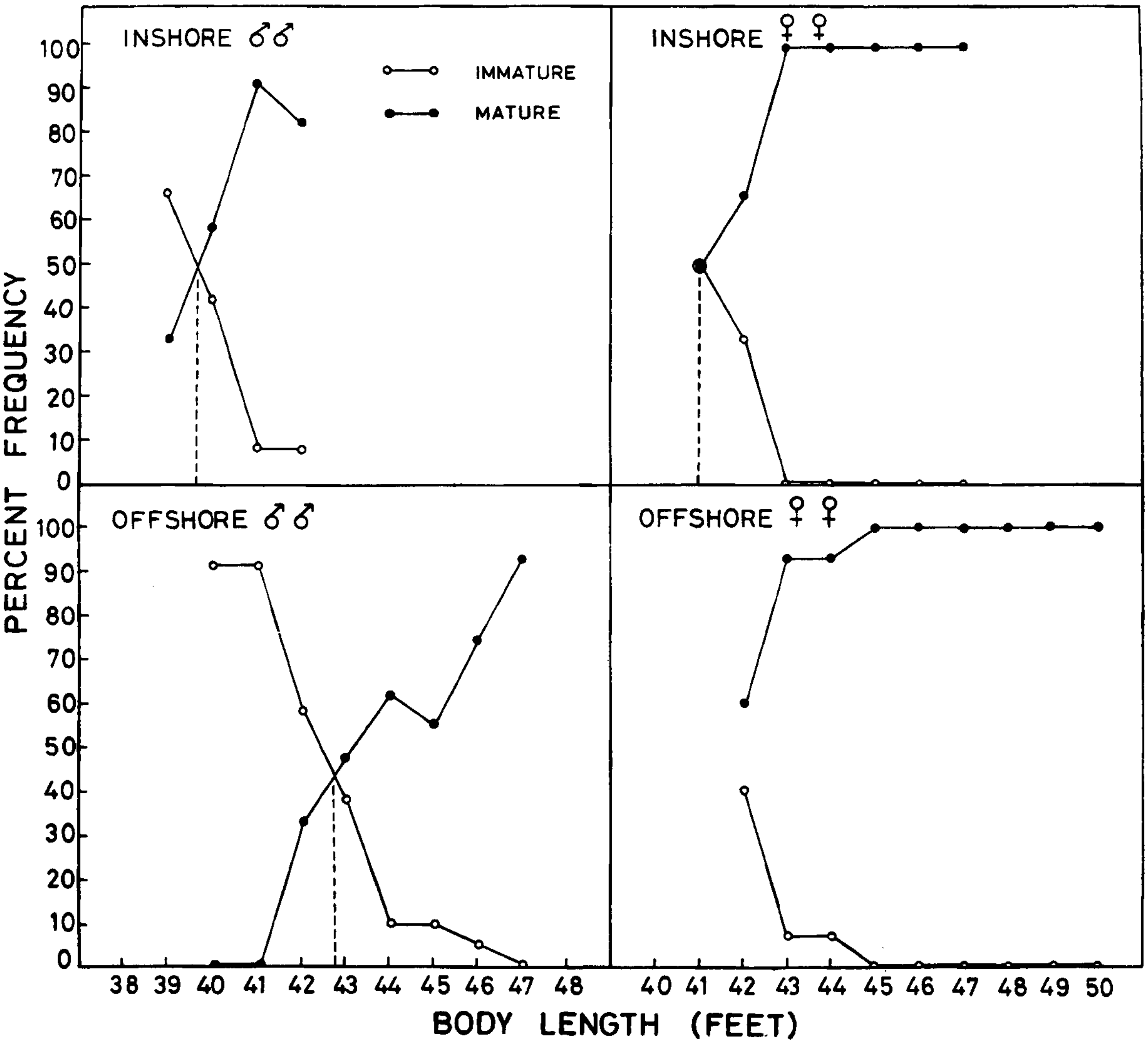

Fig. 6. Body length and sexual maturity for Bryde's whales landed at Donkergat, 1962 and 1963.

materially affect Nishiwaki *et al.'s* conclusions. A more likely explanation of the disparity is the fact that baleen whales of some species tend to be smaller in the Northern than the Southern Hemisphere. Figures quoted by Laws (1956) show that female fin whales in the North Atlantic reach sexual maturity at 61.5 feet whereas those in the Antarctic reach sexual maturity at 65.5 feet, a difference of 4/61.5 or 6.5%. This difference is quite sufficient to account for the divergence between the two estimates of the length at sexual maturity in these two Bryde's whale populations.

Using testis weight only as a criterion of maturity, Omura (1962b) classified 13 male Bryde's whales from the coast of Japan as sexually immature or mature. Due to the small sample size it is difficult to calculate an actual length at sexual maturity, but it seemed to occur between 11.8 and 12.6 m (39 to 41 feet approximately).

For the animals from the Cape Province, the small number of mature males examined (only 31) and the limited seasonal coverage (only five months) are insufficient to investigate the possibility of a reproductive cycle in this sex.

FEMALE REPRODUCTION

Length at sexual maturity

Both ovaries were collected from 68 Bryde's whales at Donkergat during the 1962 to 1965 whaling seasons. These were subseqeuntly treated exactly as described for sperm whale ovaries (Best, 1968), counts of ovarian corpora being made after sectioning on a commercial meat-slicer at a thickness of about 5 mm. These counts only included corpora lutea and albicantia and omitted corpora atretica or aberrantia. They are plotted against body length separately for inshore and offshore whales in Fig. 7.

All whales with one corpus or more were considered sexually mature, and if the percentage of mature females at each foot of body length is smoothed by threes, fifty per cent maturity of inshore whales seems to occur at a length of 41 feet (Fig. 6). The data coverage for offshore whales is unfortunately insufficient for a smoothing process to be applied, but they seem to reach maturity at less than 42 feet. From this evidence there is little difference between the size at sexual maturity of the two forms of Bryde's whale, which is in contrast to the finding for males.

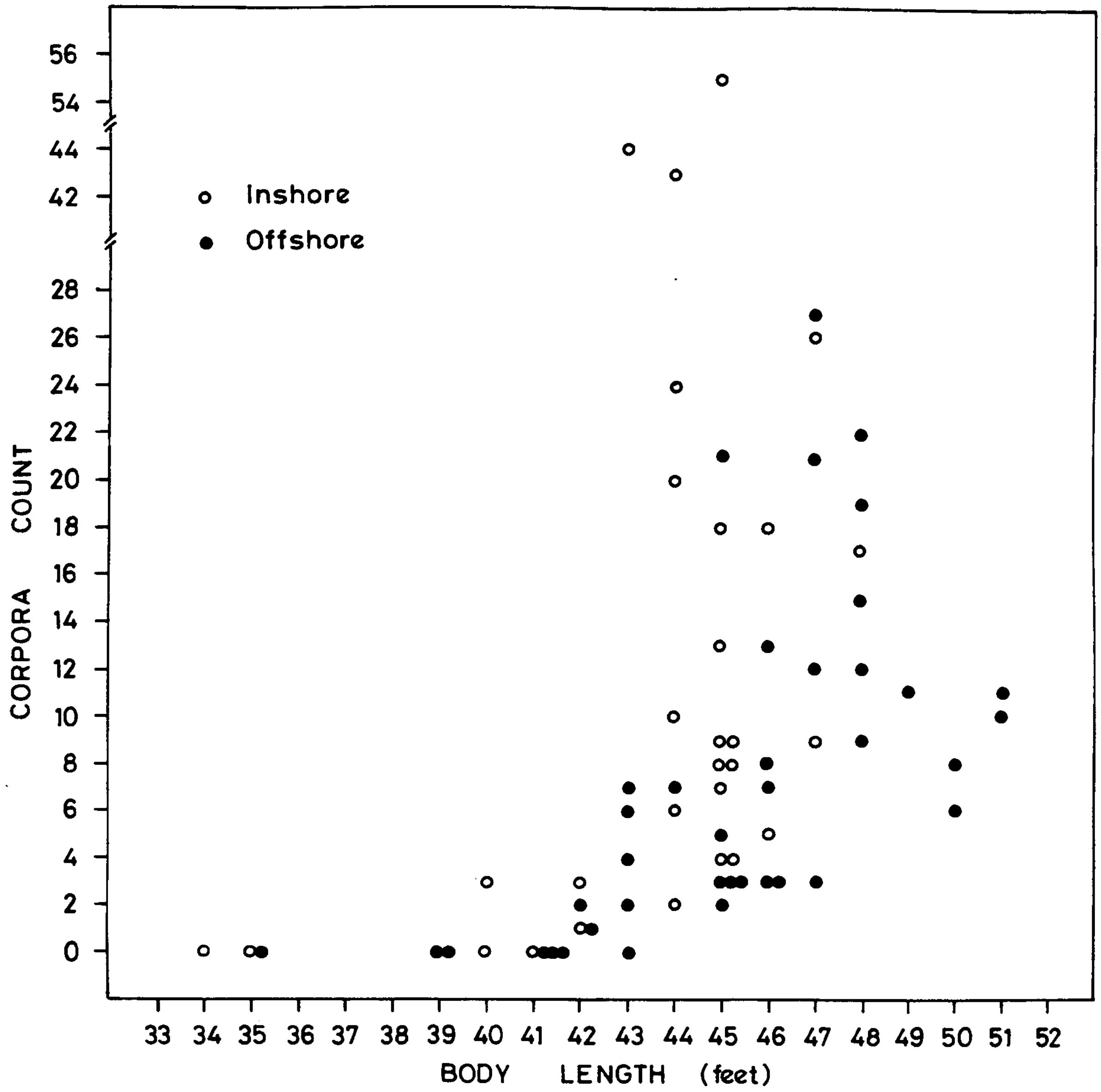

Fig. 7. Body length and ovarian corpora counts for Bryde's whales landed at Donkergat.

However the distribution of corpora counts is generally higher at each foot of body length in inshore whales. This suggests either that these whales mature at a smaller size than offshore whales, or that they have a higher frequency of ovulation (to be discussed below), or that a combination of both takes place.

Female Bryde's whales from the Bonin Islands reach sexual maturity at 41.1 feet (Nishiwaki *et al.*, 1954), but this was calculated as the stage at which 75% of the population was mature. Nishiwaki *et al.*'s data show that 50% maturity would be reached at less than 40 feet, though no animals of such a size were examined. Female Bryde's whales from the coast of Japan become sexually mature at 11.8 to 12 m (39 feet – Omura, 1962b). Both these results are somewhat smaller than the size of either form of Bryde's whale off the Cape Province at sexual maturity, but this could be attributed to the usual size difference between northern and southern baleen whales (see above).

Chittleborough (1959a) gave details of two female Bryde's whales from Western Australia, one 34 feet 8 inches long that was immature and one 38 feet 6 inches long that had 11 corpora in the ovaries. He has now sent me (letter dated 10 November 1970) details of five more females, all taken off Western Australia (Table 7). These include whales 39 feet 6 inches and 40 feet 6 inches long that were still immature, plus a female 47 feet 3 inches long that had only three corpora in the ovaries. This seems to suggest considerable variation in the size of females at sexual maturity in this locality, although the doubts concerning the specific identity of some of these animals must be borne in mind.

Table 7

Reproductive data for female Bryde's whales taken off Western Australia

Serial No.	Date killed	Position killed	Length (feet and inches)	Ovaries: Diameter of largest follicle (mm)	Ovaries: Corpora count
551/c/61	11.7.61	24°34'S 113°09'E	31'3"	6	0*
901/c/62	5.6.62	26°18'S 111°40'E	39'6"	2	0
902/c/62	5.6.62	26°08'S 111°43'E	40'6"	6	0
902/c/63	23.6.63	25°58'S 110°58'E	47'3"	17	3
903/c/63	24.6.63	26°04'S 111°21'E	53'9"	16	14

*only one ovary collected

Data are also available for the reproductive state of twelve female Bryde's whales landed at Durban from 1962 to 1970 (Table 8). Two females at a length of 38 feet were immature, one at 39 feet had a single corpus albicans and three at 41 feet had two, four and five ovarian corpora respectively. All larger animals were sexually mature. This suggests that sexual maturity occurs about 39 feet, but the data are very limited.

Foetal growth and breeding season

From an earlier analysis of records of Bryde's whale foetal lengths it was concluded that there was no restricted breeding season for the species off Cape Province (Best, 1960). Since July 1962, accurate records have been kept of the catch positions of all Bryde's whales landed at Donkergat, and the lengths of foetuses from whales killed within 20 miles of the coast have been analysed separately from those of whales killed beyond 50 miles from the coast (Fig. 8). Records are available for 24 foetuses from these 'inshore' whales and 13 from 'offshore' whales. These are too few and too widely scattered to draw any direct conclusions about the duration or pattern of foetal growth. Some interesting conclusions however, can be drawn from an indirect analysis using the closely-related sei whale as a model.

There is no published information on the size of Bryde's whale at birth, though a female 12 feet 6 inches long stranded alive (with a healed umbilicus) at Willows, Port Elizabeth, on 1 July, 1969 (photographs and measurements sent to me by G. J. B. Ross, Port Elizabeth Museum). Omura (1962b) has listed foetal lengths from 175 Bryde's whales from the Bonin Islands, and 73 foetal lengths from the Cape Province were figured in an earlier report (Best, 1960). There are now 37 additional records from Donkergat, and of this combined total of 285 foetuses, only two were 13 feet (3.96 m) or more in length. A length of 13 feet has consequently been adopted as the size at birth. As such it is in reasonable agreement with a theoretical size at birth derived from Ohsumi's (1966) allometry formula for the relationship between body length at sexual maturity of the female, L_M (here taken to be 41 feet or 12.5 m), and body length at birth, L_B. For four species of *Balaenopteridae*, this formula is

$$L_B = 0.420\ L_M^{0.900}$$

giving an L_B for Bryde's whales of 4.08 m.

In all baleen whale species so far investigated the length of pregnancy has been calculated as about a year (Laws, 1959; Rice and Wolman, 1971), and Gambell (1968) has estimated gestation to last 12 months in the southern sei whale. Pregnancy is therefore assumed to last a year in Bryde's whales. Gambell (1968) has also found that sei whale foetal growth is best described by two straight lines, one covering the first four months of pregnancy when foetal growth is considered to be slow, and the second covering the remainder of pregnancy when growth is more rapid. This pattern has been adopted for Bryde's whale foetal growth. The stage at which the initial slow growth of sei whales is superceded by more rapid growth occurs at a foetal length of about 50 cm, or 11.1% of the length at birth. This would be equivalent to a length of 44 cm in

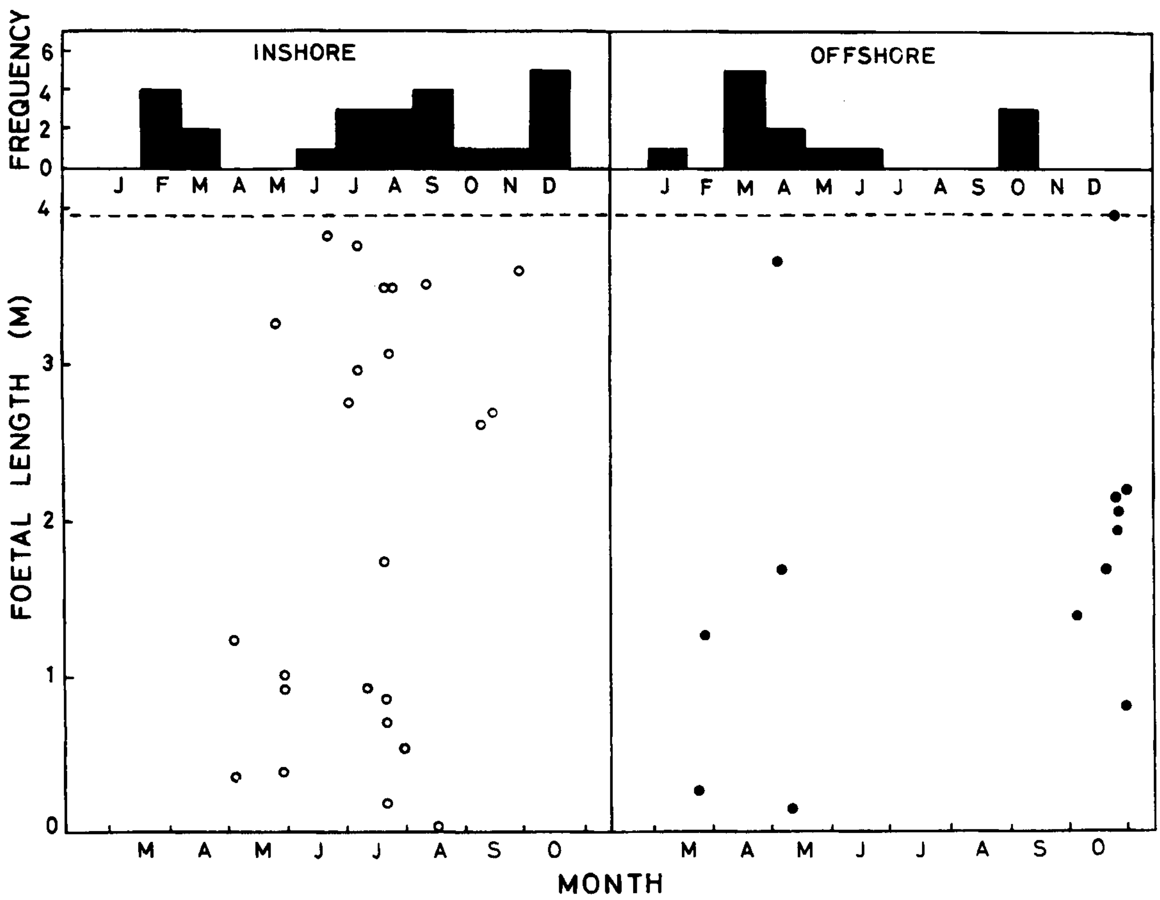

Fig. 8. Foetal lengths of Bryde's whales landed at Donkergat.

Bryde's whales, so foetal growth up to this size is assumed to occupy four months, or a mean rate of 0.37 cm per day. All foetuses larger than 44 cm must therefore grow at a mean rate of 1.45 cm per day (cf. 0.51 ± 0.01 and 1.70 ± 0.02 cm respectively for sei whales – Gambell, 1968). These hypothetical growth rates are considered to be the best possible estimates in the absence of more direct evidence.

Using these values it is possible to calculate the theoretical age of any foetus from its length, and so by back-calculating, to arrive at its conception date. The theoretical distribution of conceptions throughout the year has thus been calculated for inshore and offshore Bryde's whales (Fig. 8). Although the sample sizes are small, there appears to be a difference between the two frequency distributions. Conceptions in inshore whales apparently take place throughout the year, equal proportions being conceived in spring (September to November), summer (December to February), autumn (March to May) and winter (June to August) (chi-square test, $p > 0.20$). The majority of conceptions in offshore whales (eight out of 13, or 61.5%) take place in autumn, and the distribution of conceptions throughout the year is not at random (chi-square test, $p < 0.02$): this suggests that there is a restricted breeding season (as described for Bryde's whales from the Bonin Islands by Omura, 1962b).

The seasonal occurrence of ovulating or recently ovu-

Table 8

Reproductive data for female Bryde's whales taken off Durban

Platform No.	Date killed	Length (feet)	Mammary gland thickness (cm) and activity	Ovaries: Diameter of largest foll. (mm)	Ovaries: Corpora count	Foetus, length (feet & inches), sex
–	23.8.62	42	10 (some milk)	24	17	None
2616	1.10.63	41	6 (no milk)	16.5	5	None
2617	1.10.63	43	4 (no milk)	22.5	8	3'9" M
2102	29.6.66	43	–	–	–	2'0" F
563	12.5.67	39	5 (no milk)	28	1	None
1626	11.8.67	43	–	–	–	10'0" M
741	11.6.68	44	–	12.5	4	8'2" M
582	18.4.69	38	–	10	0	None
652	26.4.69	38	–	25.5	0	None
683	28.4.69	41	(no milk)	17	2	None
2138	25.9.69	41	4 (no milk)	16	4	3'10" M
889	28.5.70	42	milk present	–	–	None

lated Bryde's whales has been listed in a previous report (Best, 1967). Data are now available for a further 14 inshore whales and one offshore whale, and the reproductive condition of all females examined at Donkergat has been summarised for each month (Table 9). Unfortunately the data are restricted in time, being available from non-pregnant females of the inshore population for only three months, and of the offshore population for only five months. However ovulating or recently ovulated whales were caught offshore only in March and April, which agrees with the timing of the breeding season proposed from an analysis of foetal growth. Ovulating females were found in the inshore population in each of the three months for which data were available, which is not inconsistent with an unrestricted breeding season.

Table 9

Reproductive condition of mature female Bryde's whales during each month of the whaling season off Donkergat

		Inshore form					Offshore form			
Month	Preg.	Lact.	Rest.	Ov.	Total	Preg.	Lact.	Rest.	Ov.	Total
March	–	–	–	–	0	3	0	2	1	6
April	–	–	–	–	0	0	1	2	1	4
May	1	0	0	0	1	1	0	10	0	11
June	1	0	0	0	1	0	0	2	0	2
July	5	1	0	1*	7	–	–	–	–	0
August	2	3	0	4+	9	–	–	–	–	0
September	2	3	0	2	7	1*	0	0	0	1
October	–	–	–	–	0	2	3	2	0	7
Total	11	7	0	7	25	7	4	18	2	31

*Also lactating
+Two doubtful, one also lactating

The apparent difference in reproductive behaviour between the two populations of Bryde's whales may be associated with differences in their migratory behaviour, as offshore whales apparently undertake more marked seasonal movements than the more resident inshore population (see above).

The foetal sex ratio in both populations did not differ from parity, seven foetuses from offshore whales being males and six females, while 11 foetuses from inshore whales were males and 12 females. Equal numbers of male and female foetuses are also found in sei whales, though there is an excess of male foetuses in fin and humpback whales (Gambell, 1968).

Eight foetuses ranging from 0.145 m to 2.68 m in length were weighed whole, giving a length/weight relationship of $\log W = 2.8368 (\log L) - 1.6196$, where W = weight in grams and L = length in cm. Weight at birth would therefore be about 562 kg.

Frequency of ovulation

The size of the mammary gland, measured as its 'thickness' (or depth), has proved to be a good indicator of cyclical reproductive activity in whales (Best, 1968; Gambell, 1968; Laws, 1961). The distribution of gland thicknesses in immature, ovulating, pregnant, lactating and resting Bryde's whales is shown in Table 10. There is a definite increase in the size of the gland associated with the attainment of sexual maturity, all individuals with mammary glands 2 cm thick being immature whereas 90% of those with glands 3 cm thick are mature. There is little difference between the size of the glands in ovulating, pregnant or resting whales, where thicknesses range from 3 to 7 cm. Lactating animals have greatly enlarged glands from 8 to 14 cm thick, so that the thickness of the mammary gland at the end of lactation must be between 7 and 8 cm.

Changes in the thickness of the mammary gland were found to give a fair indication of the progress of lactation in the sperm whale (Best, 1968). This also seems to be true for Bryde's whale, for there is a positive correlation between the diameter of the largest corpus albicans in lactating females and the thickness of their mammary glands ($r = 0.6268$, $p < 0.02$). The largest corpus albicans in these animals should represent the regressing corpus luteum of the previous pregnancy, though unsuccessful ovulations during lactation can also produce large corpora albicantia that may complicate the picture. However there seems to be a clear linear relationship between corpus diameter and mammary gland thickness (Fig. 9), for which an estimating equation of $Y = 1.57 + 0.2125\,x$ has been calculated by the method of least squares. The few outlying points, mostly above the regression line, may represent ovulations during lactation. From this equation the mean size of the largest corpus albicans at the end of lactation (or at a mammary gland thickness of 7 cm) can be calculated as 3.06 cm.

As ovulation is suppressed during pregnancy in cetacea, the largest corpus albicans in a pregnant female must reflect its reproductive history prior to conception. These corpora seem to be generally larger in inshore than offshore Bryde's whales (Fig. 10). There is no significant difference between the size of the corpus luteum of pregnancy in the two groups, 11 inshore whales having corpora from 6.76 to 9.43 cm in diameter with a mean of 7.78 cm, and six offshore whales having corpora from 6.53 to 8.00 cm with a mean of 7.21 cm (Mann-Whitney U test, two-tailed $p > 0.10$). Consequently the size difference between the largest corpora albicantia in inshore and offshore whales must reflect a difference in their reproductive activities rather than in the initial size of the corpus.

There is a peak in the size distribution of the largest corpora albicantia in pregnant females at 2.9 cm, a secondary peak at 3.3 cm and further individual corpora up to 4.2 cm in diameter. As the largest corpus albicans is on average 3.06 cm in diameter at the end of lactation, it seems reasonable to assume that the group of corpora around 2.9 cm represents the largest corpus albicans of lactation that has undergone slight regression since lactation ended. As this corpus in turn is considered to represent the corpus luteum of the previous pregnancy, this group of animals must have conceived at their first ovulation since being pregnant previously. All five offshore animals

Table 10

Thickness of mammary gland at different stages of the reproductive cycle in Bryde's whales off Donkergat

Mammary gland thickness (cm)	Reproductive condition Immature	Ovulating	Pregnant	Resting	Lactating	Total
1	1	–	–	–	–	1
2	7	–	–	–	–	7
3	1	2	2	5	–	10
4	2	3	10	7	–	22
5	–	2	4	6	–	12
6	–	1	1	–	–	2
7	–	–	2	1	–	3
8	–	–	–	–	2	2
9	–	–	–	–	3	3
10	–	–	–	–	1	1
11	–	–	–	–	4	4
12	–	–	–	–	2	2
13	–	–	–	–	1	1
14	–	–	–	–	1	1
Total	11	8	19	19	14	71

belonged to this group, suggesting that these whales have a very low frequency of ovulation, possibly tending to be seasonally monoestrous. Only two of the 11 inshore whales belonged to this group.

The second group of corpora with a modal diameter of 3.3 cm are too large to represent regressing corpora lutea from the previous pregnancy, but on the other hand seem too small to be unsuccessful ovulations of recent origin. Although there is no confirmatory evidence apart from the fact that simultaneously ovulating and lactating inshore whales have been found (Table 9), it has been assumed that these corpora were the result of ovulations during lactation. The number of times these whales have ovulated during lactation can only be deduced after examining the size distributions of the second, third and subsequent largest corpora albicantia (Fig. 10). A corpus less than 3.05 cm in

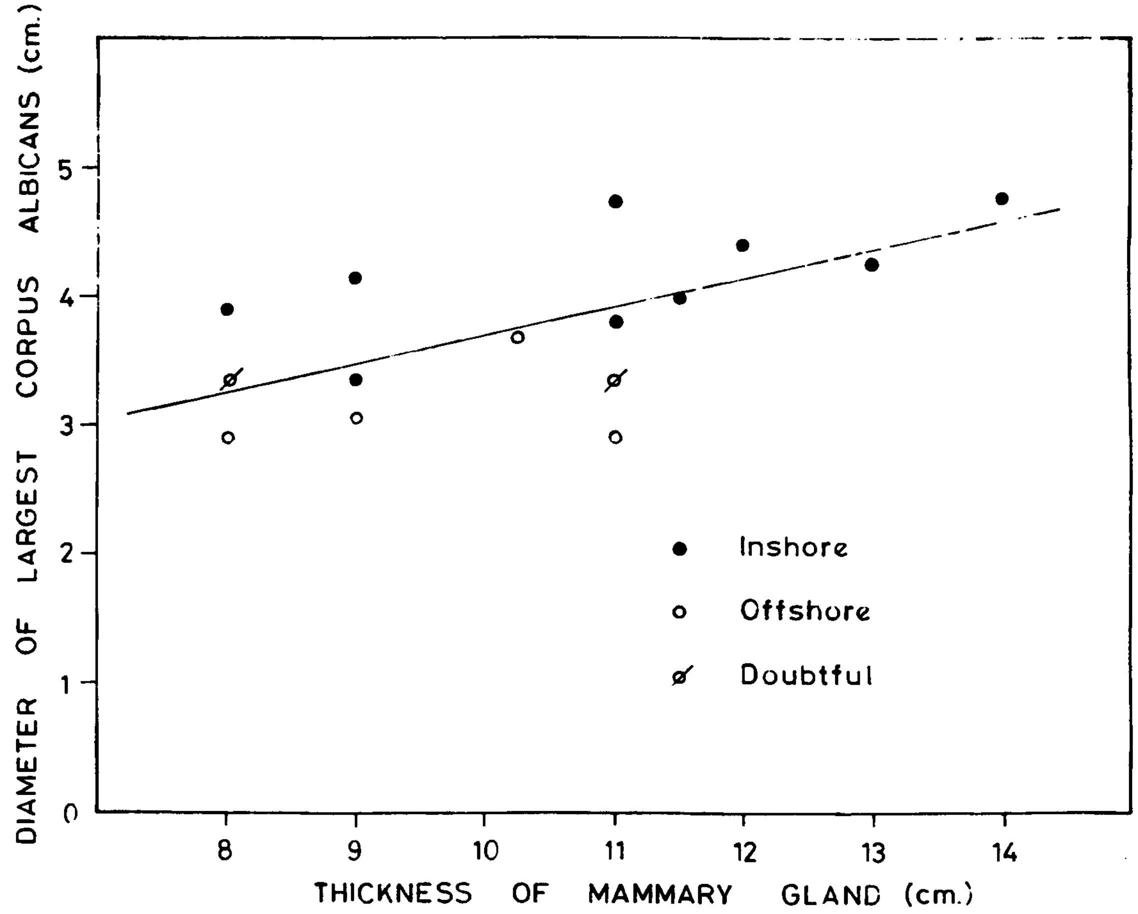

Fig. 9. Diameter of the largest corpus albicans and the thickness of the mammary gland in lactating Bryde's whales landed at Donkergat.

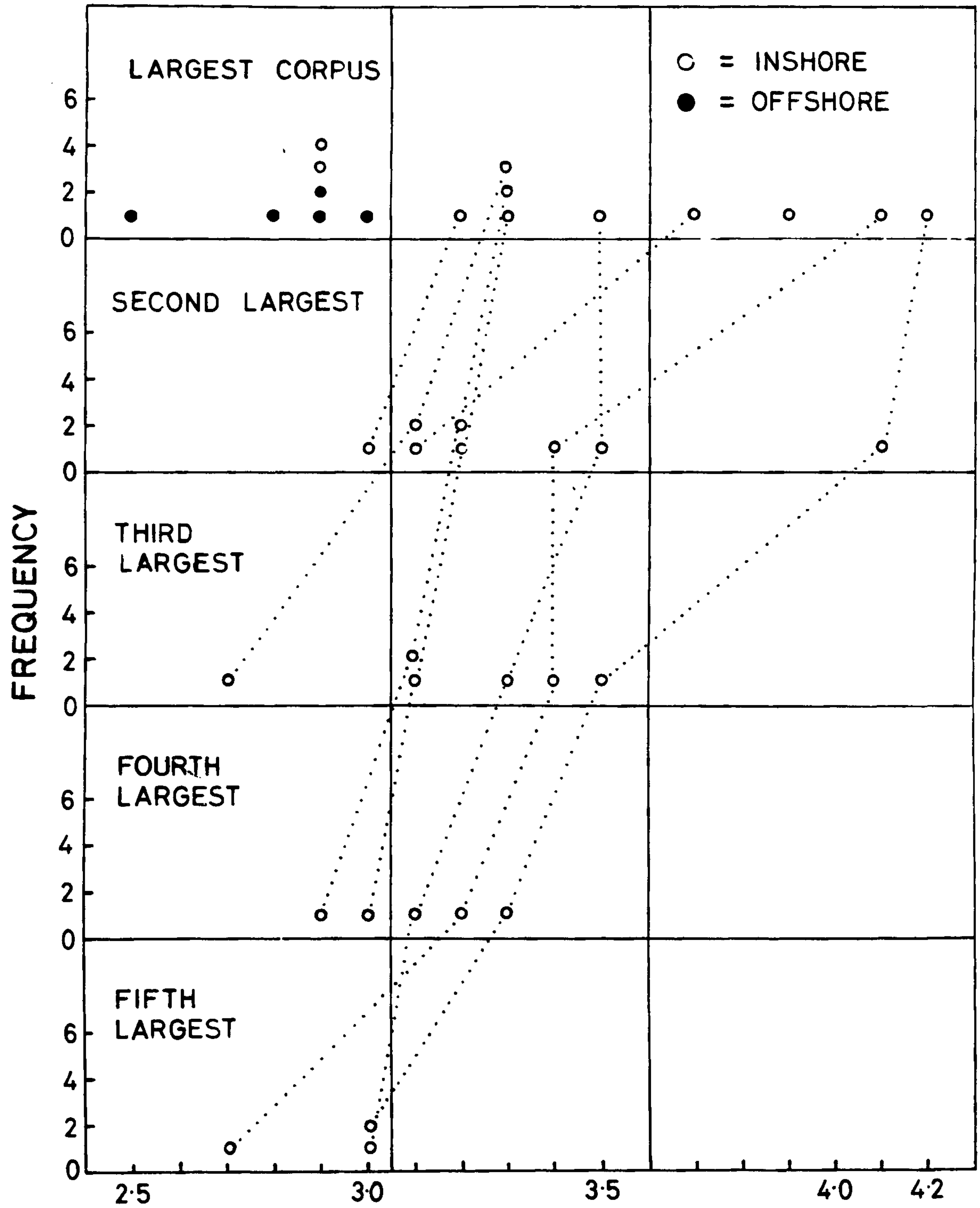

Fig. 10. Diameters of the five largest corpora albicantia in pregnant Bryde's whales landed at Donkergat.

diameter has been assumed to represent the corpus luteum from the previous pregnancy, and on this basis one female ovulated once during lactation, one twice, two three times and one four times.

Four more whales had a largest corpus albicans 3.7 to 4.2 cm in diameter. This group seems to be physiologically separate from the previous group of whales, as their second or third largest corpus was 15 to 17% smaller than the next largest, and so must have occurred some considerable time before (Fig. 10). It has been concluded that the largest corpus albicans of these whales represents an unsuccessful ovulation that took place almost immediately prior to the ovulation which resulted in conception. Only two of these animals apparently ovulated twice unsuccessfully shortly before conceiving.

Some of these animals must also have ovulated during lactation, for their second, third or subsequent largest corpus albicans was more than 3.05 cm in diameter. On this basis, one of the two whales that conceived after one unsuccessful recent ovulation is estimated to have ovulated three times during lactation as well, and the whale that conceived after two unsuccessful recent ovulations is estimated to have ovulated twice during lactation.

This information has been summarized in Table 11, where the difference between inshore and offshore Bryde's whales is readily apparent. The average number of ovulations per reproductive cycle is calculated as 3.75 for inshore whales but only 1.00 for offshore whales. Although there may be some reservations over the accuracy of these estimates, it seems that the frequency of ovulation per reproductive cycle is much higher in inshore Bryde's whales than in offshore whales.

Table 11

Calculated frequency of ovulation of Bryde's whales off Donkergat.

Reproductive history	Total number of ovulations per cycle	Frequency (inshore)	Frequency (offshore)
Conceived at first ovulation following lactation, with no previous ovulation	1	2	5
As above, but with one ovulation during lactation	2	1	0
As above, but with two ovulations during lactation	3	1	0
As above, but with three ovulations during lactation	4	2	0
As above, but with four ovulations during lactation	5	1	0
Conceived at second ovulation following lactation, having ovulated three times during lactation	5	1	0
Conceived at third ovulation following lactation, having ovulated twice during lactation	5	1	0
Total number of whales		9	5
Total number of ovulations in cycle		30	5
Average number of ovulations per cycle		3.75	1.00

This conclusion is supported by the accumulation rate of ovarian corpora per growth layer in the ear plug (for readability of Bryde's whale ear plugs see below). Assuming that one growth layer is deposited in the ear plug per year, as in the fin whale (Roe, 1967), the slope of the regression of the number of corpora against the number of growth layers should represent the annual ovulation rate (as opposed to the frequency of ovulation per reproductive cycle above). For seven inshore whales the estimating equation (by the method of least squares) is $Y = -29.28 + 2.35\,x$, and for 17 offshore whales $Y = 1.51 + 0.42\,x$, and hence the annual ovulation rate for inshore whales is calculated as 2.35 and for offshore whales 0.42. These two regression coefficients are significantly different ($t = 3.314$, $p < 0.001$, 20 degrees of freedom).

A higher ovulation rate for inshore Bryde's whales could be a natural consequence of their (apparently) unrestricted breeding season, which in turn might be associated with their lack of a strong migratory pattern compared to the offshore group.

Reproductive cycle

Because of the small numbers of whales examined, the insufficient seasonal coverage and complications arising from the unrestricted breeding season of the inshore group, it is extremely difficult to reach any definite conclusions on the duration of part or all of the reproductive cycle of the species.

Pregnancy is assumed to last 12 months from analogy with other balaenopterid species (see above). The duration of lactation is impossible to determine directly from the available data, but it is calculated that the largest corpus albicans is on average 3.06 cm in diameter at the close of lactation (see previous section). This is about 40 per cent of the average size of a corpus luteum of pregnancy (7.57 cm). According to Gambell (1968), the average size of the largest corpus albicans of southern sei whales in late lactation is 3.41 cm, which is approximately 41% of the size of a corpus luteum in late pregnancy (8.38 cm). As the corpus luteum seems to undergo a similar amount of regression during lactation in the two species, the duration of lactation itself may be similar. Gambell (1968) has estimated that lactation lasts six months in the sei whale, and this figure has been adopted for Bryde's whale.

One observation of interest in this connection occurred on 12 May, 1964, when two Bryde's whales were killed by the same catcher close to Dassen Island. One of these was a 44 feet long female with mammary glands 13 cm thick, indicating a lactating animal, though no milk was recorded in the mammary glands. The other animal killed was a female 28 feet in length whose stomach contents were recorded as milk. Examination of the growth curve for female Bryde's whales of the inshore form (see Fig. 12) suggests that the latter animal might have had two growth layers in the ear plug i.e. it would have been two years old assuming an accumulation rate of one growth layer per year. As no actual material for age determination was collected from either animal, this observation must be considered of limited significance.

The distribution of reproductive condition amongst mature inshore and offshore whales has been listed in Table 9. Only 20% of all the inshore whales examined were neither pregnant nor lactating, whereas such individuals comprised 64.5% of all offshore whales. From this it might be concluded that the resting period between the end of lactation and the subsequent conception is much shorter in inshore whales, which would seem logical if inshore whales have an unrestricted breeding season and can ovulate at any time of year. In fact, no sexually inactive mature female of the inshore type was examined at Donkergat, those females neither pregnant nor lactating being ovulating animals. Furthermore, the total number of ovulations per reproductive cycle has been calculated as 3.75 for inshore whales and 1.00 for offshore whales. For a two-year reproductive cycle (composed of 12 months pregnancy, six months lactation and six months resting period), the mean number of ovulations per year would be 1.88 for inshore whales and 0.50 for offshore whales. The actual annual ovulation rates calculated above from the regressions of corpora counts on growth layers were 2.35 for inshore and 0.42 for offshore whales. The rate for offshore whales is therefore in reasonable agreement with the expected number of ovulations in a two-year cycle, but the rate for inshore whales is much higher, suggesting that the reproductive cycle is shorter than two years. The possible duration can be calculated from the equation

$$\frac{\text{Total number of ovulations per cycle}}{\text{Duration of cycle in years}} = \text{Mean number of ovulations per year,}$$

as 1.6 years, or about 19 months. This is very close to a reproductive cycle composed solely of a year's pregnancy and six months lactation.

However the data in Table 9 may not be strictly representative of the catch, as the material collected from 12 inshore whales in 1964 by the whaling inspector included seven pregnant animals, which seems an unnaturally high proportion.

Catch statistics from the 1963 to 1966 whaling seasons at Donkergat have been analysed so that the percentage of whales declared as pregnant is calculated separately for Bryde's whales killed within 20 miles of the coast and for whales killed more than 50 miles from the coast (Table 12). Assuming all females 42 feet or more in length to be sexually mature (see above), 22.7% of mature inshore whales and 22.2% of mature offshore whales were recorded as being pregnant. As there is no reason to suppose that the efficiency of reporting foetuses was any different for the two groups, there appears to be no difference between the pregnancy rates in offshore and inshore whales. If the reproductive cycle only lasted 18 months in inshore whales, of which one year was pregnancy, the proportion of pregnant animals in the catch should be much higher than in offshore whales. Consequently it seems unlikely that the reproductive cycle is actually shorter in inshore whales, and it is suggested that all Bryde's whales off South Africa have a reproductive cycle of about two years duration. Further data are needed, however, to confirm this conclusion.

Table 12

Pregnancy rates of Bryde's whales off Donkergat 1963–1966*

	Killed within 20 miles of coast			Killed outside 50 miles of coast		
Length (feet)	Number examined	Pregnant No.	Pregnant %	Number examined	Pregnant No.	Pregnant %
37	2	0	0	–	–	–
38	1	0	0	–	–	–
39	2	0	0	2	0	0
40	7	1	14.3	1	0	0
41	5	0	0	3	0	0
42	13	1	7.7	3	0	0
43	13	3	23.1	7	1	14.3
44	21	3	14.3	2	1	50.0
45	22	7	31.8	8	0	0
46	9	3	33.3	8	1	12.5
47	7	2	28.5	9	1	11.1
48	1	1	100.0	11	2	18.2
49	1	0	0	4	1	25.0
50	–	–	–	7	4	57.1
51	1	0	0	4	3	75.0

*This includes whales examined by inspectors only

PHYSICAL MATURITY AND GROWTH

Determinations of physical maturity were made for 16 inshore Bryde's whales and 47 offshore whales (Table 13). Animals were classified as physically immature if the epiphyses of the caudal vertebrae were unfused to the centra, maturing if the caudal epiphyses were fused but the anterior thoracic epiphyses unfused, and mature if the anterior thoracic epiphyses were fused.

No physically mature males were examined, and only four physically mature females, so it is difficult to reach meaningful conclusions on the attainment of maturity. Nevertheless, it seems from the trends shown in Table 13 that offshore females may reach physical maturity at a greater length than inshore females, suggesting that offshore whales are indeed a larger form of Bryde's whale.

Ear plugs were collected from 56 male and 48 female Bryde's whales for age-determination. Only 60.7% of male plugs and 64.6% of female plugs proved to be readable, there being no significant difference between the readability of plugs from inshore (66.7%) and offshore (60.6%) whales. Bryde's whales therefore have ear plugs intermediate in readability between those of sei whales (mean 48%) and fin whales (mean 85%), if Roe's (1968) values for the latter two species are adopted. There is no significant correlation between readability and body length in either sex ($r = 0.0546$, $p > 0.8$ for males; $r = -0.2320$, $p > 0.4$ for females), whereas the readability of male sei whale plugs decreases markedly with increasing body length (Roe, 1968). With a large enough sample, therefore, valid age compositions of the catch and mortality rates could be calculated. With the small number of readable plugs examined in this report, however, such calculations are impossible.

Despite the small sample of plugs examined, plots of body length against age for inshore and offshore whales indicate differences in growth rate (Figs. 11 and 12). From the growth curves fitted by eye, and assuming that the accumulation rate of ear plug layers is similar in both forms, both sexes of offshore whales appear to grow faster

Table 13

Physical maturity of Bryde's whales off Donkergat.

Length (feet)	Males						Females					
	Inshore			Offshore			Inshore			Offshore		
	*	ϕ	+	*	ϕ	+	*	ϕ	+	*	ϕ	+
32	1	–	–	–	–	–	–	–	–	–	–	–
33	–	–	–	–	–	–	–	–	–	–	–	–
34	–	–	–	–	–	–	–	–	–	–	–	–
35	–	–	–	1	–	–	–	–	–	1	–	–
36	–	–	–	1	–	–	–	–	–	–	–	–
37	–	–	–	–	–	–	–	–	–	–	–	–
38	–	–	–	–	–	–	–	–	–	–	–	–
39	–	–	–	2	–	–	–	–	–	2	–	–
40	–	–	–	1	–	–	1	–	–	–	–	–
41	–	2	–	2	–	–	–	–	–	3	–	–
42	–	–	–	–	–	–	1	–	–	1	–	–
43	1	5	–	1	2	–	–	–	–	2	3	–
44	–	–	–	–	3	–	–	–	1	–	–	–
45	–	–	–	2	3	–	–	2	1	2	1	–
46	–	–	–	–	3	–	–	–	–	2	–	–
47	–	–	–	–	2	–	–	–	–	2	1	–
48	–	–	–	–	–	–	–	–	1	–	2	–
49	–	–	–	–	–	–	–	–	–	–	–	–
50	–	–	–	–	–	–	–	–	–	–	1	–
51	–	–	–	–	–	–	–	–	–	–	–	1
Total	2	7	–	10	13	–	2	2	3	15	8	1

* = immature
ϕ = maturing
\+ = mature

and reach a larger final size than those of inshore whales (see above).

Because of the relatively few animals that it was possible to age accurately, estimates of the age at sexual maturity have to be made from the growth curves, using the lengths at sexual maturity calculated previously. Male inshore whales reach sexual maturity at 9 to 10 layers and male offshore whales at 10 to 11 layers. The age of female whales at sexual maturity is similar, at 10 layers for the inshore form (maybe slightly less for the offshore form). If the accumulation rate of growth layers in the ear plug is the same as in fin whales, i.e. one per year (Roe, 1967), these values can be expressed as the equivalent number of years from birth. Omura's (1962b) estimates for Bryde's whales from Japan are very similar, males reaching sexual maturity at 9 to 13 layers and females at 9 to 10 layers. Both sets of results are also in good agreement with the figures for other whalebone whales – 9 to 10 layers in male and 10 to 11 layers in female fin whales (Ohsumi, 1964); 8 to 10 layers in female humpback whales (Chittleborough, 1959b).

The growth curves for male Bryde's whales tend to an asymptote at body lengths of 42 to 43 feet for inshore

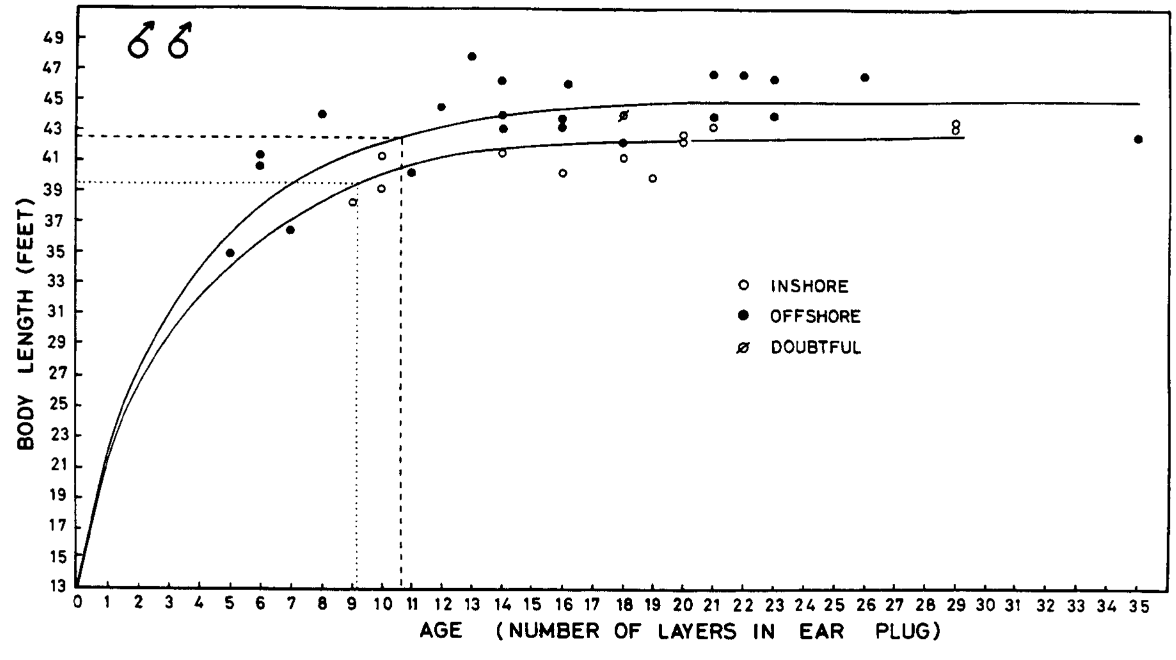

Fig. 11. Growth curve of male Bryde's whales landed at Donkergat.

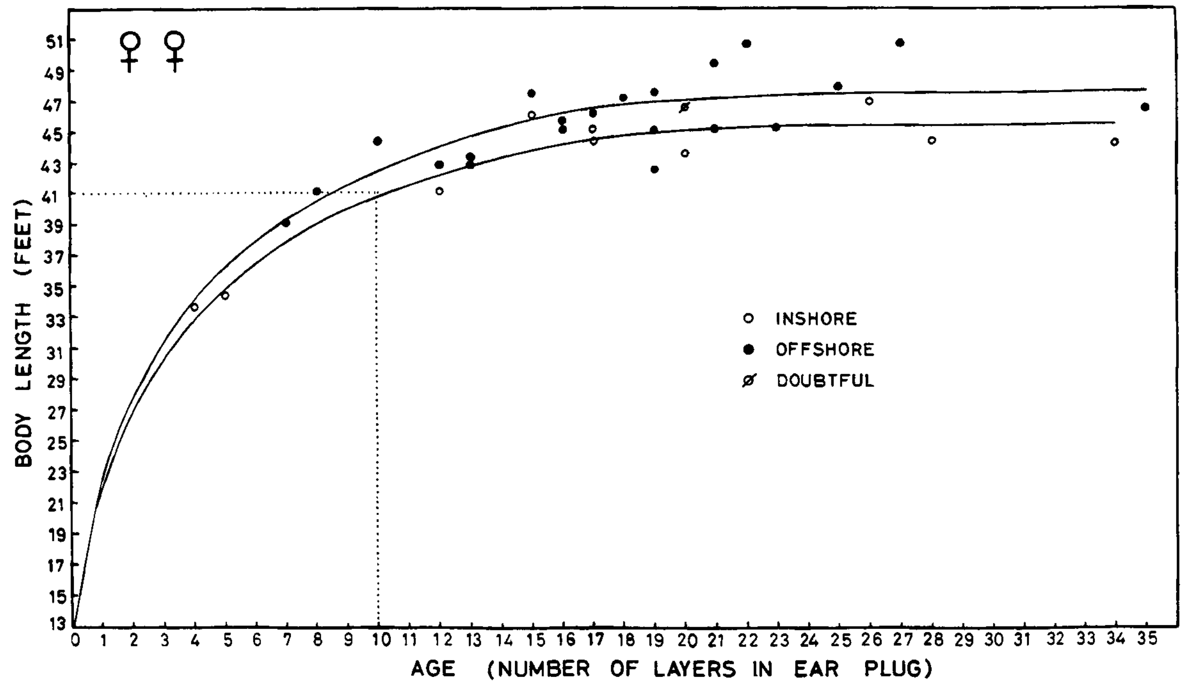

Fig. 12. Growth curve of female Bryde's whales landed at Donkergat.

whales and 45 feet for offshore whales (Fig. 11), while the growth curves for female Bryde's whales become asymptotic at 45 to 46 feet in inshore whales and 47 to 48 feet in offshore whales (Fig. 12). These body lengths should approximate to the size of the whale at physical maturity.

These lengths also correspond in each case almost exactly with the modal length in the Donkergat catch (see Fig. 3), suggesting that the populations have been subjected to a low level of exploitation. Total reported catches from the stock prior to 1968 had in fact been very small (Best, 1974).

TAXONOMIC POSITION

The differences between inshore and offshore Bryde's whales are summarized in Table 14. Using a combination of these characters it was possible to assign 116 (or 90.6%) of the 128 Bryde's whales examined at Donkergat to one of the two groups or forms. The distinction between them is therefore not absolute, but is sufficiently clear at least for their consideration as separate populations, e.g. for stock assessment purposes. Before making any decisions on their taxonomic status, however, the relationship of these forms to Bryde's whales in other parts of the world must be investigated.

The similarity between Bryde's whales of the offshore form and those from the Bonin Islands in the North Pacific has already been mentioned. Both populations are exceptionally heavily scarred (giving many individuals a 'galvanised' appearance), and the length:breadth quotient of their baleen plates is much less than that of sei whales. Both groups have similar feeding habits, mainly taking euphausiids but also myctophid fish, and both have a restricted breeding season. Comparative measurements, however, indicate that the Bonin Islands animals have a proportionally longer rostrum than Bryde's whales off South Africa. A Bryde's whale taken off Chile also resembled this form in its baleen shape, as did one from Brazil, though there were no data on scarring or feeding habits in either case. All Bryde's whales so far examined from the Natal coast of South Africa have had similar baleen shape to the offshore form.

Unfortunately the identity of Bryde's whales from the coast of Japan (as distinct from those from the Bonin Islands) is not clear from the published data. The species has been taken in three localities, Sanriku, Oshima and the west coast of Kyushu (Omura, 1962b). There is no information on scarring amongst these animals, and baleen shape data for seven animals has been combined with that for 265 animals from the Bonin Islands and so cannot be extracted. Three individuals marked in Bonin Islands waters, however, have been recovered off Sanriku, establishing a link between the two populations (Nemoto, 1959). Whales of the offshore group must therefore exist off Sanriku. Animals taken at both Sanriku and Oshima have been recorded as eating krill and anchovy (Omura, 1962b), so it is possible that Bryde's whales of both inshore and offshore forms exist in these two localities, though allopatrically, much as they do off Donkergat. Dr H. Omura of the Whales Research Institute, Tokyo, has informed me, however, that all the Bryde's whales he has examined at Sanriku and Oshima have belonged to the offshore form (*in litt.*, 28 July 1970), and he sent a photograph of a baleen plate from a whale killed off Sanriku which resembles that of the offshore form in shape.

There is evidence that animals of the inshore form occur in the third locality on the coast of Japan, the west coast of Kyushu. Bryde's whales caught here are smaller on average than those from Sanriku or Oshima by three to four feet (Omura, 1962b), are recorded as feeding exclusively on anchovy and horse mackerel (Nemoto, 1959), and from the evidence of one baleen plate seem to have a baleen shape similar to that of the sei whale. Bryde's whales with such relatively narrow plates have also been recorded from Brazil and Baja California.

On the biological evidence available for the species throughout its range, therefore, the separation into two

Table 14

Distinguishing characteristics of the two forms of Bryde's whales off Donkergat

Characteristic	Inshore form	Offshore form
Distribution	<20 miles off the coast	>50 miles off the coast
External appearance	very few oval scars—several with scrapes under tail	numerous oval scars—no scrapes under tail
Baleen shape (length : breadth quotient)	2.22–2.43	1.83–2.24
Food	Anchovies, pilchards, maasbankers	Euphausiids, myctophids, *Lestidium*
Size at sexual maturity	Males 39–40 ft. Females 41 ft.	Males 42–43 ft. Females 41–42 ft.
Breeding season	Unrestricted	Principally autumn
Mean number of ovulations per reproductive cycle	3.75	1.00
Calculated ovulation rate	2.35	0.42
Size at physical maturity (= $L\infty$)	Males 43 ft. Females 45 ft.	Males 45 ft. Females 47–48 ft.

forms observed so far only off the west coast of South Africa may be more widespread. The animals examined from Australia, however, seem to be somewhat anomalous. While their baleen shape is similar to that of the offshore form, the occurrence of a female 38 feet 6 inches long with 11 ovarian corpora seems inconsistent with the trend of corpora numbers against body length in Fig. 7. Furthermore, animals from the west coast of Australia seem to differ from 'normal' Bryde's whales in the relative position of the posterior end of the throat grooves and their umbilicus. Bannister (1964) has commented 'There have now been four sei whales and eight Bryde's whales taken at Australian stations since Bryde's whales were first taken on this coast in 1958 (Chittleborough, 1959). Material and data from these specimens do not conform precisely with the published descriptions of specimens from other parts of the world. Further material from the west coast of Australia, where these whales are common but not sought commercially at present, might show that localized populations differ in their morphology'.

The possibility of there being different forms of Bryde's whale should also be viewed against the controversy that exists over the taxonomic identity of *Balaenoptera edeni* Anderson and *B. brydei* Olsen. Junge (1950) and Omura (1959) considered these two species to be synonymous on osteological grounds, though both authors found certain consistent differences between skeletons of *edeni* and *brydei*.

Soot-Ryen (1961) investigated these differences further, comparing data from three skeletons of *edeni* from the Bay of Bengal to Sumatra with data from four skeletons of *brydei* from Curacao, South Africa and Japan. He found three (possibly four) osteological ratios in which there was a greater difference between *edeni* and *brydei* than between these two and *B. borealis*. Omura (1966) however, considered these differences less significant than those between *edeni-brydei* and *borealis*. Nevertheless, in 1959 the same author commented that the Pulu Sugi specimen of *edeni* described by Junge (1950) had a skull about 32 cm shorter than that from a specimen from the coast of Japan, though it was a full-grown adult while the Japanese animal was still adolescent. This size difference is strongly reminiscent of that between the inshore and offshore Bryde's whales from Donkergat. From this characteristic alone, therefore, it could be deduced that inshore Bryde's whales are referable to *edeni* and offshore Bryde's whales to *brydei*, though body size is not a good taxonomic character because of its possible relationship to environmental conditions.

However, in his original description of *edeni*, Anderson (1878) gave no details of the external appearance that would enable one to identify whether it was an inshore or offshore form, apart from measurements of six baleen plates. One of these was apparently a fragment of a plate, while the five remaining plates were described as 'triangular, with about 12 inches of length and a maximum breadth at the base of 6 inches'. These proportions would place the animal as an offshore form of Bryde's whale. Its length was given as 37 feet, and Anderson considered it to be a mature animal based on the condition of the vertebral epiphyses, with a maximum length for the species of 38 to 40 feet. The specimen of *edeni* from Pulu Sugi described by Junge (1950) had a skeletal length of slightly over 12 m and was also classified as a mature animal from the fusion of all vertebral epiphyses. *B. edeni* therefore seems to be a much smaller animal than either form of Bryde's whale off South Africa. The shape of the baleen plates of animals from this general region is confirmed by a partly damaged plate measuring 24 cm by 13 cm from an animal stranded in Malaysia (Berry *et al.*, 1973).

It also seems probable that Olsen (1913) was referring to both forms of Bryde's whale in his description of *brydei*. He mentioned reports of whalers in Saldanha Bay that two varieties of 'seihval' existed in that area, one called the 'bastard', with the baleen of a fin whale and some other characteristics of the sei whale, and a second, smaller variety with exceedingly dark-coloured baleen and different behaviour. The latter variety was seen in approximately the same numbers all the year round, and in the same localities as the 'bastard', but seemed to occur in greater numbers north of Saldanha Bay. Olsen stated however that he did not examine any specimens of this smaller variety. From his earlier remark that in March 1913 while he was present at

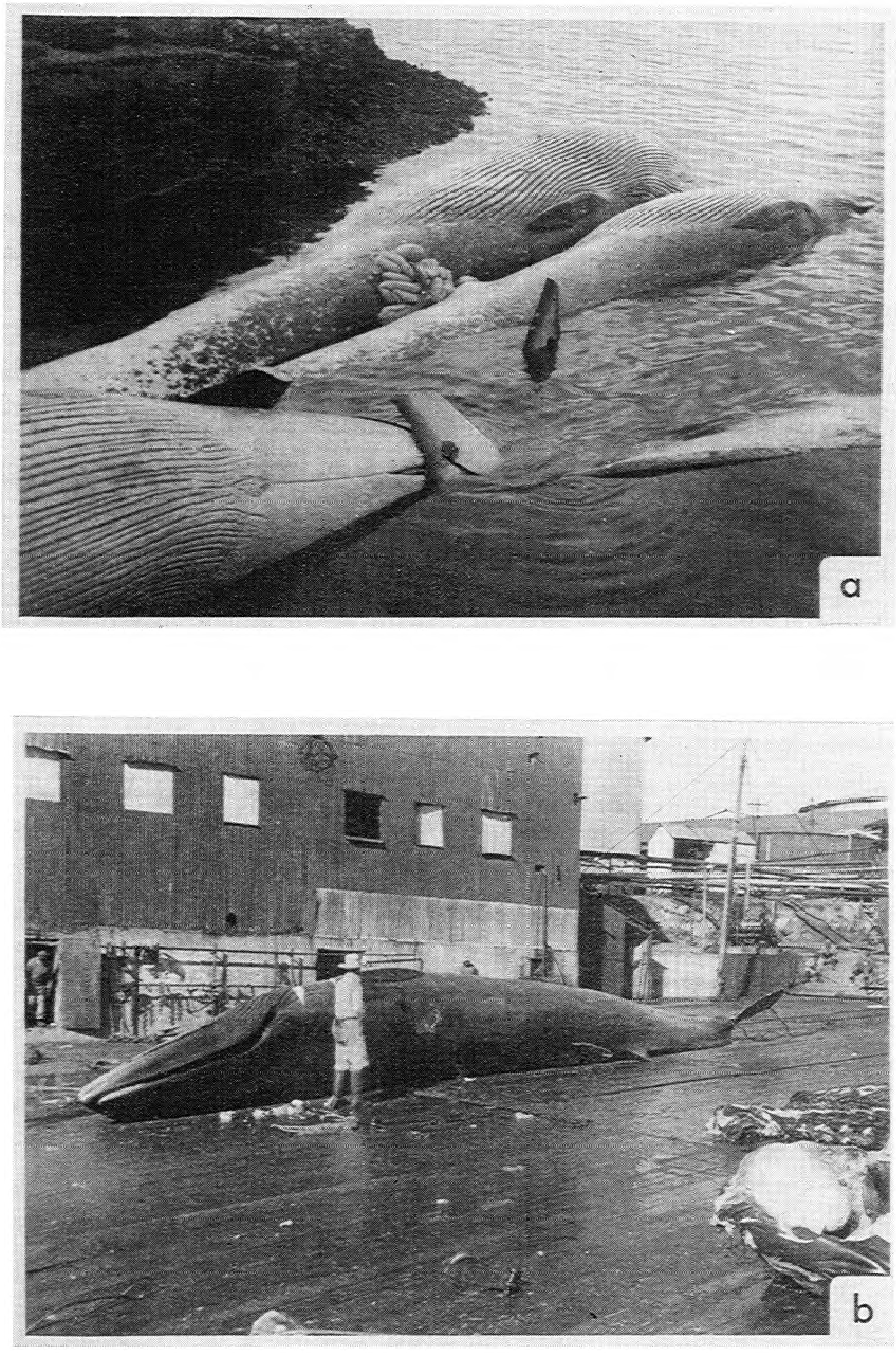

Fig. 13. Bryde's whales landed at Donkergat. (a) Offshore form (b) Inshore form.

the station eleven specimens of *brydei* were brought in that had been mostly found 40 to 70 miles from the coast surrounded by large numbers of euphausiids, it would seem that his description was based chiefly on the offshore form. However the baleen measurements given for four animals clearly indicate that Olsen must have examined at least some Bryde's whales with narrow plates, corresponding to the inshore form. The illustrations published with his description also include photographs of a typically unscarred inshore form (Figs. 3 and 4) and a heavily scarred offshore form (Fig. 8). As he published no osteological details, and no reference material was apparently preserved, the name *brydei* could be equally applied to either form.

The first skeleton described as *brydei* was from a 43 feet 6 inches long female that from the figures of the vertebral column published was clearly very far from being physically mature (Lönnberg, 1931), and so must have been from a very much larger form than the *edeni* described by Anderson (1878) and Junge (1950). Unfortunately no other information on its baleen or external appearance is known, and its locality is not stated (though given as South Africa by Soot-Ryen, 1961).

At present, therefore, it is not possible to reach a definite conclusion about the number of 'forms' of Bryde's whale found throughout the species' range, though there are clearly two off the west coast of South Africa. Nor is it possible to be certain of their taxonomic status in the *edeni-brydei* complex. Animals from the west coast of South Africa are referable to *brydei*, without distinction as to form. *B edeni* is apparently a much smaller animal than either form of *brydei*, with baleen plates resembling the larger, offshore form in shape. Possibly the anomalous Bryde's whales from western Australia are referable to *edeni* also, as those described by Chittleborough (1959a) seemed to be smaller-at-age than either form off South Africa, but had baleen plates similar to the offshore form in shape.

For the moment, although it is clear that *edeni* has systematic priority over *brydei*, it would seem best to keep the two nominal taxa separate, as suggested by Soot-Ryen (1961). As with many other problems in cetacean taxonomy, a final solution must await a thorough investigation of specimens from as many different localities as possible and for which both external and osteological characters are known. A comparison of the genetic variation of different populations using biochemical methods would also prove especially interesting.

The conclusions of the present paper, that different populations of Bryde's whales may have different growth and reproductive rates, should also be taken into consideration when population models or assessments are being prepared for the species.

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Appendix I

Measurements of Bryde's whales at Donkergat, South Africa

				Measurement (inches)													
Date	Whale number	Form¹	Sex	TL	1	2	3	4	5	6	7	8	9	10	11	12	13
1962																	
13.8	119	I	M	470	343	348	81	59	90	130	–	183	58.5	–	13	15.5	–
13.8	120	I	M	516	371	374.5	90	72.5	94	146.5	–	133	51.5	–	13.5	10.5	–
13.8	121	–	M	508	366	385	90	79.3	93.3	155	–	214	59	–	14	14.5	–
13.8	122	I	M	494	351.5	377	95	75	94	133	–	179	57	–	12.5	15	–
13.8	123	I	M	458	321	335.5	79.5	71	86	127	–	192	45	–	11	13	–
13.8	124	–	F	410	295	294	72	66	77	107	–	166	43.5	–	6.5	10.5	–
14.8	133	I	F	495	354	352.5	82.5	76	88	140	–	212	53	–	12.5	13.5	–
22.8	180	I	M	479	337	363	82	74	84	132	–	197	56	–	12.5	10	–
22.8	181	–	M	499	352	367	91	78	93	146	–	187	50.5	–	12.5	14	–
22.8	182	–	M	522	347	386	91	78	95	150	–	216	64.5	–	14	18.5	–
4.9	303	I	M	492	349	353	82	89	74	134	–	213	50	–	13	–	–
4.9	304	I	M	482	335	364	80	67	85	141	–	198²	55	–	12.5	13.5	–
4.9	305	I	M	431	291	317	71	61	79	116	–	176	47	–	11	13.5	–
10.9	320	I	F	535	372	406	86	78	90	149	290	–	59	–	14	13	21
10.9	321	I	F	554	378	408	98	82	103	164	–	220²	59	–	15	–	–
17.9	381	I	F	417	288	–	72	52	–	–	–	–	–	–	–	11	–
18.9	382	–	M	528	379	406	98	86	102	144	–	246	60	47	14.5	16	13.5
11.10	624	O	M	528	364	380	98	82	103	–	–	208	55	–	13.5	12.5	–
11.10	625	O	M	525	380	385	98	87	101	–	–	204	56	–	14	17	–
13.10	656	O	F	566	415	414	105	95	102³	166	–	192	70	49	15.5	18	–
13.10	657	O	M	561	399	418	101	91	98	158	–	184	70.5	52	15.5	15.5	–
13.10	658	O	F	611	435	447	118	101	110	188	–	216	63.5	57	16.3	–	–
17.10	685	O	M	557	395	–	100	90	90	156	–	188²	68	51.5	14	14.5	–
20.10	704	O	F	548	394	402	106.5	89.5	104	155	–	196	64	52	15.3	15.5	–
21.10	705	O	M	527	387	401	102	87	97	157	–	187²	67	44.5	15	10.5	–
23.10	716	O	M	551	401	401	103	91.5	97	160.5	–	188	67	46	15.5	12.8	–
31.10	786	–	F	502	357	–	88	71.5	84.3	138	–	212²	–	45	11.5	–	–
31.10	787	O	F	583	418	431	105	96	105	166	–	242	61	–	15	10.5	–
31.10	788	O	F	543	395	391	103	98	91	163	–	217	68.5	51	15	–	–
1963																	
26.3	1,109	O	F	580	408	394	111	92	112	163	–	–	65	50	14.5	–	–
26.3	1,110	O	F	602	422	440	97.5	90	94	168	–	254	63	54	15	–	–
26.3	1,111	O	F	610	410	460	115	100	116	173	–	248	66	54	15	–	–
26.3	1,112	O	M	519	372	381	97	84	93.5	157	–	210	61	50	14	15	22
26.3	1,130	O	F	494	351	–	–	–	–	156	–	–	55	42.5	13	14.5	22
31.3	1,133	O	M	419	300	314	77	65	73.5	127	–	162	52	39	10	12	17
31.3	1,134	O	M	523	362	386	89	73	87	143	–	196	67.5	48.5	13.5	12.5	23
9.4	1,143	O	F	576	410	429	104	93	101	161	–	212	–	–	–	–	–
9.4	1,144	O	F	520	378	385	97	82	92	152	–	208	66	42	14	12.5	19.5
9.4	1,145	O	M	574	416	431	104	92	102	163	–	196	71	54	15.8	14	22
9.4	1,146	O	M	487	347	369	88	76	84	134	–	204	58	44	13	13	21
9.4	1,147	O	M	536	396	393	101	92	99	153	–	190	63	47	14.5	14	21.5
10.4	1,148	O	M	468	338	349	85	71	84	131	–	196.5	57.5	43	12	11	17
10.4	1,149	O	F	470	336	341	89	77	84	131	–	180	58.5	45	12.5	14.5	18.5
10.4	1,150	O	M	557	410	422	112	84	110	168	–	198	70	55	15	13.5	20
10.4	1,151	O	M	555	403	414	109	92	106	161	–	206	63	48	14.5	–	–
22.4	1,217	I	M	519	372	364	88	80	86	163	262	219	58	44	13	14	21

Date	Whale number	Form[1]	Sex	Measurement (inches)													
				TL	1	2	3	4	5	6	7	8	9	10	11	12	13
24.4	1,238	O	F	415	305	293	79	62	77	134	–	184	46	33	11	12.5	15
24.4	1,239	O	M	540	398	399	100	87	96	167	–	200	66	50	14	12.5	19
24.4	1,240	O	M	561	413	411	104	92	99	–	308	208	69	53	15	12	16
24.4	1,241	O	F	571	421	435	118	95	111	180	–	194	66	51	14	14	22
25.4	1,242	O	F	465	337	335	86	74	80	136	–	180	57.5	44.5	13.5	14	19
25.4	1,243	O	F	579	424	427	106	95	98	169	–	236	65	47	13.5	–	–
25.4	1,244	O	M	482	343	351	88	82	–	153	–	–	62	48	13	13	18
26.4	1,253	O	M	513	373	377	96	84	91	148	–	196	65	47	13.5	14.5	22
26.4	1,254	O	M	535	388	391	99	86	93	154	–	190	66	49	13.5	12	18
26.4	1,255	O	F	512	370	378	94	84	86	150	–	200	57	43	13	13	21
26.4	1,256	O	M	542	390	401	90	85	87	160	–	222	69	49	14	13	18
26.4	1,257	O	M	535	388	393	101	83	97	158	–	186	64	48	12.5	13	22
2.5	1,269	O	M	535	382	402	98	85	94	156	–	–	65	52	14	13.5	19.5
2.5	1,270	O	M	490	353	347	86	78	82	146	–	196	–	–	–	–	–
2.5	1,271	O	F	550	400	400	102	88	94	163	–	–	62	48	14	14.5	21
2.5	1,272	O	F	559	408	415	106	97	98	178	–	230	63	49	15	–	–
6.5	1,273	O	M	436	315	320	82	71	77	133	–	184	53	41	12	–	–
6.5	1,274	O	F	544	405	392	102	83	96	173	–	–	64	52	14	13.5	19
8.5	1,297	I	M	387	–	278	58	56	–	110	–	–	40	31	9	–	–
13.5	1,367	O	F	543	–	398	103	84	100	162	–	194	67	52.5	14	–	–
13.5	1,368	O	F	556	391	407	103	92	99	172	–	–	66	51	14	14.5	19
13.5	1,369	O	M	495	364	374	89	79	86	137	–	210	–	–	–	–	–
13.5	1,370	O	F	487	349	367	89	75.5	85	137	–	180	60	43	12.5	14	18
14.5	1,376	O	F	528	386	395	103	85	100	159	–	200	63	49	13	–	–
14.5	1,377	O	F	556	387	411	100	88	97	161	–	242	66	51	14.5	–	–
14.5	1,381	O	F	505	359	375	94	82	90	141	–	180	–	–	–	–	–
17.5	1,389	O	M	506	364	373	87.5	79	83	159	–	182	56	44	12	12	16.5
17.5	1,392	O	F	572	407	435	114	106	109	177	–	224	66	50.5	14	13	19
18.5	1,397	O	F	534	388	395	96	83	92	157	–	202	–	–	–	13	20
2.6	1,529	I	M	456	–	–	–	–	–	–	–	–	51	39	10	9.5	12
2.6	1,530	I	F	566	–	–	–	–	–	–	–	–	68.5	52.5	15	–	–
2.6	1,531	O	F	550	–	–	–	–	–	–	–	–	–	–	–	14	22
18.6	1,614	O	F	560	404	405	109	96	99.5	171	–	220	–	–	–	–	–
2.8	1,768	I	M	496	–	372.5	82.5	75	81.5	140	269	194	54	40.5	12	11.5	18
19.8	1,916	I	M	552	400	410	94	85	91	171	304	207	–	–	–	–	–
19.8	1,917	I	F	544	388	385	94	87	90	166	319	218[4]	64	47	14	14	22
23.8	1,972	I	M	518	373	388	87	79	84	149	277	216	63	45	13.5	14	24
24.8	1,973	I	F	564	398	407	98	89	93	167	309	191	–	–	–	17	24
24.8	1,974	I	M	495	349	364	76	66	76	133	266	197	–	–	–	–	–
24.8	1,975	I	M	512	366	378	88	80	86	136	275	204	59	44	13.5	13	18
24.8	1,976	I	M	494	368	374	87	77	85	139	277	204	59	44	13.5	–	–
24.8	1,977	I	F	538	394	408	95	88	93	140	306	210[4]	62	50	13.5	13	23
30.8	2,040	I	M	510	369	373	86	81	84	139	265	222	62	43	13	15	23
30.8	2,041	I	F	506	362	380	91	77	87	144	283	196	64	49	13.5	13.5	23
30.8	2,042	I	F	535	393	390	96	84	93	146	286	222	64	48	14	17	23
2.9	2,060	I	F	508	363	368.5	87	76	84	142	266	209	58	42	13	14.5	23.5
2.9	2,061	I	F	407	291	290	68.5	58	66	111	212	157	46	35	10	12.5	20
2.9	2,062	I	F	526	393	395	95	84	91	153	297	214	–	–	–	13	22
2.9	2,063	I	M	519.5	381	379	83	75.5	78	141.5	280	225	58	44	12.5	14	22.5
10.9	2,180	O	F	541	391	419	105	93	99	152	318	243	70	53	15	17	24
13.9	2,201	I	F	483	349	359	80	73	76	129	270	216	55	40	12	14	22

Date	Whale number	Form[1]	Sex	Measurement (inches)													
				TL	1	2	3	4	5	6	7	8	9	10	11	12	13
13.9	2,202	–	F	561.5	411.5	421	95	86	92.5	155	318	235	67	50	15	18	28
17.9	2,249	I	F	480	343	368	83	75	79	138	277	212	56	41	12	17.5	24
26.9	2,296	O	M	497	347	366	89	74	85.5	137	272	187	62	46	13	12.5	19.5
28.9	2,330	O	M	560	402	416	106	91	100	164	314	173	72	57	14	15	19
30.9	2,345	I	F	531	390	394	87	93.5	90	133	287	235	62	46	13.5	14	21
30.9	2,356	O	M	556	397	409	104	87	101	157	303	202	70	52	14.5	15	25
4.10	2,419	O	F	535	380	395	101	84	98	161	290	170	65	51	14.5	13	20
11.10	2,544	O	F	509	356	387	91	80	87	151	288	182	63	50	13	13	21
13.10	2,557	O	F	596	435	436	107	94	105	171	277	227	65	52	14.5	16.5	24.5
28.10	2,685	O	M	526	–	394	101	98	96	–	293	204	59	47	14.5	15.5	21.5
1964																	
30.5	420	O	F	516	376	382	97	86	98	154	294	192	65	47	14	15	–

[1] I = Inshore, O = Offshore

[2] Measured after blubber removed

[3] Measured to inner corner of mouth in this and all subsequent whales. Previously measured to outer corner of mouth.

[4] Measured after blubber cut longitudinally but not removed.

SC/SP 74/Doc 6

Some Results of Sei Whale Marking in the Southern Hemisphere

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Abstract

A total of 395 sei whales has been marked up to 1974 on the Antarctic whaling grounds south of 40° South latitude as part of the International and USSR whale marking schemes. Marks have been recovered from 46 of these whales. An additional 155 animals were marked north of 40°S and marks have been returned from 15 individuals.

The mark recoveries indicate that the movements of sei whales in the Southern Ocean are similar to those of fin and blue whales in the same waters, with some individuals returning to the same region of the feeding grounds year after year and others showing dispersal movements. There is evidence to suggest that movements within the Antarctic whaling Areas may be more restricted in sei whales than in fin whales but movement between some of the Areas is recorded. Migration northwards between the Antarctic and Brazilian waters, and southwards from South African and Australian waters to the Antarctic has been demonstrated.

Since the 1966–67 whaling season, more sei whales have been marked in the Antarctic whaling Areas and north of 40°S by vessels co-operating in Antarctic marking under the International scheme and more marks have been returned. The separate USSR marking scheme has also continued and some results of this have become available (Ivashin, 1973). The present account is based on this additional material, together with some results from the sei whale marking carried out elsewhere in the Southern Hemisphere under the two marking schemes.

ANTARCTIC MARKING AND RETURNED MARKS

A total of 266 sei whales has been marked under the International scheme in the six Antarctic whaling Areas in the post-war period up to the close of the 1973–74 whaling season (Table 1). Under the USSR scheme 129 sei whales have been marked in the same Areas to the close of the 1970–71 whaling season (Ivashin, 1973, Table 3). The distribution of these marked whales by 10° 'squares' within the six Areas is shown on the chart (Fig. 1). Areas II, III and IV together include 299 whales (76% of the total) and very few have been marked in Areas I and VI.

An additional 54 whales have been marked north of 40°S during this Antarctic marking under the International scheme. Precise details of any such marking in the USSR scheme are not available but Ivashin (1973, Table 2) lists 59 sei whales marked in the region from 40°S to the Equator.

Forty-one marks have been returned from 35 sei whales marked in the Antarctic or north of 40°S under the International scheme up to the close of the 1973–74 season. i.e. 11% of the 320 whales marked. They are listed by year-group and marking season in Table 2. Three of the returns are from the 54 whales marked between 30°S and 40°S. There are 17 returns in the O-group (whales shot in the same season as marked), and eight in 1-group. There are no returns older than 5-group. There are marks from 21 whales returned in the USSR series up to and including the 1971–72 season (seven of which were from whales marked north of 40°S) but it has not been possible to prepare a similar table of returns by year-group and marking season from the available data. However, there are six 0-group returns and six 1-group returns. There are also single returns in four older year-groups than in the International scheme series (7, 8, 10 and 11-groups).

MOVEMENTS OF SEI WHALES IN THE ANTARCTIC

Information on the movements of sei whales in the previous analysis (Brown, 1968) was almost entirely restricted to the western half of Area II. Only six marks were recovered from whales captured outside this region and of these only two showed movements of more than 20 degrees of longitude.

The more recent returns considerably extend the area from which information is available, and there are recoveries from each of the six Areas. It is now possible to make a comparison between the range of longitudinal movement shown by marked sei and fin whales captured during the same period – the 12 seasons 1962–63 to 1973–74 inclusive. In Table 3 all the sei and fin whales marked and captured within the six whaling Areas in this period are tabulated according to the range of movement, measured in units of 10 degrees of longitude, between the positions of marking and capture. Since the numbers in the individual year-groups are small, they are combined into four series of three year-groups each. All of the sei whales in both International and USSR schemes in this marking/capture category have been included in the table but only fin whales from the International scheme returns. No correction has been made to the numbers of returns in the different longitude units to allow for the differential distribution of catches of the two species.

Even using the combinations of year-groups, the

Table 1

Sei whales estimated to have been effectively marked in the Antarctic whaling Areas

	Whaling Areas						
	I	II	III	IV	V	VI	All Areas
International scheme (1955–56 to 1973–74 inc)	2	61	36	87	66	14	266
USSR scheme (1954–55 to 1970–71 inc.)*	10	25	20	14	46	14	129
Total	12	86	56	101	112	28	395

*Figures from Ivashin (1973) Table 3

Table 2

Returns of marked sei whales in each year group – International Scheme

Number of whales marked			Returns						
Marking season	Areas I–VI	North of 40°S	Same season 0–group	1st season 1–group	2nd season 2–group	3rd season 3–group	4th season 4–group	5th season 5–group	Returns to date
1955–56	–	2	–	–	–	–	–	–	–
1956–57	–	–							
1957–58	3	–	–	–	–	–	–	–	–
1958–59	–	–							
1959–60	2	–	–	–	–	–	–	–	–
1960–61	10	–	–	–	–	–	–	–	–
1961–62	7	–	–	–	–	–	–	1	1
1962–63	7	5	–	–	–	–	–	2*	2*
1963–64	19	–	1	2	1	–	1	2	7
1964–65	47	2	10	3	1	–	–	–	14
1965–66					No marking programme				
1966–67	20	4	2*	1	–	–	–	–	3*
1967–68	21	10	–	–	–	–	–	–	–
1968–69	29	–	–	–	–	2	–	–	2
1969–70	24	1	2	–	–	–	–		2
1970–71	6	13	–	–	–	–			–
1971–72	15	6	1	–	–				1
1972–73	22	9	–	2*					2*
1973–74	34	2	1						1
	266	54	17	8	2	2	1	5	35

*includes one return from a whale marked north of 40°S

numbers in each series are small but the table does suggest that the range of movement within the whaling Areas may be rather more restricted in sei whales than in fin whales.

There are no records of exceptional movements among the returns which have accumulated since the 1966–67 season except for those of movements between the Antarctic whaling Areas.

MOVEMENTS BETWEEN THE ANTARCTIC WHALING AREAS

Among the 21 marked whales captured up to the 1966–67 season there were two records of movements between the whaling Areas, both in the 1-group returns. One whale had moved eastwards from the eastern boundary of Area I into the western half of Area II. A second animal had moved eastwards from the western half of Area II into the western half of Area III.

In the 25 additional returns from whales marked and captured within the whaling Areas in both marking schemes since that season, there are five more records of movements between the Areas. A whale marked in the western half of Area II at the end of December was captured in early January in the western half of Area III, having moved eastwards through 50 degrees of longitude, approximately 2,200 miles, within 10 days. This is a quite exceptional record as regards sustained rapid speed of movement over a long distance compared with O-group returns showing movements over similar distances in blue and fin whales.

In the 1-group returns a whale marked near the western boundary of Area II in February was captured just across the boundary in Area I in December of the following season. Another whale marked in the eastern half of Area IV was captured a year later just inside Area V.

A whale marked in Area V was killed four years later in the western half of Area VI, and an animal marked in the eastern half of Area II was killed five years later in the western half of Area III.

In Table 4 all but one of these movements eastwards and westwards between the six whaling Areas have been used to compare the amounts of movement taking place between the different Areas. (The movement in the 1-group return from Area IV eastwards into Area V is not included in the table which was prepared before this record was received). The assumption is that the marked whales were a fair sample of the population, then for example, 33.3% of the sei whales in Area I moved into Area II during the period concerned. With the very small numbers of marked whales involved, the figures can of course only be used to draw the broadest of comparisons between the different movements. The tentative suggestion is that there is roughly twice as much movement eastwards between Area II and III as between Areas I and II, and IV and V, and that there is very little movement between any of the other whaling Areas. This suggestion is supported by the earlier conclusion that the range of movement of sei whales within the whaling Areas may be more restricted than is the case of fin whales, in which species movements in both directions have been recorded between all of the whaling Areas.

MARKING NORTH OF 40°S LATITUDE AND RETURNED MARKS

In addition to the 54 sei whales marked north of 40°S during Antarctic whale marking cruises under the International scheme and the 59 whales marked between the Equator and 40°S in the USSR scheme noted above, a further 42 sei whales have been marked off the coasts of Australia, South Africa, South America and New Zealand, and among some island groups of the southwest Pacific Ocean up to the close of the 1973 whaling season. Although the total of 155 whales marked north of the whaling Areas is small, there have been several important returns among the 15 recoveries from them.

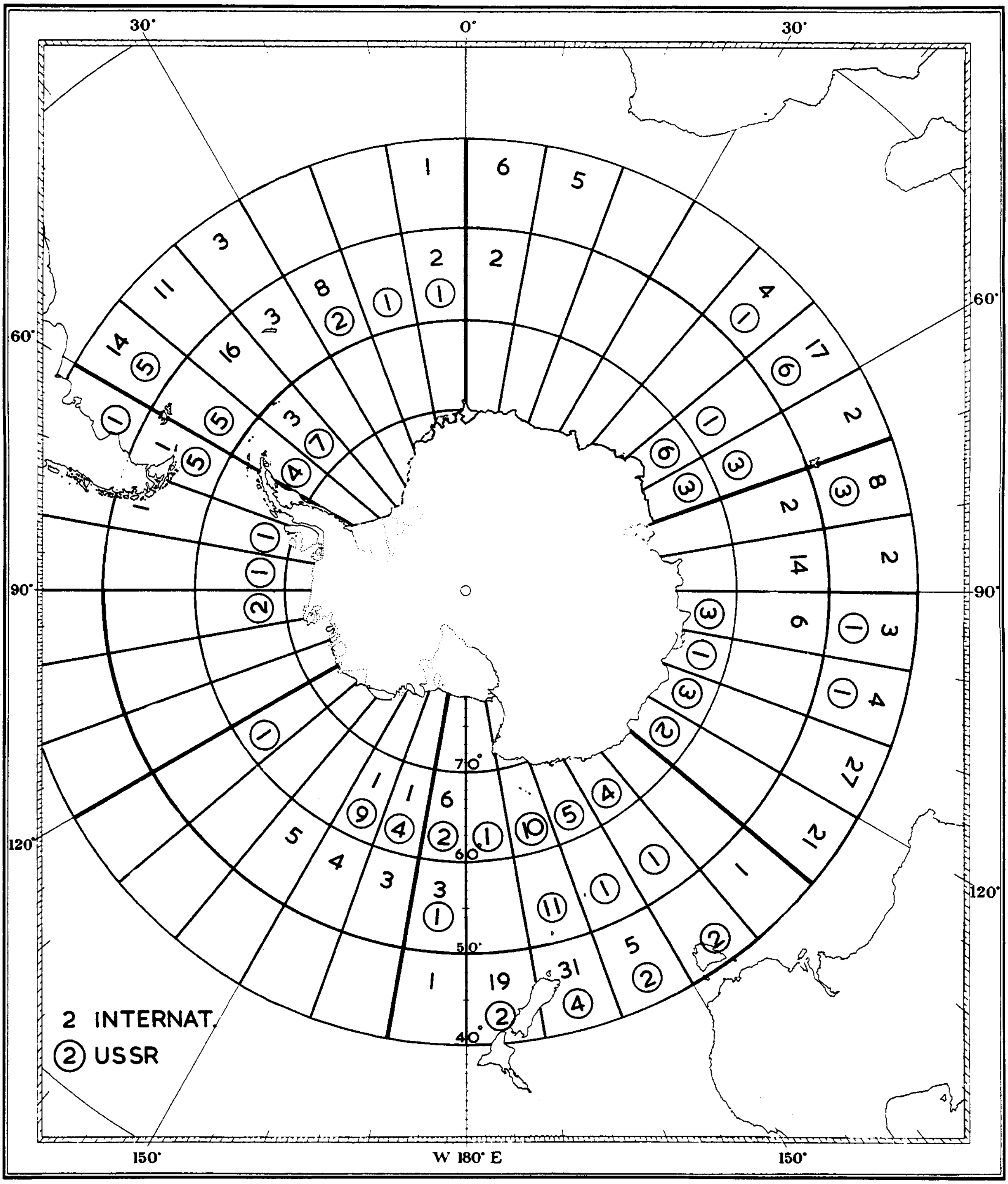

Fig. 1. Distribution of marked sei whales in the Antarctic whaling Areas – International Scheme to 1973–74 inclusive, USSR scheme to 1970–71 inclusive.

Four whales marked in August 1969 in the Indian Ocean off Durban, South Africa, have been captured in Areas III and IV. Two were captured in the Antarctic whaling season immediately following marking (½-group returns), one in position 44°04'S, 50°54'E on 11 February 1970 and one from around 45°30'S, 71°25'E about 24 February. The mark from the latter was returned from a refrigerator vessel so the date and position of capture are only approximate. Similarly in the 1973 season, the other two whales were captured (as 3½-group returns), one in position 45°50'S, 51°24'E on 28 March, and one from around 43°18'S, 82°26'E about 1 April (the mark was recovered in a cooker). These four returns suggest that at least some of the whales found off Durban in August migrate southwards annually into the eastern half of Area III and that they may move further east into the western half of Area IV during the southern summer.

Further east in the southern Indian Ocean there are 1-group returns from two whales marked in the region around 32°/36°S, 79°/85°E. One whale marked on 19

Table 3

Comparison of movements in sei and fin whales within the whaling Areas.

Year group	Species		Total recoveries	Movement (degrees longitude)						
				0–10	10–20	20–30	30–40	40–50	50–60	60 plus
0–2 groups	Sei	No.	30	27	1	–	–	–	2	–
		%		90%	3%				7%	
	Fin	No.	41	24	6	3	6	2	–	–
		%		59%	15%	7%	15%	5%		
3–5 groups	Sei	No	10	5	1	4	–	–	–	–
		%		50%	10%	40%				
	Fin	No.	12	3	2	4	1	1	–	1
		%		25%	17%	33%	8%	8%		8%
6–8 groups	Sei	No.	2	–	2	–	–	–	–	–
		%			100%					
	Fin	No.	30	12	7	6	3	1	1	–
		%		40%	23%	20%	10%	3%	3%	
9–11 groups	Sei	No.	2	2	–	–	–	–	–	–
		%		100%						
	Fin	No.	13	6	4	–	1	1	1	–
		%		46%	31%		8%	8%	8%	

Table 4

Movements between Areas I–VI in sei whales – marking under the International and USSR marking schemes to 1972–73

Whales marked in		Marked whales crossing into	Number of whales marked in	Number of these marked whales recovered in	Ratio of chances of capture in	Corrected number of marked whales crossing into	Corrected number as % of whales marked in
Movement eastwards							
I–II	I 12	II 1	II 86	II 21	II $\frac{86}{21}$ = 4.1	II 1 x 4.1 = 4	I 33.3
II–III	II 86	III 3	III 66	III 4	III $\frac{66}{4}$ = 16.5	III 3 x 16.5 = 50	II 58.1
III–IV	III 66	IV Nil	IV 97	IV 7	IV $\frac{97}{7}$ = 13.9	IV –	III –
IV–V	IV 97	V Nil	V 95	V 4	V $\frac{95}{4}$ = 23.8	V –	IV –
V–VI	V 95	VI 1	VI 25	VI 1	VI $\frac{25}{1}$ = 25.0	VI 1 x 25.0 = 25	V 26.3
VI–I	VI 25	I Nil	I 12	I Nil	I –	I –	VI –
Movement westwards							
I–VI	I 12	VI Nil	VI 25	VI 1	VI $\frac{25}{1}$ = 25.0	VI –	I –
VI–V	VI 25	V Nil	V 95	V4	V $\frac{95}{4}$ = 23.8	V –	VI –
V–IV	V 95	IV Nil	IV 97	IV 7	IV $\frac{97}{7}$ = 13.9	IV –	V –
IV–III	IV 97	III Nil	III 66	III 4	III $\frac{66}{4}$ = 16.5	III –	IV –
III–II	III 66	II Nil	II 86	II 21	II $\frac{86}{21}$ = 4.1	II –	III –
II–I	II 86	I 1	I 12	I Nil	I –	I [1]	II [1.2]

November 1966 in position 35°44'S, 79°16'E was captured on 13 January 1968 in 51°29'S, 73°49'E. A second whale marked on 22 November 1970 in 32°20'S, 85°20'E was captured on 9 January 1972 in 41°53'S, 97°20'E. A 5-group return from the same region is from a whale marked on 16 November 1962 in 35°36'S, 80°50'E and captured on 15 February 1968 in 51°02'S, 72°47'E. The first two returns, and to a lesser extent the 5-group return also, suggest that sei whales migrating southwards in this central region of the southern Indian Ocean may move southwest or southeast and perhaps eventually pass into Area III as well as into Area IV.

A whale marked off Albany in Western Australia was captured in early January in 43°11'S, 129°19'E having moved almost due southwards to the eastern boundary of Area IV.

A whale marked on 6 November 1972 in 37°49'S, 156°41'E off south east Australia was captured and the mark found on a refrigerator vessel on 13 December 1973 in 42°04'S, 124°00'E, showing a movement westwards into Area IV.

In the south Atlantic Ocean a whale marked on 17 November 1965 in 36°19'S, 12°57'W was captured on 10 September 1966 in approximately 34°S, 17°E. This return suggests that some whales moving southwards in the central region of the South Atlantic in one season may change their route in the following season. There is evidence of similar behaviour in fin and blue whales in the south Atlantic from mark returns.

Two whales marked on 17 November 1965 in 36°22'S, 12°48'W (very close to the marking position of the above animal) were captured later in the same season southwest of this position in 44°01'S, 32°44'W on 21 January 1966 and 46°10'S, 18°39'W on 9 February.

One whale marked in February 1962 in the extreme west of Area II (position 46°18'S, 58°18'W) was killed on 14 May 1963 in 24°18'S, 40°45'W off the coast of Brazil, presumably when it was migrating northwards in the season following marking.

CONCLUSIONS REGARDING SEI WHALE MOVEMENTS

The total number (64) of marked sei whales captured from which marks have been returned to date is small and any conclusions based on them must be regarded as provisional. However, analysis of the additional mark returns received since the 1966–67 season from the International scheme and of the published records of returns from the USSR scheme, confirms the earlier conclusion that the movements of sei whales in the Southern Ocean are similar to those of fin and blue whales in the same waters. The return to the same region of the feeding grounds year after year demonstrated in some fin and blue whales also occurs in some sei whales and there is evidence of dispersal movements in other sei whales as is the case in the other two species.

The movement of sei whales within the Antarctic whaling Areas may be more restricted than is the case in fin whales, but movements have been recorded between Areas II and III, and Areas IV and V in an eastwards direction, and both eastwards and westwards between Areas I and II. There may be more movement between Areas II and III than between the other two pairs of Areas. No movements have been recorded between any other Areas. At present there is no evidence from marking results to suggest that any modification of the boundaries of the six whaling Areas is necessary to reflect more accurately the distribution of sei whale population groupings in the Antarctic.

In the south Atlantic Ocean there is evidence linking sei whales off the coast of Brazil with the western half of Area II. In the southern Indian Ocean, sei whales off Durban are linked with the eastern half of Area III and the western half of Area IV. Sei whales in west Australian waters are linked with Area IV, as are whales off south east Australia.

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A Review of Population Assessments of Antarctic Sei Whales

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Abstract

Sei whales in the Southern Hemisphere appear to have the same general patterns of seasonal movements and dispersal as the larger baleen whales. Stock units are not known precisely, but the Antarctic statistical Areas have been used as convenient sub-divisions for assessment purposes.

Population assessments during the development of the Antarctic sei whale fishery in the 1960s were based on analyses of catch-per-unit-of-effort data, mark recoveries, sightings, and a theoretical sustainable yield curve model. Subsequently, modified DeLury method analyses have been employed which indicated that there are some 50,000 to 55,000 exploitable whales remaining from an initial population of around 150,000. The replacement yield is estimated as about 4,100 to 5,000.

Variations between observed density trends and predictions for the stocks in some Areas suggest that the models currently used are not wholly accurate. Additionally these models take no account of possible interaction between whale species.

DISTRIBUTION AND MIGRATION

The basic pattern of the seasonal migrations of baleen whales in the Southern Hemisphere is a southward movement from the tropical and sub-tropical seas after the winter breeding season and a return migration from the productive cold waters of the Antarctic after the summer feeding period. Evidence for these movements has been obtained, particularly for humpback and fin whales, from the times and places of whaling, seasonal population densities, direct observations of movements and recovered whale marks (see Mackintosh, 1965). Much less information is so far available on the migrations of sei whales, but they seem to have the same general pattern of movements as most other baleen whales, although it is timed a little later and the whales do not penetrate to such high latitudes (Gambell, 1968).

At South Georgia the population densities, estimated from catch-per-unit-of-effort (CPUE) data, increased after the beginning of the year. Evidence from mark recoveries suggested a southward drift of the population in January, consistent with the sharp fall in diatom film infection at this time which indicated that the new arrivals had come from outside the Antarctic zone. There appeared to be a northward movement in late February and early March.

Density estimates from catches and aircraft sightings at Durban (approx. 30°S) showed a slow influx of sei whales in May, increasing rapidly after June to high levels in August and September, with a probable reduction in October. Direct observations of whale movements from spotter aircraft pointed to a northeastward trend in May and June, which was reversed from July to September.

STOCK UNITS FROM WHALE MARKING

Relatively few sei whales have been marked in the Southern Hemisphere, because they were not a species of major interest until very recently. Brown (1968) reviewed the records available under the International whale marking scheme up to the close of the 1966/67 season. He reported 140 sei whales marked (64 in the Antarctic between 20° and 60°W), and recoveries from 21 animals. The latter comprised 13 recoveries in the same season of marking, 5 in the following season, 2 in the second year after marking and 1 return after an interval of 5 years.

The returns suggest that the sei whale movements are similar to those of fin and blue whales in the same waters. One sei whale showed an eastward longitudinal movement south of South Africa of some 1,100 miles in 35 days during the whaling season. A whale captured the year after marking had moved over 51° of longitude across the South Atlantic sector of the Antarctic. The other marks recovered after the season of marking indicated a return to the same region of the feeding grounds year after year.

Recoveries in the 1969/70 season (Brown, 1971) included 2 sei whales marked off Durban in August 1969 and caught in February 1970 in the Antarctic, and another sei whale which had moved about 2,200 miles eastwards in 10 days in the South Atlantic sector. Under the Soviet marking scheme, 21 sei whales have been caught out of 172 marked up to 1971/72 (Ivashin, 1973). One of these showed a northward movement from the Antarctic to the sub-tropical waters of the South Atlantic. Two returns indicated an eastward movement of 30° of longitude, one across the South Atlantic to the west coast of South Africa, the other from 166°E to 166°W. The remainder, including 12 recoveries from 1 to 11 years after marking, were returned from much the same regions as at marking.

Clearly, more mark returns are needed before firm conclusions can be drawn about the frequency and extent of dispersal in sei whales but it does not seem to be any more marked than in blue and fin whales. In the mean time, the statistical Areas of the Antarctic (I, 120°W–60°W; II, 60°W–0°; III, 0°–70°E; IV, 70°E–130°E; V, 130°E–170°W; VI, 170°W–120°W) have been used as convenient units for sub-division of the whole region in assessment studies.

POPULATION ASSESSMENTS

The rapid development of the pelagic fishery for sei whales in the Antarctic during the 1960s made assessment of the populations unusually difficult at that time. Different countries varied in their emphasis on catching this species, and the whaling grounds shifted considerably between seasons, so that catch-per-unit-of-effort data needed to be used with extreme caution. The biological information necessary for assessments was scanty but increasing.

There were two main sets of assessments for sei whales which were discussed and reviewed at a special working meeting of the Scientific Committe of the International

Whaling Commission (IWC) held in Tokyo in June 1968, and which have been developed subsequently. Scientists from FAO made use of changes in catch-per-unit-of-effort data, and Japanese workers employed several approaches culminating in a theoretical model.

FAO ESTIMATES

For several seasons estimates of the Antarctic sei whale populations were made for Areas or sub-Areas. The assumption was made that there are several more or less discrete stocks of sei whales, which may correspond to the statistical Areas, and which have been exploited to varying degrees and so require separate assessment (FAO, 1968). The estimates were based on the relative decrease in the indices of the catch per catcher day. They assumed that the decrease was proportional to the change in the stock abundance, and that the decrease in the stock was equal to the average catch in the two seasons, less the net annual recruitment in that period.

The catch-per-unit-of-effort data were calculated in three ways: 1) as total catch-per-unit-of-effort; 2) as CPUE for the whole 10° latitudinal series; and 3) as CPUE by month and by series. Because of the changes in whaling grounds from one season to another, the last two methods were only used where comparable data were available in two successive seasons.

There was no direct measure of net recruitment available, and so by comparison with the values thought at that time to apply to blue and particularly to fin whales a rate of 10% of the population was adopted. This figure was applied to the current population.

In addition to the direct population estimates calculated between seasons in each Antarctic Area, estimates were also made by comparison between catch per catcher day in other Areas and that in Area II in 1966–67 and Area III in 1967–68. These Areas in these and the immediately subsequent seasons showed rather little change in the composition of the fleets working in them and so were thought to be the most reliable standards. Calculations were carried out separately for fleets of different nationalities to overcome their differing species preferences and allowance was made for the varying longitudinal widths of the Areas.

The average estimates for the sei whale population sizes at the beginning of the 1967–68 season, based on the 1965–66, 1966–67 and 1967–68 catches and the various comparisons were then derived, and extrapolations to the start of the 1968–69 season are shown in Table 1.

The sustainable yield (SY) and maximum sustainable yield (MSY) were recognised to be known even less precisely than the size of the population (FAO, 1967). An almost arbitrary method of calculating the yields was adopted. It was assumed that the population giving the MSY was half the original population size, and that MSY was the MSY population size multiplied by the net recruitment rate. This recruitment was guessed to be 15%, by comparison with the then estimated values for blue and fin whales. The original population size was determined as the current estimated population plus the cumulative catch since 1960 (roughly when the more intensive catching of sei whales began), less an allowance for recruitment since that time. The current sustainable yield was based on an assumed net rate of recruitment of 10% for a population depleted below the level giving the MSY, this rate decreasing to zero in the unfished population. How the 15% net recruitment value at MSY fitted in this scheme was not explained. The resulting estimates for the yields are shown in Table 1.

JAPANESE ESTIMATES

The first major assessment of the Antarctic sei whale population by Japanese workers was produced by Doi, Ohsumi and Nemoto (1967). They made use of three main methods for estimating population size.

Rate of exploitation

This makes use of the relationship:

$$N = \frac{C}{E}$$

where N = population size
C = catch
E = rate of exploitation.

The catch is known, and E was estimated from the recovery rate of whale marks and a comparison of sightings and catches.

Of 57 sei whales marked in the Antarctic, 17 had been recaptured (it is not clear what marking results are included in this analysis). The natural mortality rate (M) was estimated as the total mortality rate before 1963–64 from logarithmic regressions of age frequency distributions. Values for M ranged from 0.059 to 0.079, and averaged 0.065. Allowing for natural mortality, the rate of mark recoveries was compared with the number of marked whales available, and gave estimates of 10.1%, 21.7% and 10.9% in the seasons 1963–64, 1964–65 and 1965–66 respectively. Only Japanese recovery information was available for the latter season at the time, and so a figure of about 20% was suggested for the overall recovery rate for the seasons under consideration. No allowance was made for unreported mark recoveries, which could well have been a significant proportion of the total.

A second estimate of the exploitation rate was calculated from a comparison of the number of sei whales observed and taken by Japanese expeditions in 1964–65 and 1965–66. These gave values of 0.35 (recalculated) and 0.28.

The greater part of the sei whale catch in these early seasons of the fishery came from Areas II and III. Estimates of the population at the beginning of the 1965–66 season were therefore calculated as shown in Table 2.

Table 1

Estimates of Antarctic sei whale populations and yields (× 10^3) (FAO, 1969).

Area	IIW	IIE	III	IV	V	VI	II–VI
Stock 1968–69	9.9	3.8	8.6	5.9	12.0	12.0	52.0
SY	0.90	0.37	0.70	0.45	0.85	0.85	4.10
Stock for MSY	16.0	5.9	11.0	6.5	11.0	8.0	58.0
MSY	1.20	0.45	0.85	0.50	0.90	0.65	4.50

Table 2

Estimated sei whale populations (x 10^3) in Areas II and III at the beginning of 1965–66, from rate of exploitation.

Area	II	III
Catch	12.8	2.7
N, with E = 0.3	42.7	9.0
N, with E = 0.2	64.0	13.5

Sightings estimate

An estimate of the population in the higher latitudes of Area II was derived from the sightings of sei whales, using the formula:

$$N = \frac{A}{LD} \times \frac{n}{p}$$

where A = the total area surveyed
L = length of sighting track (n. miles)
D = sighting distance of whales (n. miles)
n = number of whales seen
p = probability of seeing whales.

Observations at sea suggested that D = 10 miles and p = 0.27. This led to estimates of populations of 28,100 and 44,300 for February and March respectively, during the 1963–64 season.

Comparison of the numbers of sei whales seen per catcher days worked by Area gives a relative index of population sizes, which can be translated into numbers if the population in one Area is known. Observations in Areas III–VI in 1960–61, Areas II–IV in 1961–62 to 1962–63 and Areas I and II in 1963–64 led to the results shown in Table 3, assuming a rounded average population in Area II of 50,000 from the other methods of assessment.

Total abundance was then calculated by comparison with the Area II value. Assuming the Area II population was 40,000 led to an estimated total Antarctic population for 1965–66 of

$$40{,}000 \times \frac{7.663}{2.640} = 116{,}000$$

It is not clear why the Area II population was taken as 40,000 here when a figure of 50,000 was assumed previously. The catch data seem to indicate a big discrepancy with the sightings for the abundance of sei whales in Area I. The extent to which sei whales were the preferred species may also vary between Areas by nations even with one season, so there could be various biases in these results.

Sustainable yield

The model developed by Doi *et al.* (1967) was elaborated in greater detail by Doi and Ohsumi (1970).

Notation:
tm = mean age at sexual maturity (= 10 years)
Ro = number of whales of age tm
tc = age at first capture (= 17 years)
R = number of whales of age tc (i.e. recruits)
N = number of catchable whales
A = number of sexually mature whales
M′ = natural mortality rate, immature whales
M = natural mortality rate, mature whales (= 0.065)
F = fishing mortality rate
So = survival rate from tm to tc
S = survival rate after tc
P = pregnancy rate
E = exploitation rate
C = sustainable yield
K = reproduction rate
T = catching period (= 0.3 year)

Table 3

Estimated sei whale populations (x 10^3) for 1963–64 from sightings per catcher days work.

Area	I	II	III	IV	V	VI	Total
	48.6	50.0	28.1	24.5	93.0	11.0	255.2

A major problem with these estimates is that it is not certain that they properly represent the whole sei whale population in the Antarctic, since the sightings do not cover the total region. The bias of sightings data by commercial whaling fleets tends to give over-estimates of population abundance. This was thought to be particularly the case in Area V, and it was suggested that a more reasonable figure for the whole Antarctic was 150,000 (Doi *et al.*, 1967).

Catch-per-unit-of-effort analysis

The catch-per-catcher-day's-work was used as a relative index of population size in each Area in the 1965–66 season (Table 4).

The following relationships were then derived, based on an assumed equilibrium stock situation with an equal sex ratio;

$$Ro = KA$$
$$R = Roe^{-(tc-tm)M}$$
$$So = e^{-M}$$
$$S = e^{-(M+F)}$$
$$E = \frac{F}{F+TM}\left(1 - e^{-(F+TM)}\right)$$
$$N = \frac{R}{1-S}$$
$$C = EN$$
$$A = Ro\,\frac{1 - So^{(tc-tm)}}{1 - So} + \frac{So^{(tc-tm)}}{1 - S}$$

Table 4

Sei whale catch-per-catcher-day's-work by Areas in 1965–66.

Area	I	II	III	IV	V	VI	Total
	1.231	2.640	1.468	0.952	0.539	0.833	7.663

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It was assumed that the reproduction rate K increases as the number of mature whales A decreases. The exact form of the relationship is not known and four possible curves were suggested.

$$\text{Now } Ro = \frac{P}{2} Ae^{-10M'} \quad (\text{where tm} = 10)$$

$$\text{and } K = \frac{Ro}{A}$$

$$\text{so } K = \frac{P}{2} e^{-10M'}$$

The observed pregnancy rate in the catches was about 61%, but allowing for the protection of lactating females, a true value might be around 50%. Using this figure led to an estimate of the upper limit of M′ as 0.138, and the lower limit was taken as 0.065. In fact, a single figure of M′ = 0.10 appears to have been adopted, leading through several steps involving the relationships derived above to an estimate of E = 0.075 for a sustainable exploitation rate. Depending on the exact pattern of the change in reproduction rate with population size chosen, the MSY was then shown to be generated when the population is 50 to 60% of its initial adult size, or about 33% of the initial catchable stock size.

Adopting an initial catchable stock size of 150,000 from the earlier analyses, the sustainable yields at various population levels were calculated assuming linear and convex reproductive relationships (Table 5).

Table 5

Sei whale sustainable yield estimates at various population sizes ($\times 10^3$) from reproductive relationship curves.

Linear relationship			Convex relationship		
Mature	Catchable	SY	Mature	Catchable	SY
7.4	1.8	0.5	7.4	1.8	0.5
32.0	10.0	1.9	83.7	26.3	4.9
81.3	30.5	3.7	140.4	52.7	6.5
118.2	51.4	4.2	169.9	73.9	6.0
152.7	74.6	3.9	194.6	95.0	5.0
179.8	96.9	3.1	211.8	114.1	3.6
211.8	122.3	1.9	229.1	132.3	2.1
243.8	150.0	0.5	243.8	150.0	0.5

Up-dated estimates

The earlier estimates of population size were updated as more material became available in succeeding seasons. In particular, sightings data from the *Chiyoda Maru No. 5* expedition in the area between 110°E and 140°W, 40°S and 60°S in 1966–67 were analysed, together with further analyses of catch-per-unit-of-effort data and sightings from expedition scouting boats. The analyses presented by Doi and Ohsumi (1969) are outlined below.

1. Catch-per-unit-of-effort comparisons were made between Areas, using the now heavily fished Area III as a standard. Its population was derived from a sustainable yield curve analysis. Estimates were made using data of all pelagic whaling nations, or of Japanese expeditions alone.
2. The ratio of sei to fin whale catches in 1967–68 was 4.81. Assuming a population size of 41,800 fin whales, a sei whale population estimate could be derived that was biased on the high side by the preference for this species.
3. Sightings of fin and sei whales by Japanese expedition boats were used to develop a sei/fin ratio (10.4, 5.4, 1.7 in 1965–66, 1966–67, 1967–68 respectively) which was applied to the estimated fin whale populations in each season to find the numbers of sei whales. This assumed no bias in sightings (which depended on the areas surveyed) and an accurate fin whale assessment.
4. The sustainable yield curve method was used to extend population estimates forward taking the latest season's catches into account. The initial population size was taken as 180,000, with an MSY of 6,300 from a population of 70,000.
5. The sustainable yield curve method was also used to estimate sei whale populations by Areas (Table 6). The exact reproductive relationship used was not indicated.

The results from these five approaches are summarised in Table 7.

Table 7

Summary of sei whale population estimates, 1967–68. Japanese analyses.

Method	Population ($\times 10^3$)	Remarks
1a	94.6 – 117.7 (+ I, IIW)	Total effort
1j	63.1 – 78.6 (+ I, II)	Japanese effort
2	201	
3	204–68	1966–67 to 1967–68
4	105	
5	118.6	

SUBSEQUENT ANALYSES

At the 1968 Tokyo meeting of the IWC Scientific Committee the estimates given in Tables 1 and 6 were discussed in detail. The Area II population was re-estimated, together with its sustainable yield. Averaging the estimated sustainable yields for the other Areas and adding the new Area II figure (1,900) gave a total sustainable yield of 5,375 sei whales.

Gulland (MS) reviewed the discussions held in Tokyo and re-analysed the recruitment model developed by FAO, incorporating some of the Japanese data. In this new recruitment model, r was calculated as 0.18 for low population levels, and the immature natural mortality was set at

Table 6

Sei whale population estimates and yields calculated by the sustainable yield curve method ($\times 10^3$).

Area		I	II	III	IV	V	VI	Total
Initial stock		10.0	55.0	32.5	20.0	45.0	20.0	182.5
MSY	stock	3.8	20.7	12.4	7.6	17.1	7.6	69.2*
	yield	0.31	1.68	1.00	0.62	1.11	0.62	5.34*
1968/69	stock	7.6	24.9	17.6	11.5	36.0	13.9	111.5
	yield	0.11	1.54	0.82	0.48	0.41	0.34	3.70*

*The published figures differ slightly.

0.03 to give $(r - M)$ as 0.15, as previously assumed. In the unexploited population $r = M = 0.085$, from Japanese age composition data for females.

This new model and the current catches gave estimates of populations and sustainable yields by Areas as shown in Table 8.

Catches of sei whales from 1968–69 onwards were around 6,000 animals a season, and thus close to the estimated sustainable yield of about 5,000. This meant that catch-per-unit-of-effort data would show little change from season to season, so that any analyses were unlikely to be conclusive.

Table 8

Sei whale population and yield estimates ($\times 10^3$) by Gulland (MS).

Area		I	II	III	IV	V	VI	Total
Initial stock		12.6	45.4	24.8	13.5	19.6	15.5	131.4
MSY	stock	6.3	22.7	12.4	6.8	9.8	7.8	65.8
	yield	0.47	1.70	0.93	0.51	0.73	0.58	4.92
1968/69	stock	11.3	19.8	12.4	6.8	12.2	10.9	73.4
	yield	0.17	1.67	0.93	0.51	0.69	0.49	4.46

However, Chapman (1971) showed that the cumulative catches ($C_1, C_2 \ldots C_k$) with constant recruitment derived from the unexploited populations gives an estimate of the reduction in the populations in k years of:

$$C_1 e^{-M(k-1)} + C_2 e^{-M(k-2)} + \ldots + C_{k-1} e^{-M} + C_k$$

The natural mortality rate M was taken as 0.065 from Doi and Ohsumi (1967), and this gave the reductions shown in Table 9.

If the original catchable population was 150,000 the remaining whales numbered about 75,000. This can be compared with the updated Japanese yield curve analysis (Doi, Ohsumi and Shimadzu, 1971) giving an estimate for the 1970/71 population of 82,720 and a sustainable yield of 5,010.

Chapman (1974) also carried out an analysis for Antarctic sei whales to take account of the fact that in addition to the exploited component of the populations south of 40°S with an age at recruitment of 15 years (Nasu and Masaki, 1970) there is an unexploited component in lower latitudes which supplies recruits to the fishery. This unexploited component was estimated from the parameters $M = 0.065$, pregnancy rate = 0.50, and age at maturity = 10 years. It was calculated that the mature population from ages 10 to 14 years is 38.4% of the exploited population aged 15 years and older. This proportion was then applied to calculate the unexploited component of the initial, effectively unfished, population of 1961–62.

Using a modified DeLury type analysis, the catch data for Areas II to V were used with two indices of abundance (1) catch-per-unit-of-effort in latitudes 40–50°S, the main sei whaling grounds and (2) Japanese sightings indices. A natural mortality rate of 0.065 was applied, and the populations at the start of intensive sei whale catching in each Area (variously 1965–66 to 1967–68) were calculated. These estimates were extrapolated backwards to 1961–62 and forwards to 1973–74, with mortality applied in the season of catching but recruitment derived from earlier years (Table 10).

By reference to fin whales, it was assumed that a net yield of 4% of the total population was reasonable. This result was extrapolated to Areas I and VI on the basis that these two Areas have provided 10% of the catch of sei whales, so that the present total sustainable yield was estimated as 4,000.

This method of analysis takes no account of possible parameter changes in response to exploitation or interaction with blue, fin or other whales.

Ohsumi and Fukuda (1975) carried out a modified DeLury analysis similar to that of Chapman (1974), but used total catch-per-unit-of-effort data for the indices of abundance since 1964–65. This presents a problem because of the lesser interest in sei whales in certain seasons, but their population estimates for 1973–74 of 52,000 and 54,000 (mean and expected) exploitable sei whales were in close agreement with Chapman's (1974) estimate (pro-rated for Areas I and IV) of 53,000.

They suggested that since the catch-per-unit-of-effort in the three seasons 1971–72 to 1973–74 was almost constant (0.670, 0.499 and 0.660 respectively), the average catch of 5,160 sei whales must be close to the present sustainable yield. However, the calculated yield they obtained from the equation:

$$N_{j+1} = (N_j - C_j)(1 - M) + R_{j+1}$$

where N_j = catchable population at the start of season j
C_j = catch in season j
M = natural mortality rate (0.065)
R_j = number of recruits in season j
gave a replacement yield of 4,100.

CONCLUSIONS

All the current assessments of the Antarctic sei whale populations are in general agreement that there are some 50,000 to 55,000 exploitable whales remaining from an

Table 9

Reduction in sei whale populations, 1959–60 to 1969–70 ($\times 10^3$).

Area	I	II	III	IV	V	VI	Total
Reduction	1.7	31.0	16.5	9.9	11.2	5.1	75.4

Table 10

Estimated exploited and unexploited populations of sei whales (x 10^3).

Area	II	III	IV	V	II–V
Exploited 61–62	40.0	25.0	27.0	22.0	114.0
73–74	17.0	6.4	12.9	12.0	48.3
Unexploited	15.4	9.6	10.4	8.4	43.8
Total 73–74	32.4	16.0	23.3	20.4	92.1

initial population of around 150,000. The replacement yield from these whales is about 4,100 to 5,200. There is no firm evidence to fix the MSY level accurately, but it is thought to be about the present population level.

The general picture is of a population which has remained relatively unchanged over the past three or so seasons. However, there has been a downward trend of catch-per-unit-of-effort data and sightings indices in Areas IV and V during this time, and the Area III indices are very low, which suggests that the population models used are not giving a true reflection of the state of the populations.

In particular, the presumed changes in recruitment depending on population size changes need reconsidering in the light of possible interactions between whale species (Gambell, 1975).

Estimates of Southern Hemisphere sei whale stock sizes and yields for the six statistical Areas were prepared by Chapman (1976) for use in connection with the IWC's new management classification scheme. The results, set out in Table 11, are based largely on a re-working of the method used by Chapman (1974) which gave the results shown in Table 10.

The original exploited population estimates were taken directly from Chapman (1974), and represent the stock aged 11 years and over. The original mature stock was recalculated as being composed of whales aged 8 years and over. These revised ages at recruitment and sexual maturity arose from new work on age, and mean that the unexploited component of the mature stock is 25% of the exploited stock.

The current stock size estimates were also taken directly from Chapman (1974), with the addition of the original component aged 8–10 years under the assumption that this has remained unaffected by exploitation. In the absence of firm information or models, 60% of the mature stock was taken as the appropriate value for the MSY level, and the MSY was estimated as 4% of the MSY level, by analogy with southern fin whales.

Because of the lack of direct data on which to calculate comparable stock estimates for Areas I and VI, the original mature stock was taken to be the same percentage of Areas II–V stocks as the accumulated catches of Areas I and VI are of the catches in Areas II–V. The current mature stock was then derived from these values by extrapolation, taking into account the intervening catches and calculated recruitment.

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Table 11

Estimated stock sizes and yields (x 10^3) of Southern Hemisphere sei whales.

Area	Original exploited (1961/62)	Original mature	Current mature	MSY level (60%)	Ratio of current to MSY level	MSY
I	?	7	4.2	4.2	1.00	0.2
II	40	50	17.0 + 10 = 27.0	30	0.90	1.2
III	25	31.4	6.4 + 6.4 = 12.8	18.8	0.68	0.8
IV	27	33.8	12.9 + 6.8 = 19.7	20.3	0.97	0.8
V	22	27.5	12.0 + 5.5 = 17.5	16.5	1.06	0.7
VI	?	12	7.8	7.2	1.08	0.3

SC/SP 74/Doc 10

Sei and Bryde's Whales in Waters Around New Zealand

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Abstract

Data on sightings and catches of sei and Bryde's whales in the vicinity of New Zealand are summarised and discussed. The sightings are correlated with synoptic surface temperature records collected during December 1966 and March 1967. The presence of Bryde's whales was confirmed only in coastal waters off the north east coast of the North Island of New Zealand. This population appeared to be small and local. Observations from *Chiyoda Maru No. 5* between December 1966 and March 1967 indicated that large summer concentrations of sei whales occur in the areas bounded by latitudes 40 to 50°S and longitudes 150 to 170°E, and latitudes 50 to 60°S and longitudes 150 to 170°W, within the region discussed. The animals in these areas appeared to concentrate respectively along the northern face of the Subtropical Convergence, and to the north of the Antarctic Convergence, particularly where steep horizontal surface temperature gradients were present in the form of 'salients'.

INTRODUCTION

This paper summarizes available data on catches and sightings of sei and Bryde's whales within the region bounded by latitudes 30°S and 80°S and longitudes 140°E and 120°W, with specific reference to the immediate vicinity of New Zealand bounded by latitudes 40°S and 60°S and longitudes 150°E to 150°W. An attempt is made to correlate the summer distribution pattern with oceanographic phenomena.

MATERIALS AND METHODS

Data sources

Sighting records were collected by Dr Keiji Nasu (Far Seas Research Laboratory, Shimizu, Japan) and the author from the whale research vessel *Chiyoda Maru No. 5* between 22 December 1966 and 22 March 1967. Four experienced personnel maintained a lookout at all times except in the most severe weather or limited visibility. Data in this paper are drawn only from those records obtained when visibility was clear to about 8 km (5 miles), the swell was less than about 2 m (6 ft.) high, and the wind force 6 (40–50 km.h^{-1}; 25–31 mph) or less on the Beaufort scale.

Previously published sighting and catch records from New Zealand coastal waters (Gaskin 1968, 1972), were available, as well as sundry distant water sightings collected during the 1962 to 1964 New Zealand Marine Department whale survey by the author and his colleagues.

Use has also been made of previously published catch records of sei whales taken by pelagic whaling expeditions between 40°S and 80°S and longitudes 140°E and 120°W (Omura 1973).

Oceanographic data

Sea surface temperature records were taken aboard *Chiyoda Maru No. 5* by a constant recording surface thermograph, checked at regular intervals (twice each day) by manual thermometer readings. These records were used to plot surface isotherms for the region synoptic with the survey sightings of whales (Fig. 1). The positions of isotherms in the Tasman Sea are centred on early January, but those drawn east of New Zealand are centred on late February.

RESULTS

The survey by *Chiyoda Maru No. 5* was carried out mainly north of latitude 60°S, and covered Antarctic whaling Areas IV, V, and VI. The exact cruise pattern in the area east of New Zealand has been previously figured by Gaskin (1973), and the positions of sei whale sightings (not accompanied by surface isotherms) by Nasu (1973). However the captions for Nasu's Figs 1a and 1b have unfortunately been reversed by the printer, which makes them very difficult to interpret. Information on recent catches of sei whales in this area has also been figured by Nasu and Masaki (1970), together with surface isotherms. A comparison of that figure with Fig. 1 of the present paper shows immediately the necessity of obtaining oceanographic data synoptic with the whale sightings or catches, since over the summer periods of 1967/68 and 1968/69 the surface isotherms can be seen to lie as much as several hundred miles further south than in 1966/67, a season in which relatively cool surface temperatures were recorded in the region.

Sighting per unit effort values, based on whales sighted in good whaling weather per hour, are shown in Fig. 2, by 10° latitude-longitude squares. The same information has been processed by Nasu (1973), but analysed in terms of whales and contacts per hundred nautical miles steamed (13,055 nautical miles steamed on watch, for 1,355 hr 37 min). and estimations are applied to only four much larger areas A to D, rather loosely defined. The present author thinks that the sample sizes are large enough to permit analysis in a little more detail. However sighting per unit effort values in Fig. 2 are based only on watch periods when the good whaling weather watch in a given 10° square exceeded a total of 40 hr.

Records of Bryde's whales are very sparse in this region, and confined to square C where for a time they were exploited by a small coastal whaling station on Great Barrier Island (Gaskin, 1972). An animal of this population which stranded near Auckland was figured in the same publication. The Japanese catches from 1967 to 1969 appear to confirm that no Bryde's whales occur among the large numbers of 'sei' whales in the open Tasman Sea south of latitude 40°S.

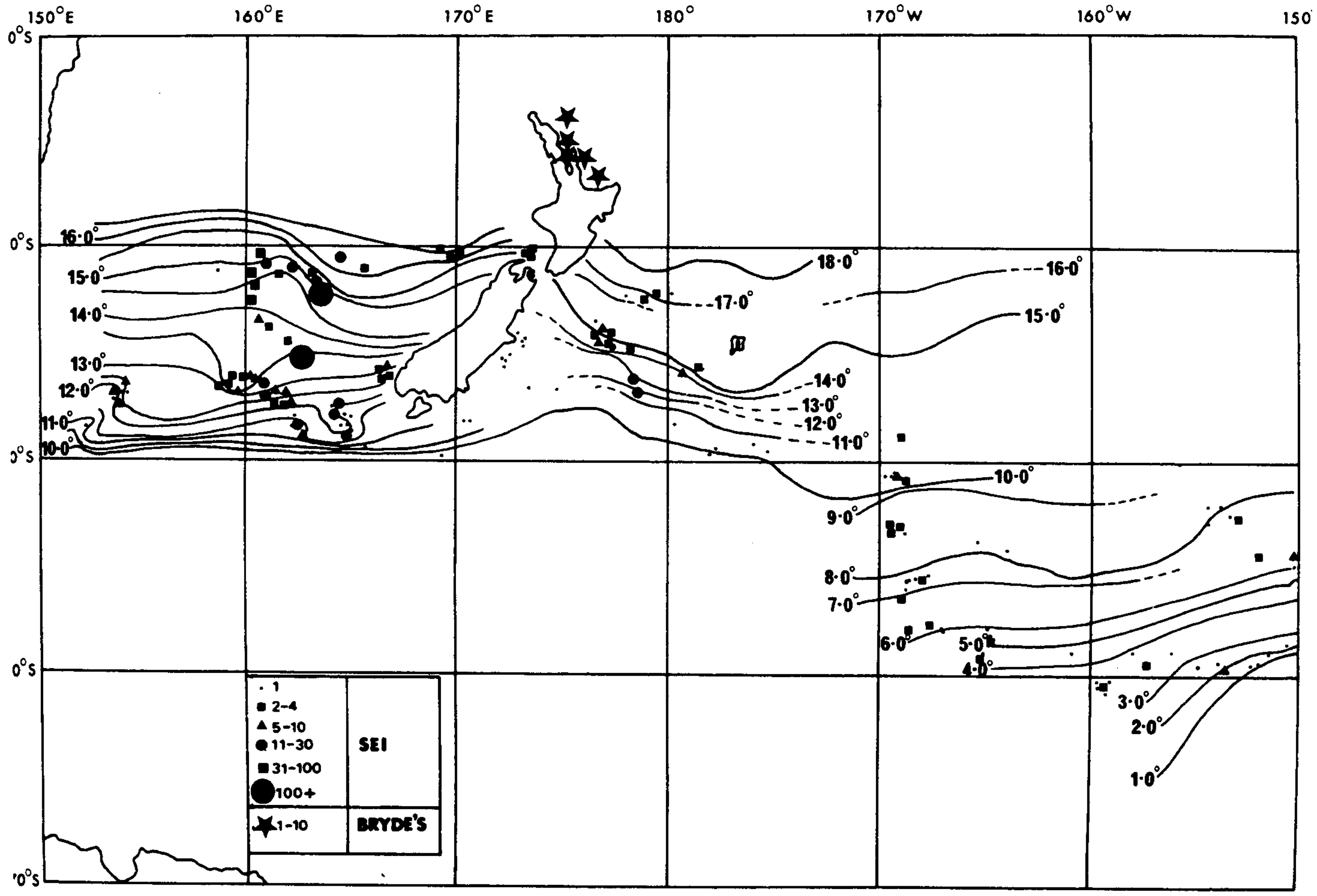

Fig. 1. Distribution of sei and Bryde's whales in waters adjacent to New Zealand. Relative numbers sighted at each contact are indicated by symbols (see inset key). Solid and dotted lines represent surface isotherms, and all temperatures are in degrees centigrade. With the exception of the Bryde's whales, all sightings were made from *Chiyoda Maru No. 5* in the period December 1966 to March 1967.

DISCUSSION

Such limited information as is available on Bryde's whales in New Zealand waters has already been discussed elsewhere (Gaskin, 1968, 1972). The population appears to be small, with a low rate of replacement, and cannot be considered as economically significant. Whether or not it is continuous with Bryde's whale populations which might occur around the Kermadecs and other islands of the western South Pacific is completely conjectural. Observations on the seasonal occurence of the New Zealand population suggests that it is largely confined to the area between North Cape and East Cape on the eastern side of the North Island, and migratory only in the sense that groups of these whales appear to follow local movements of pelagic fish schools.

Observations from *Chiyoda Maru No. 5* result in a distribution pattern of sei whales which conforms closely to the distribution of catches published by Omura (1973), and by Nasu and Masaki (1970). During the summer months large concentrations of sei whales occur in square H (40–50°S, 160–170°E), and relatively large concentrations are also found in square G, and as far west as longitude 130°E. Further east still catches are much lower until longitude 110°E, suggesting sub-populations centred on migration routes approximating to the east and west coasts of Australia. Within the same general region, but between latitudes 60°S and 70°S, very high catches have been taken in proximity to the Balleny Islands and the adjacent sea mounts. To the east of New Zealand very high catches have been recorded in the vicinity of squares Q, W, and X, and highest of all between latitudes 60°–70°S, 150°–140°W outside the main region surveyed by *Chiyoda Maru No. 5.* The generalized and specific areas of the Subtropical Convergence and the Antarctic Convergence in the western South Pacific have been figured by Gaskin (1973) and by Nasu and Masaki (1970). The author agrees with Nasu and Masaki that sei whales appear to favour zones to the north of the Antarctic Convergence. In the case of the Tasman Sea population the sei appear to concentrate along the northern face of the Subtropical Convergence, which is the southern edge of part of the East Australian current. In both regions feeding conditions are presumably exceptionally favourable.

The diet of sei whales in Antarctic waters has been considered in detail by Kawamura (1970), who also usefully summarised earlier literature, and information on sei whales feeding in particular on the amphipod *Parathemisto gaudichaudii* was published by Nemoto and Yoo (1970). Kawamura reported that in the whaling grounds south of New Zealand and in the Tasman Sea the most important food species was *Calanus tonsus.* In this region both *Euphausia* species and *Parathemisto gaudichaudii* appeared to be of relatively minor importance as food items. *E. vallentini*, was found in larger quantities in middle latitudes of Antarctic Areas III and IV, and *P. gaudichaudii* in Areas III and IV. An earlier paper by Nasu (1963)

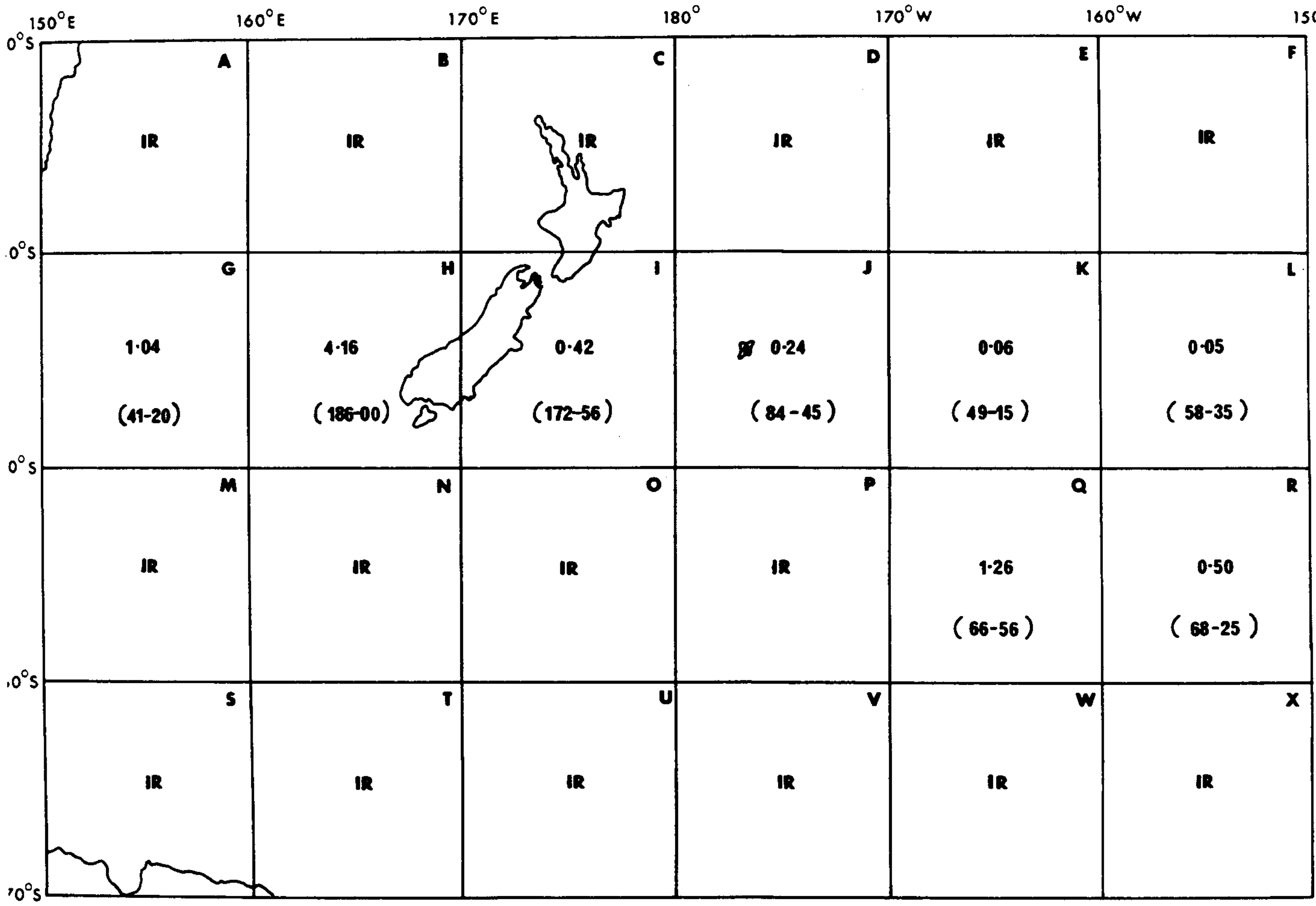

Fig. 2. Sightings of sei whales collected as described in Fig. 1, converted to numbers of whales sighted per hour of good whaling weather. The number of hours and minutes on watch are given in parentheses. Square letters conform to those used by the author in a previous paper (Gaskin 1973). IR indicates insufficient records, or area not surveyed by *Chiyoda Maru No. 5.*

suggested that baleen whale feeding grounds were characterised by relatively shallow thermoclines and local upwellings. The distribution of sightings shown in Fig. 1 of the present paper also indicates that in general sei congregate in regions to the north of convergence regions in the Southern Hemisphere, and particularly where reasonable steep horizontal temperature gradients occur in the form of surface isotherm 'salients'.

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SC/SP 74/Doc 16

Mortality Rates for Mature Southern Sei Whales

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Abstract

Estimates of total mortality rate which are close approximations of natural mortality rate for sei whales at Durban, South Africa, and South Georgia, have been calculated from a logarithmic regression of age frequency distributions in the catches. Age has been determined from growth layer counts in the ear plug. Results of mortality rate calculated in this way indicate that 0.047–0.068 is the most likely range, with an average of about 0.060.

INTRODUCTION

The work on population assessment for Antarctic sei whales by Doi, Ohsumi and Nemoto (1967) included estimates of mortality rates for sei whales. These estimates were for total mortality rate, Z, and were calculated from an analysis of the logarithmic regression of age frequency distributions. The age frequency distributions were based on a combination of length distribution in the catch and age-length keys to give the age composition of the catches. This combination was effected to reduce biasses introduced by shifts in location of the catching operation.

Values of Z were calculated for all Areas (I–VI) in the Antarctic for each sex for several seasons between 1957 and 1965. Because fishing rate and therefore fishing mortality, F, was small prior to the 1961–62 season, values of Z up to and including 1963–64 were taken as being close approximations of the natural mortality rate, M. The most likely estimates of M were taken to be between 0.059 and 0.079 with a mean of 0.065. Females were found to have an apparently higher value of M, but because of sampling biasses for this sex, 0.065 was taken to be the best estimate of natural mortality for both sexes.

The Institute of Oceanographic Sciences has age data from catches of sei whales between 1960 and 1965. Data are available for Durban, seasons 1962, 1963, 1964 and 1965. Prior to 1965, catching of sei whales at Durban was a very small operation. Season 1965 yielded the largest catch, although still relatively small, after which the sei whale population dramatically declined and this fishery collapsed. Similar age data for sei whales at South Georgia are available for seasons 1960–61, 1963–64 and 1964–65. The earliest season's catch was very small. These data have been used to produce further estimates of natural mortality rate.

METHODS

The age compositions of the catch samples at Durban are shown in Figures 1 and 2, and at South Georgia in Figures 3, 4, 5 and 6. The age compositions shown have been assessed directly from ear plug age readings, and also indirectly from the length frequency distributions of the total catch in conjunction with the relevant age-length keys for the particular location in order to check any possible bias in ear plug sampling. The readable ear plug sample generally averaged about 82% of the catch at South Georgia between 1963 and 1965, although in the 1960–61 season ear plug collections averaged 40%. The ear plug collections at Durban averaged about 38% for all seasons except 1965 when about 73% of the catch was sampled.

The total mortality rate, Z, has been calculated for both derivations of the age compositions between the ranges of ages indicated in the Figures, by a least squares regression analysis of the logarithm of whale numbers, n, on age, t. In Table 1 the resulting estimates of total mortality rate (with their confidence limits) are given for the ear plug based sample, with estimates for the length frequency based sample in parentheses. Confidence limits were calculated from the function

$$\frac{S_{nt}\,\text{`t'}}{\sqrt{(\Sigma t^2 - \frac{\Sigma(t)^2}{N})}}$$

where n = number of whales, t = age in years, N = number of age classes, 't' = 'Students' t – distribution, and S_{nt} = standard deviation of Z.

RESULTS AND DISCUSSIONS

The mortality rates in Table 1 do not differ greatly when the confidence limits are applied because there is considerable overlap. The values for both sexes are very similar, although it is unfortunate that the female samples at Durban are too small and biassed to give any useful result, and have therefore been omitted.

The value of Z at Durban must be very close to the natural mortality rate M because of the small scale of fishing, and is probably in the range 0.047–0.066.

The values of Z at South Georgia are rather higher, ranging between 0.064 and 0.115. The most reliable estimates (when the variance is relatively small) are probably 0.073–0.094 for males, and 0.064–0.101 for females. The widest likely range for Z on this basis, using confidence limits, is then 0.054 to 0.124 for females, and 0.068 to 0.114 for males. It is difficult to assess how much pelagic whaling operations in Antarctic Area II during 1960–61 and 1962–63 could have affected the population at South Georgia, but even allowing for this factor, the estimates of Z are probably fairly near to M. The lower limits of these ranges, 0.054 and 0.068, would possibly be closest to M and are also of the same order as at Durban.

The estimates of total mortality rate for adult whales given here are probably quite close to the natural mortality rate, and probably range between 0.047 and 0.068, giving an average of about 0.060. These results are in quite close agreement with estimates of natural mortality rate given by Doi *et al.* (1967), 0.059 to 0.079, mean 0.065, and are based on data independent of, and in mostly different locations to, the Japanese whaling operations.

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Table 1

Estimates of total mortality rate, Z, for sei whales taken in operations 1960–65.

Locality	Season(s)	Sex	Age range (years)	Z	Variance	95% Confidence limits
Durban, South Africa	1965	♂	8–24	0.065	0.207	±0.048
	1962, 1963 1964 and 1965	♂	8–23 (12–24)	0.066 (0.047)	0.308 (0.001)	±0.064 (±0.006)
South Georgia (Antarctic Area II)	1963–64	♂	20–36 (20–30)	0.099 (0.094)	0.263 (0.009)	±0.054 (±0.020)
	1964–65	♂	20–36 (19–30)	0.115 (0.073)	0.249 (0.001)	±0.053 (±0.005)
	1960–61, 1963–64 and 1964–65	♂	20–36	0.111	0.121	±0.037
	1963–64	♀	18–34 (21–30)	0.106 (0.101)	0.230 (0.008)	±0.051 (±0.023)
	1964–65	♀	18–34 (21–30)	0.068 (0.064)	0.297 (0.002)	±0.057 (±0.010)
	1960–61, 1963–64 and 1964–65	♀	18–34	0.085	0.134	±0.039

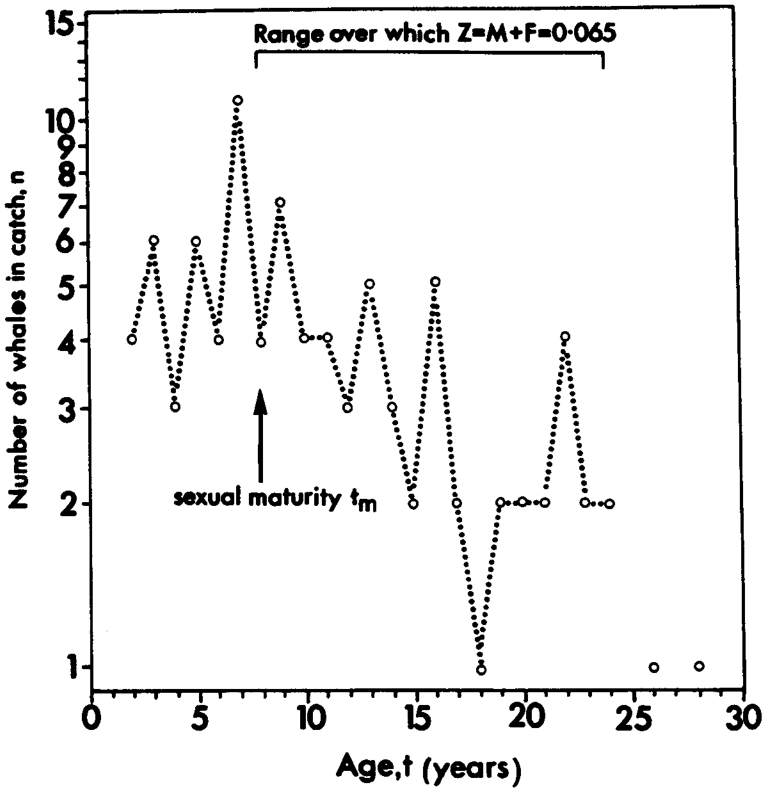

Fig. 1. Age composition of 98% of the readable male sei whale ear plug sample at Durban 1965.

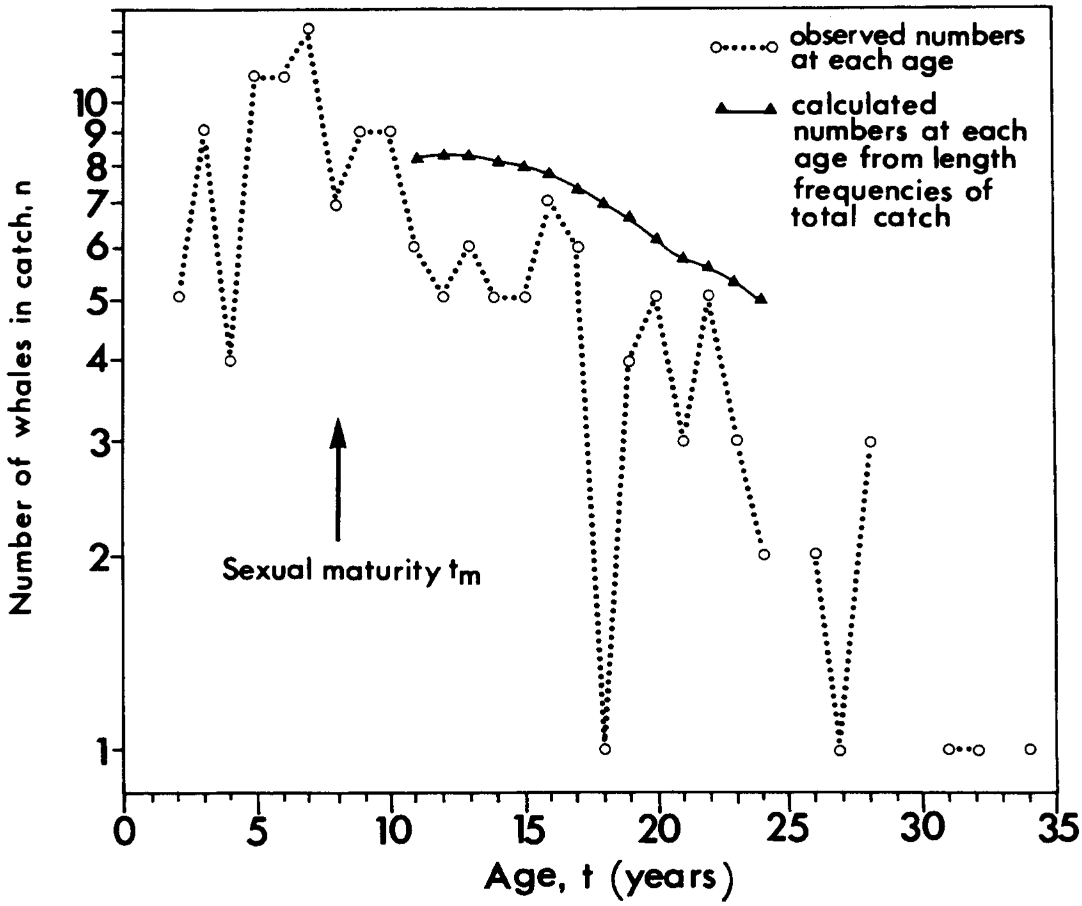

Fig. 2. Age composition of 99% of the readable male sei whale ear plug sample for Durban seasons 1962, 1963, 1964 and 1965.

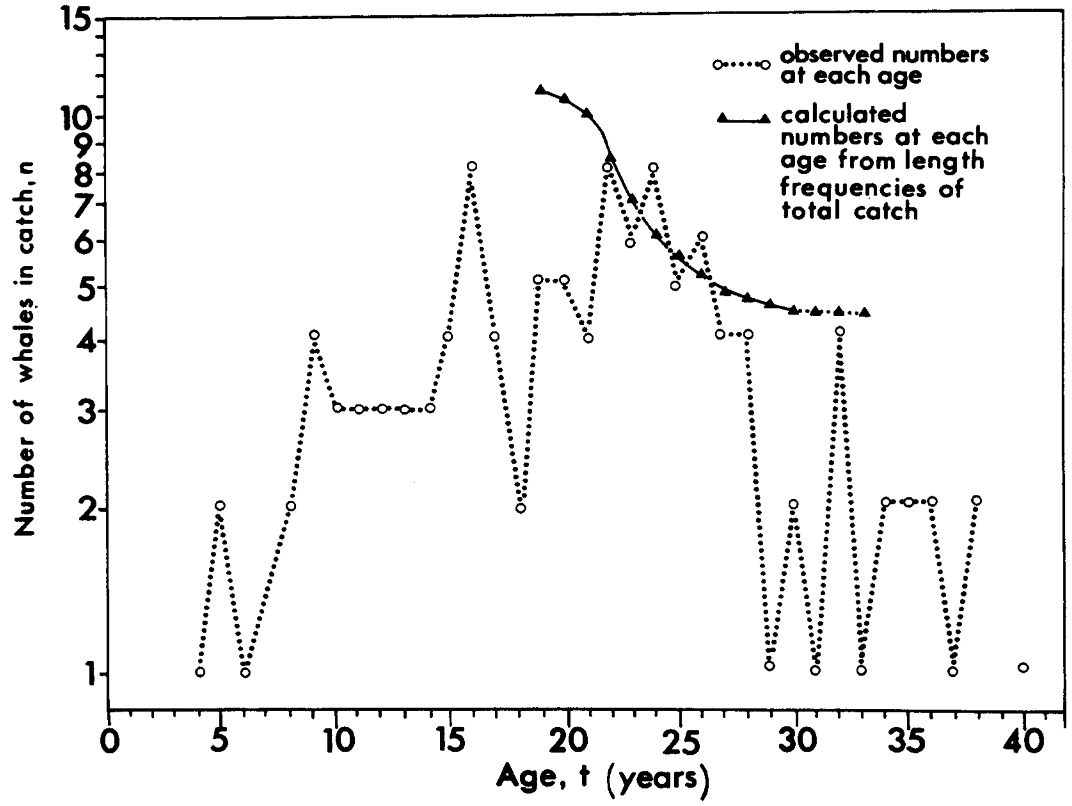

Fig. 3. Age composition of 97% of the readable male sei whale ear plug sample at South Georgia 1963–64.

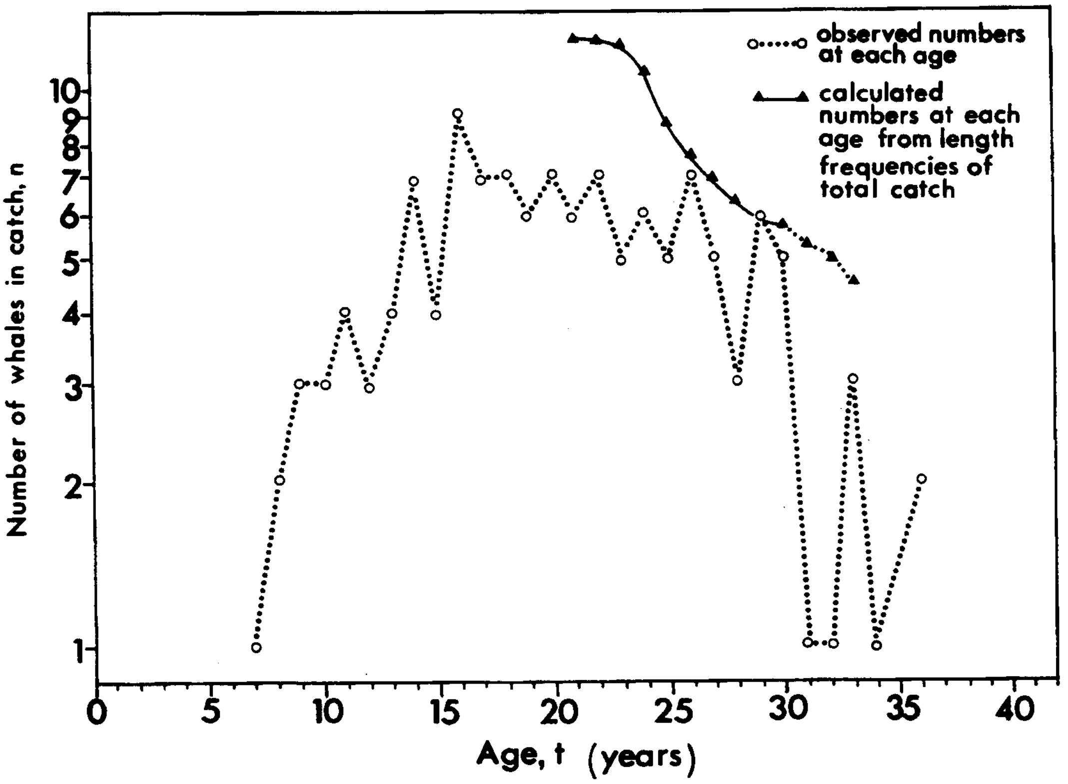

Fig. 4. Age composition of 98% of the readable female sei whale ear plug sample at South Georgia 1963–64.

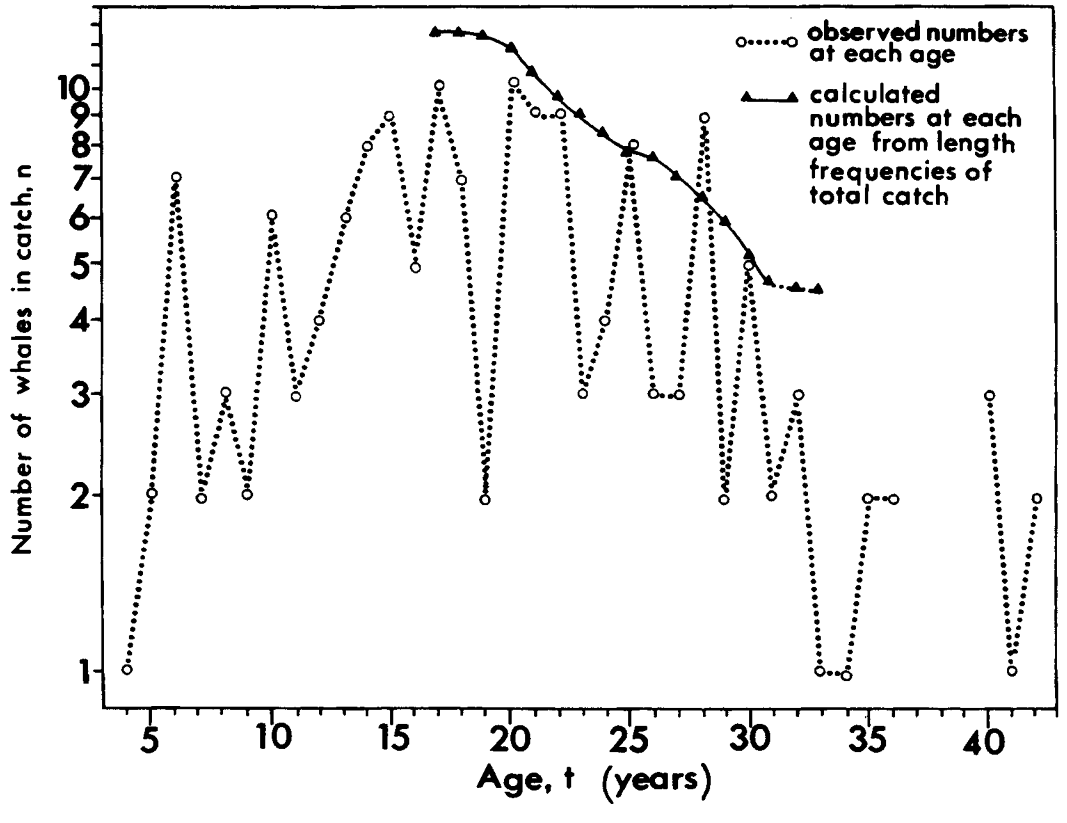

Fig. 5. Age composition of 96% of the readable male sei whale ear plug sample at South Georgia 1964–65.

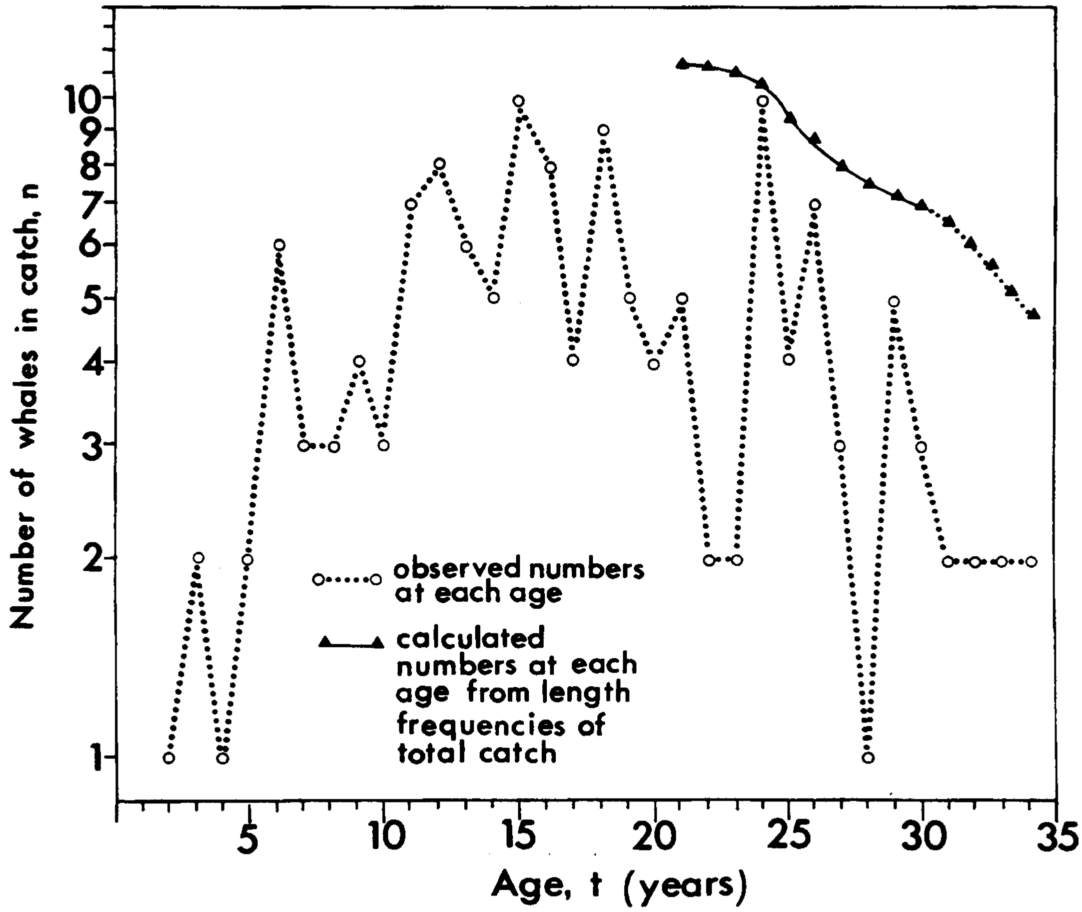

Fig. 6. Age composition of the readable ear plug sample from female sei whales at South Georgia 1964–65.

SC/SP 74/Doc 17

Some Estimates of Growth in the Sei Whale, *Balaenoptera borealis*

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Abstract

Growth rates of the sei whale in the foetal and post-natal phases are examined, and compared with some mathematical predictions for these stages. Overall growth in the foetus is geared to co-ordinate with the feeding and migratory habits of the adult, and confirms the predictions of Huggett and Widdas (1951) that $W^{1/3} = a(t - t_0)$.

Bertalanffy (1938) growth equations of the form $L_t = L_\infty(1 - e^{-k(t+t_0)})$ are found to apply well to sei whales in the post-natal growth phase, although the growth rate between birth and the end of the first year is exceedingly high and greater than that anticipated from Bertalanffy-type mathematical models. However, growth rates in sei whales are compared with the related fin whale.

FOETAL GROWTH

There are many records of lengths of sei whale foetuses together with the date on which the mother was caught. Matthews (1938) gives data for 151 foetuses recorded in the British Museum (Natural History), and for a further 55 foetuses examined during the *Discovery* Expedition between 1926 and 1931. Gambell (1968) refers to these and other foetal data, chiefly in the Reports of the Bureau of International Whaling Statistics (Oslo), and has constructed composite curves of growth. Gambell also gives separately the data for 346 foetuses collected by biologists at Durban, Saldanha Bay and Antarctic Area II (0°–60°W), and the curve of monthly mean lengths for these foetuses is shown in Fig. 1. Laws (1959) has discussed the pattern of balaenopterid foetal growth which is slow during the initial four to five months, and then much accelerated during the remainder of approximately 11 months' gestation period. Laws noted the correlation of the two growth phases with the seasonal feeding status, the fast phase commencing during the summer feeding period and enabling the foetus to grow to full term within a year and so fit the adult migratory habits.

Published records of sei whale foetal weights are not numerous, although there are 134 weighings (19 from Durban, 115 from Antarctic Area II) in the records of the Institute of Oceanographic Sciences (IOS), which enable a weight/length relationship to be studied. These data have been analysed by the method of least squares to evolve the formula $W = 0.000014L^{2.9198}$, where W is body weight in Kg, and L is body length in cm. By substituting the relevant weight for length, a probable curve of growth in weight with time has been constructed in Fig. 2, using Fig. 1 for reference. The most rapid phase of growth occurs after about the fourth to fifth month of gestation. The energy cost of this growth spurt is very high relative to the initial growth phase so that it is not surprising to find that this stage of foetal development coincides with the intense summer feeding period. The length at birth is about 4.5 m (Matthews, 1938; Gambell, 1968) and the weight would probably be about 780 kg. In terms of energy of growth in flesh weight the full-term foetus would represent some 1.17×10^6Kcal (calorific value of flesh meat $\simeq$ 1,500Kcal/Kg according to Petrides and Swank, 1965; Brody, 1968), about 95% of this amount accumulated during the rapid growth phase. This estimate does not include the metabolic energy cost of the foetus, which is probably comparatively small.

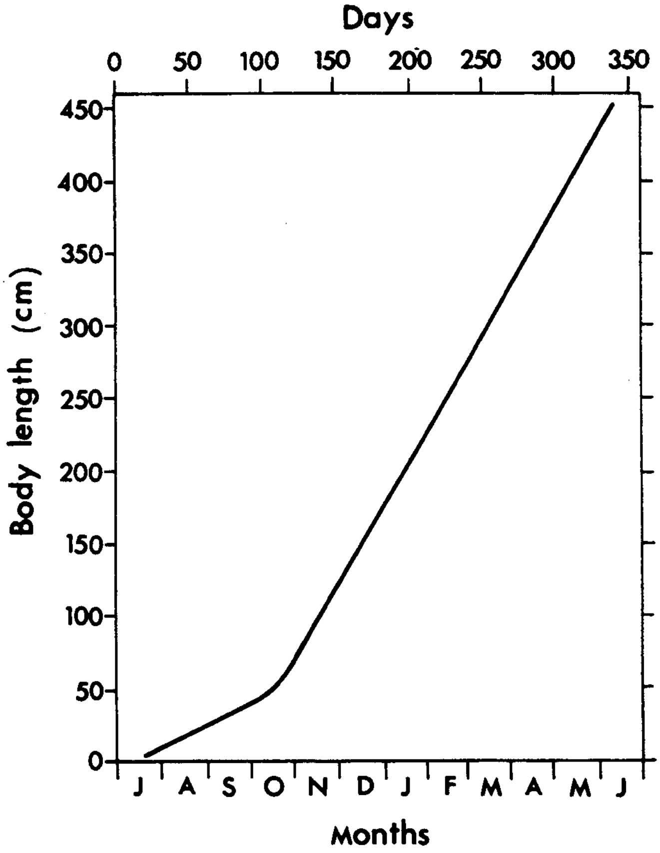

Fig. 1. Observed mean foetal body length with time, based on catch data of Gambell (1968).

In Fig. 3, the cubed root of the foetal body weight is plotted against time in days since conception, assuming that the observed gestation period, t_g, is just over 11 months, or 342 days (see Fig. 1). The relationship of $W^{1/3}$ with t is found to be linear from about the fourth month. The point where this line cuts the gestation time axis is 74 days, and may be considered to be comparable with t_0 in the formula $W^{1/3} = a(t - t_0)$ proposed by Huggett and Widdas (1951). The value of the growth velocity constant (a) is found to be 0.3436, when W is in g (0.03436 in Kg), t_g = 342 days t_0 = 74 days. The value of t_0 is close to the predicted value according to the Huggett and Widdas theory i.e. that for gestation periods between 100 and 400 days, t_0 can be expected to have a value of about 0.2 X t_g in this case 0.2 X 342 $\simeq$ 68 days. It is worth noting that Gambell (1968) believed that the gestation period for sei whales might be as long as 12 months, when t_g = 365 days, and the predicted t_0 should be about 73 days. He based his estimates on an application of the Huggett and Widdas' theory to growth in body length rather than weight. However, the value of t_g cannot be assessed directly, and in any event the constant (a) would not be affected by a prolongation of t_g. Predicted t_0 increases by only about 4 days when t_g is extended, although the data no longer fit the predictions if about 12 rather than 11 months' gestation period is assumed, observed t_0 being approximately 94 days.

In Table 1, the monthly percentages of ovulating females in the mature female catch at Durban show that (disregarding the small May sample) ovulations are most frequent in June and July. According to the foetal growth curve in Fig. 1, conception on average occurs in early July, which is therefore not likely to be far wrong; neither is the average time of birth in early June, if the length at birth is 4.5 m. This is in good agreement with Laws' (1959) original estimate of a gestation period of about 11 months for sei whales, although 11 to 11½ months might be a better estimate. Huggett and Widdas predicted that the constant (a), might be about 0.5, for large Cetacea such as blue and fin whales, which is very high compared with values of 0.05 to 0.15 for the majority of other mammals which they examined. The observed value of (a) for sei foetuses suggests that their growth rate is indeed very rapid in comparison with other mammals.

POST-NATAL GROWTH

Growth in length

Length at birth has been established at about 4.5 m (14.7 ft), when the body weight will be approximately 780 kg. Intensive nursing follows for about six months (Gambell 1968), before the calf is weaned during the summer feeding period in the Antarctic. The pattern of growth is little known at this time because apart from brief observations at sea or on the rare accidental capture of a calf, very young whales are protected by the International Whaling Commission (IWC) and so are not available for examination. The youngest animals caught are generally into their second or even third year, and most are much older in the Antarctic. Overall, the sizes of whales at each age in the youngest age classes taken in the catch can be biassed; the current minimum lengths set by the IWC being 35 ft (10.7 m) at land stations such as Durban and South Georgia, and 40 ft (12.2 m) for pelagic whaling.

The IOS has several data on length at age for sei whales taken by land-based operations both at South Georgia and Durban between 1960 and 1965, and also during Antarctic pelagic operations. However, for an analysis of growth, the data collected at Durban have been selected as the most suitable for the following reasons. Firstly, the size limit is the lower permissible length, 35 ft, and secondly, very young immature whales seldom venture far south beyond 45°S because of differences in migratory habits between mature and immature whales. An analysis of the catch in Antarctic Area II below 50° shows that at least 90% of the whales are mature and there are no whales of 40 ft (12.2 m) in length. The data available for the length at age of Durban-caught males and females respectively are presented in Figs. 4 and 5. These curves only represent mean length at

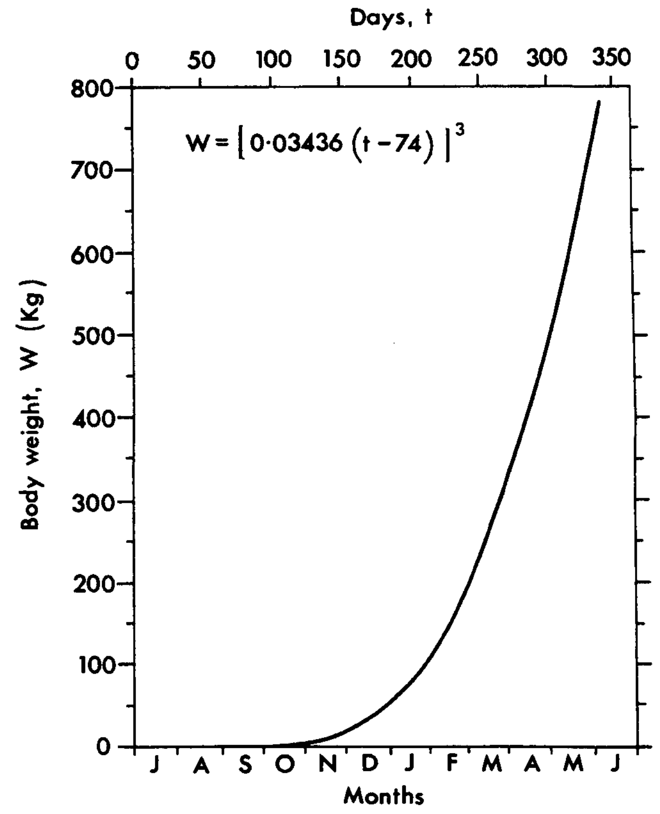

Fig. 2. Predicted growth in weight of the foetus throughout 11 months' gestation commencing about July.

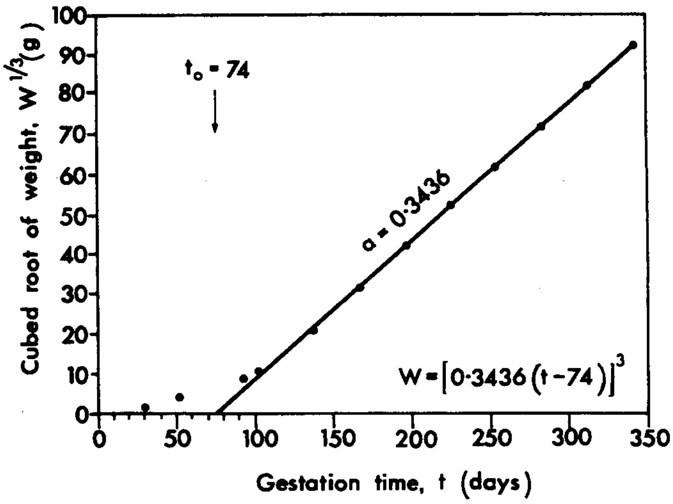

Fig. 3. Derivation of the Huggett and Widdas (1951) growth parameters for sei whale foetal growth.

Table 1

Ovulating females at Durban as a percentage of all mature females except lactating whales.

Month	Sample size	% ovulating
May	6	(50)
June	11	54.6
July	23	30.4
August	29	10.3
September	21	9.5

age for particular catches at Durban, and it is worth noting the following points.

Firstly, the maximum observed body lengths at Durban are lower than the sizes seen at South Georgia. The values for L_∞ in Figs. 4 and 5, from the Bertalanffy (1938) growth formula $L_t = L_\infty(1 - e^{-k(t+t_0)})$, are 48.5 ft for males and 50 ft for females. At South Georgia males over 25 years attain an average length of 50.7 ft, and females 54.2 ft, so that L_∞ may be somewhat greater for populations in higher latitudes than Durban. Secondly, the exponential Bertalanffy growth formulae shown in Figs. 4 and 5 describe the observed mean length at age curves well except for the first year. This is not surprising because the actual size of one year old animals is not well documented from the catch, as they are probably at about the length of the present legal minimum size limit for the Durban fishery.

Although the minimum size limit is 35 ft, noticeably few animals of sizes between 35 and 37 ft are ever taken; less than 5% in the past Durban fishery where the catch comprised about 40% juveniles. This indicates two possibilities, either these small whales are in a different area or they are still calves accompanying their mothers. I consider the first possibility unlikely, at least for the entire season, because the whaling grounds off Durban appear to be nursery areas. Therefore the second possibility is more likely. In Table 2, the proportional growth with time of the southern sei whale is compared with the related fin whale. Measurements for the fin whale are based on data used by Lockyer (1972) and for the sei whale on data used by Matthews (1938), Gambell (1968) and Lockyer (1974). The relative growth in each species is so similar that a prediction of length for sei whales at the end of the first year seems valid, particularly as the current ages at sexual maturity, 6 to 7 years in fin and 8 years in sei, are not too different (Lockyer, 1972; 1974); this length probably falls in the range 34 to 35 ft (10.4 to 10.7 m). This strongly supports the argument just given that the legal length limit of 35 ft represents the average size of some calves and first year whales. Now this raises two important matters. One is that the mean lengths at age for juveniles in Figs. 4 and 5 are unlikely to be greatly biassed, and the other is that the minimum size limit of the catch needs careful examination.

In conclusion, growth in length is very rapid up to puberty. The mean lengths observed at sexual maturity for Durban whales are 44.5 ft (13.6 m) in males and 45.7 ft (14.0 m) in females (Lockyer, 1974), representing about 90% of the maximum mean length. These estimates of length at sexual maturity are similar to those given for Antarctic Area III, 43.4 ft (13.3 m) for males and 45.6 ft (13.9 m) for females, by Nasu and Masaki (1970). Therefore the estimated growth rate between birth and sexual maturity is unlikely to be inaccurate, although maximum sizes reached will be greater in Antarctic Area III, so that at sexual maturity only about 86% of the maximum body size will have been attained.

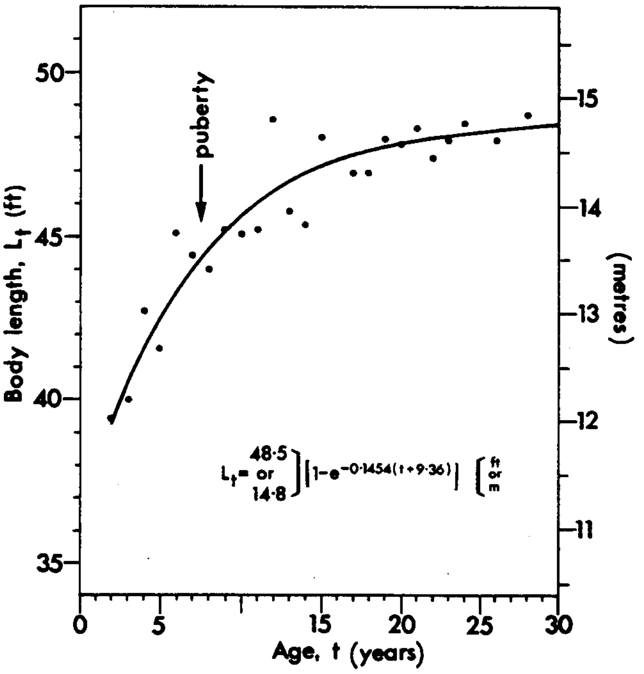

Fig. 4. Mean length at age for a sample of 152 male sei whales taken at Durban, 1960–65. (After Lockyer, 1974).

Growth in weight

Omura (1950) has published weights of 16 sei whales taken off Japan and gives a formula describing the relationship between body weight in tonnes W, and length L. Lockyer (1976) has corrected this formula to allow for about 6% fluid loss during flensing and gives a formula $W = 0.001436L^{2.43}$ for L in ft, or $W = 0.025763L^{2.43}$ for L in m. Bearing in mind that different populations, even of the same species, may vary slightly in shape (Machin, 1974; Machin and Kitchenham, 1971), one can only derive an approximate curve of growth in weight by substituting W for L in Figs 4 and 5. The resulting curves for males and females are shown in Figs 6 and 7 respectively.

Table 2

Comparison of relative size in sei whales and fin whales from Antarctic Area II.

Body lengths, and ratios relating body size to length at birth

				1 year		Sexual maturity		Physical maturity		Legal minimum size	
Species	Units	Birth	Weaning	♂	♀	♂	♀	♂	♀	Land station	Pelagic
Fin	Feet	21	37.5	49	50.4	63.5	65.5	69	73	55	57
	Metres	6.4	11.5	15.0	15.4	19.4	20.0	21.1	22.3	16.8	17.4
	Ratio	1	1.8	2.3	2.4	3.0	3.1	3.3	3.5	2.6	2.7
Sei	Feet	14.7	26	[34]*	[35]*	44.5	45.7	48.5	50	35	40
	Metres	4.5	8.0	[10.4]*	[10.7]*	13.6	14.0	14.8	15.3	10.7	12.2
	Ratio	1	1.8	[2.3]	[2.4]	3.0	3.1	3.3	3.4	2.4	2.7

*Estimates, assuming same ratios as for fin whales.

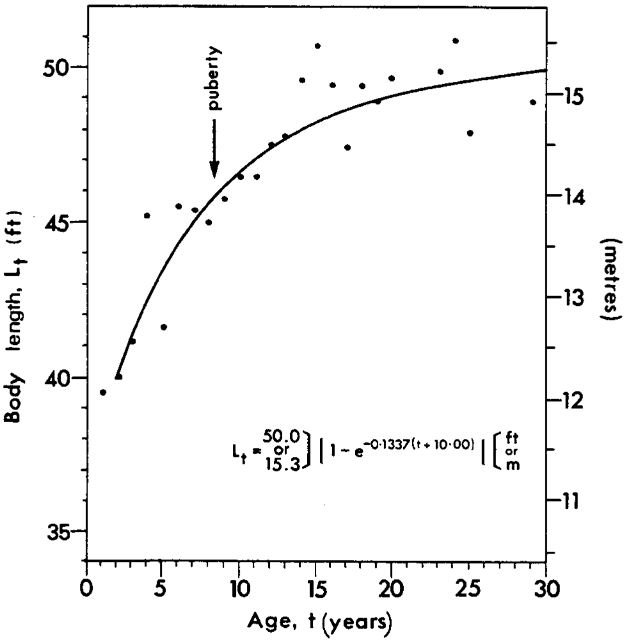

Fig. 5. Mean length at age for a sample of 92 female sei whales taken at Durban, 1960–65. (After Lockyer, 1974).

The cubic modification by Laws and Parker (1968) of the exponential Bertalanffy growth formula

$$W_t = W_\infty (1 - e^{-k(t+t_0)})^3,$$

has been applied to the data here. The formula for weight in tonnes is $W_t = 18.5\ (1 - e^{-0.1454(t+9.36)})^3$ for males, and $W_t = .20\ (1 - e^{-0.1337(t+10.00)})^3$ for females. These formulae predict body weights in fairly close agreement with the values plotted in Figs. 6 and 7, but do underestimate by as much as one tonne in the youngest age classes. This is not unexpected because the estimates of W_∞ are almost certainly too low: an increase in weight may continue after increase in length has ceased. Estimates of W_∞ nearer 20.5 and 22 tonnes for males and females respectively might be more likely for whales at Durban. In the Antarctic, however, some 58 ft sei whales are likely to reach up to 28 tonnes, and none of these estimates of W_∞ allows for seasonal increases in body weight during feeding, which may amount to some 50% of initial weight in other rorquals (Lockyer, 1972a).

The main observation is that growth is most rapid before puberty at which time the body weight attained is about 75 to 78% of the maximum.

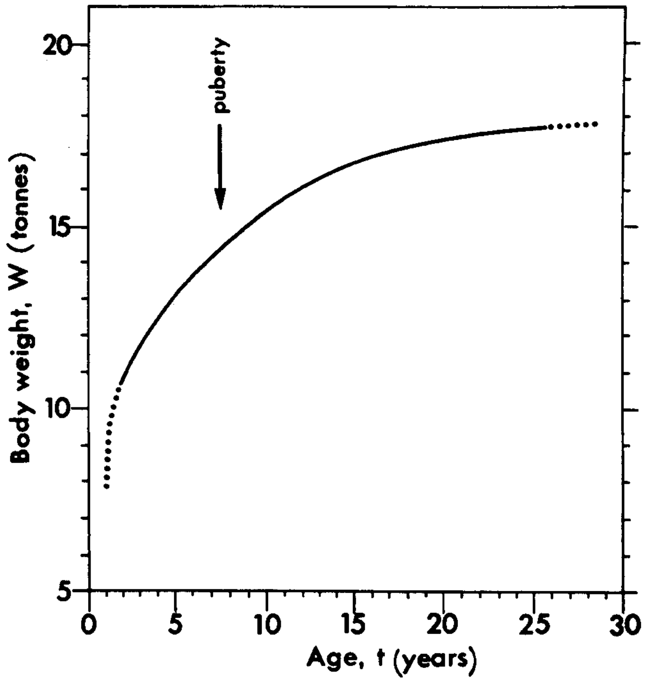

Fig. 6. Expected growth in weight with age for male sei whales, applying the conversion formula $W = 0.001436L^{2.43}$ to Fig. 4.

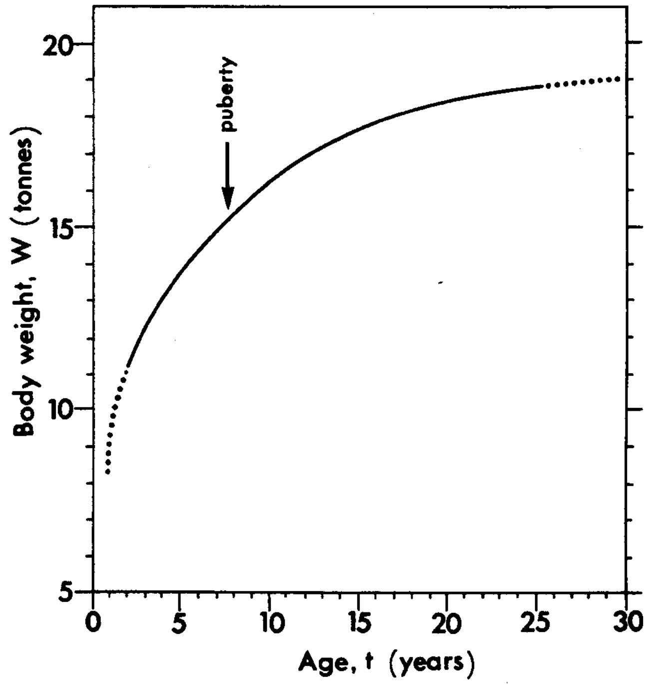

Fig. 7. Expected growth in weight with age for female sei whales, applying the conversion formula $W = 0.001436L^{2.43}$ to Fig. 5.

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Some Possible Factors Affecting Age Distribution of the Catch of Sei Whales in the Antarctic

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Abstract

Catches of sei whales in Antarctic Area II in latitudes greater than 50°S have been analysed by age, date of capture, sex and reproductive status, in order to detect whether any or all these factors can affect the dispersion of whales. Results suggest that there is considerable seasonal aggregation by sex, age and reproductive status, chiefly because of the order of migration of different groups. Young adults are generally preceded by older ones in abundance, and pregnant females appear to reach peak abundance before the rest of the population.

Additional information on group sizes of sei whales show that usually one to four whales are found swimming together.

The conclusion is that because of seasonal age and sex associations and actual groupings of whales, a short whaling season and very small catches could yield biassed age distributions.

INTRODUCTION

Special groupings by sex, age and maturity are well documented for many species of animals particularly mammals, for example, elephants (Sikes, 1971), red deer (Delap, 1970) and buffalo (McHugh, 1972), which usually exhibit herding and migratory habits. Sperm whales are a good example of a cetacean species which is found to form highly complex school structures, with separate bachelor schools, nursery schools, harems and also lone bulls (Ohsumi, 1971; Gambell, 1968, 1972). Blue, fin and sei whales are known to migrate in waves of mature animals, then immature ones (Mackintosh and Wheeler, 1929; Matthews, 1938); and pregnant females of the humpback species are known to migrate in waves out of phase with the rest of the population (Dawbin, 1965). It would not be surprising then, if it were found that the seasonal dispersion of whales of different age groups on the feeding grounds was not random, particularly for the sei whale, which is well known for the latitudinal segregation of different sizes and ages, only the larger and older animals migrating far south below 50°S (Gambell, 1968a; Lockyer, 1974).

Bannister and Gambell (1965) gave evidence that off Durban (at a latitude of about 30°S) the majority of sei whales were immature and thus young and of small size. From the evidence of sei whale catches, Doi, Ohsumi and Nemoto (1967) concluded that the average size of animals taken increased with latitude, the largest whales being predominant in latitudes 45° to 60°S. Small whales only appeared in any numbers in latitudes less than 45°S. All this information indicates that there is considerable segregation by size and maturity, and therefore age, with latitude. The observations which are made here, in latitudes greater than 50°S, therefore apply only to a section of the total sei whale population, chiefly the older animals. Doi *et al.* (1967) showed that the bulk of the total sei whale population is in fact present in latitudes less than 50°S, indicating that the main feeding grounds are also below 50°S, so that the sei whale is more sub-Antarctic in its choice of habitat. The results of investigations in this paper are therefore intended only to describe the pattern of distribution of sei whales which enter the Antarctic proper.

MATERIAL

The Institute of Oceanographic Sciences (IOS) has age data (from ear plug examination) for sei whales taken off South Georgia in latitudes 52° to 57°S (in the western half of Antarctic Area II) for the 1960–61, 1963–64 and 1964–65 seasons (sample sizes of 119, 259 and 306 respectively). Data are also available from pelagic operations of the *Southern Harvester* in latitudes 58° to 62°S of the western half of Antarctic Area II in the 1962–63 season (sample size 83). These age samples represent about 80% of the whales taken in the catches. The date and approximate position of capture of the whales are also known. For the 1963–64 and 1964–65 seasons there is some information available about the number of whales observed swimming together before capture, from the gunners' reports. However, although the sex and usually the age of the whales taken are known, the same are rarely known for the rest of the group, so that the usefulness of such data is limited.

AIMS, METHODS AND RESULTS

The overall aim of this paper is to discover whether there may be some degree of seasonal association by age, sex and reproductive status, which might then affect the age distribution of the catch. The following items have been examined.

The frequency of capture of animals of similar age in a particular area on a particular day

The age of captured whales was determined from ear plug layer counts (assuming one layer per year). Because of difficulties in reaching exact agreement on layer counts by different persons, ages of less than 30 years were generally allowed a latitude of ±1 year, and ages of 30 or more years a latitude of ±2 years. This is unlikely to have introduced serious biasses. The main purpose was to distinguish whales which could be of similar age from those of obviously different age, and observe whether age is a factor influencing dispersion.

IOS has no reliable records on whether the whales of similar or disimilar ages were actually swimming together before capture, so that, even when an age association is observed, it is possible only to say that the whales were within a ship's day's steaming distance of each other. The 'position of capture' is not always exact or meaningful. For example, many whale catchers have only logged the ship's noon position. Other catchers may have recorded individual catch positions but these are not directly useful because after one has been caught the remaining whales in a group flee or split up into smaller groups, when they may escape or be taken in other positions than the original one.

An observed day's steaming distance can be up to 120 nautical miles although whales taken on any one day are almost invariably less than 60 miles apart, and more usually less than 10 miles. So, a 'particular area' is taken to mean in practical terms, a radius of less than 60 miles.

The age distribution of the daily catches throughout the months mid-November to mid-April is shown in Fig. 1 for all data and both sexes combined, showing the separate distributions of the frequencies when ratings of none, one, two, three, four or five whales of similar age were taken on the same day. The observed age distributions show similar trends for the ratings one or more, with the same age groups generally dominant in each.

The probability of capturing a whale of any age at any time should be proportional to its actual frequency in the total age distribution of the catch of a randomly dispersed population. However, even if whales are randomly dispersed with respect to age, one would expect the same age groups to be dominant in all ratings. For such a system, the expected frequency of each rating in any one age group might follow the predictions of a Poisson type distribution. In other words, the probability of capturing none, one or more whales of a particular age at any one time can be calculated for a randomly dispersed population.

In Fig. 1, the expected age distribution in each rating is illustrated together with the observed one, calculated from the formula

$$\frac{e^{-np}(np)^x}{x!} \times N.$$

The maximum observed rating is five, so that expected frequencies have been calculated within the range $x = 0$ to 5. The mean number of whales of any one age taken in a catch throughout the season is taken to be equivalent to np, and is simply the total number of whales of age t taken throughout the season divided by N; here, $N = 139$, and represents the number of age-sampled daily catching operations.

The observed and expected frequencies for whales of age t in each rating have been compared by a variance ratio. The value of np is taken to be an approximation of σ^2, the true variance, and is compared with the observed variance S^2, to give a value of χ^2 (Chi-squared)

$$\left(\chi^2 = \frac{S^2 N}{\sigma^2}\right),$$

This is then tested for significance by the formula

$$'x' = \sqrt{2\chi^2} - \sqrt{2n-1},$$

where n = degrees of freedom, >30. Here the chances of observing the calculated value of 'x' outside the range given at a particular probability level can be estimated from the table of deviation in the normal distribution in terms of the standard deviation. For all age groups the probability is less than 1%, so that the results are significantly different from a random distribution. There must be considerable association, or aggregation of whales by age.

The overall age distribution of the catches, when taken throughout the entire feeding season, is unlikely to be biassed because all age groups frequenting the area are represented. However, when the length of the whaling season is considerably less than the whales' feeding season, certain biasses might be introduced into the apparent age distribution of the sampled population. Possibly this could partly explain the variations in year class strengths in successive seasons if any of the seasons are short.

The succession of sexual classes of whales by age on the feeding grounds

The catches at South Georgia and in Antarctic Area II are comprised of more than 90% mature whales, so that no reasonable analysis can be made of actual monthly frequencies of immature whales. All that can be said is that none appear in the catches before mid-January, but that their peak abundance occurs in late February.

By the end of the whaling season the sex ratio of the mature catch shows that there are more males than females. This could be in part because lactating females, which are protected by fishery regulation, are absent from the catch. However, lactation is usually over by the end of summer, so that an excess of males over females in the catch may actually reflect latitudinal sexual segregation at this time of year.

In comparing the numbers of whales present on the feeding grounds, certain adjustments have to be made. Firstly, because of small sample sizes, November and December have been combined, and also March and April. Both January and February have been divided into first and second halves. Secondly, the number of catching days varies according to the month, and this is in turn reflected in the number of age-sampled days of operation in each month. Generally, peak catches and whale densities occur around January. The relative frequency of whales observed in each month category has therefore been expressed in the form n/N_m, where N_m, is the number of age-sampled operations in each category, and n is the number of whales taken. The relative frequencies of whales during the whaling season, by sex and age group are shown in Fig. 2, with all age groups, except those over 30 years, combined in Fig. 3.

The graphs for whales 30 to 34 years old are based on very sparse data, and whales 35 to 72 years old in the samples number only 44 or 6% of the total catch and are omitted. Because of deficiencies in data for 30 to 34 year old whales in some months, the adjusted frequencies are not considered to be reliable. Examining the remaining graphs in Figs. 2 and 3, the following trends emerge.

(1) Mature males: The peak abundance of mature males of 19 years or less occurs in the latter half of January, whereas those 20 years old or more are most abundant in the first half of January. There is also a suggestion that there may be a dip in abundance in the early part of February (Fig. 3), which is also noticeable for very young whales and whales between 25 and 29 years. Perhaps this is the result of sampling errors or whales leaving the feeding grounds.

(2) Non-pregnant females: Resting and ovulating females appear to remain at a fairly steady density throughout the season, although they too, in all age groups, exhibit the same dip in early February already noted in the male population. Judging from the separate age groups in Fig. 2, the peak abundance of non-pregnant whales 19 years or less occurs later than for whales 20 years or more in age.

(3) Pregnant females: The overall peak abundance of pregnant females precedes both males and all other classes of females by about half a month (Fig. 3). There is also a dip in abundance in late January, a half-month prior to that

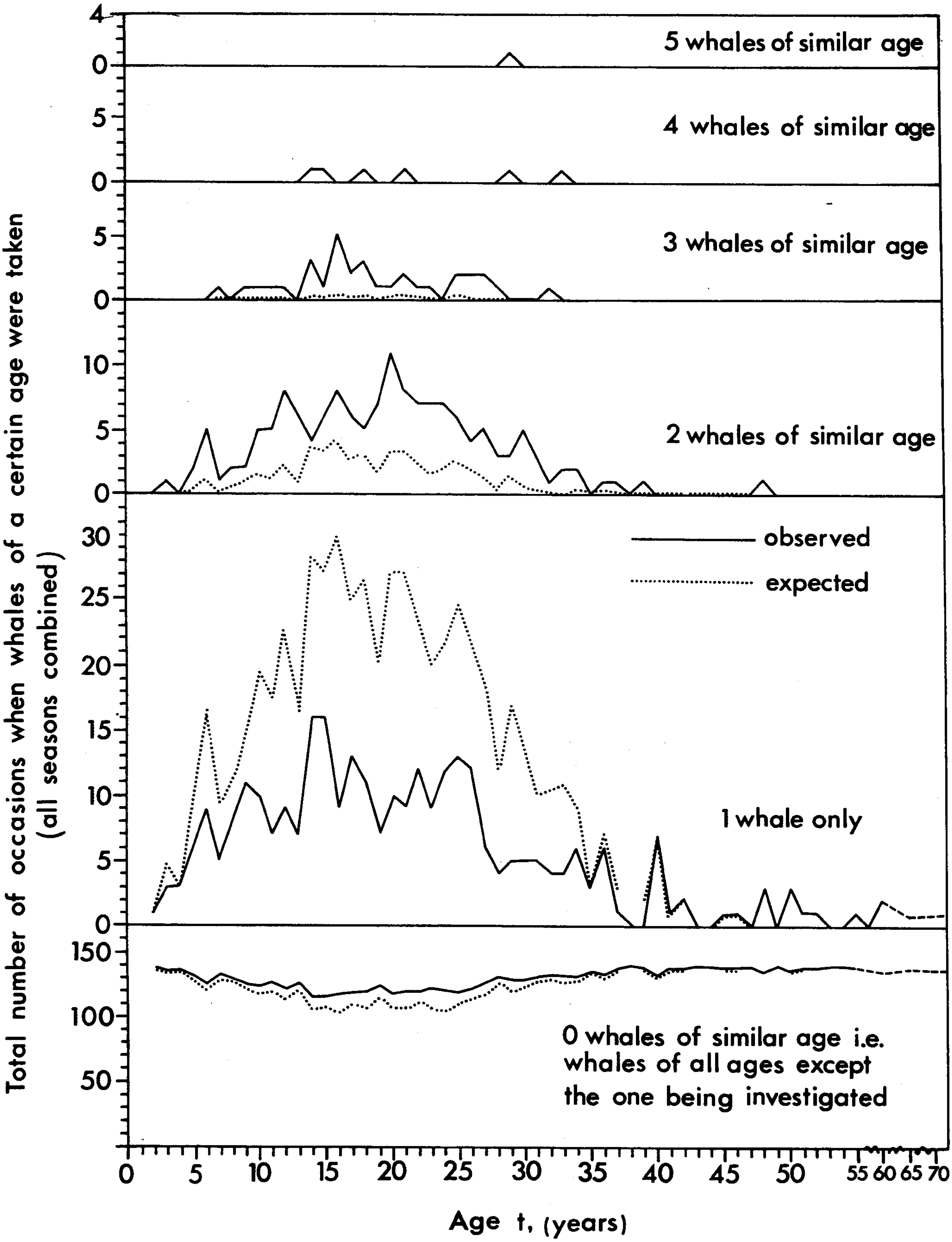

Fig. 1. Age distribution of sei whales in the catches for all seasons combined. The distributions are shown for the frequency of occasions when none, one, two, three, four or five whales of a particular age were all taken in a successful day's catching operation. Observed and expected frequencies are shown.

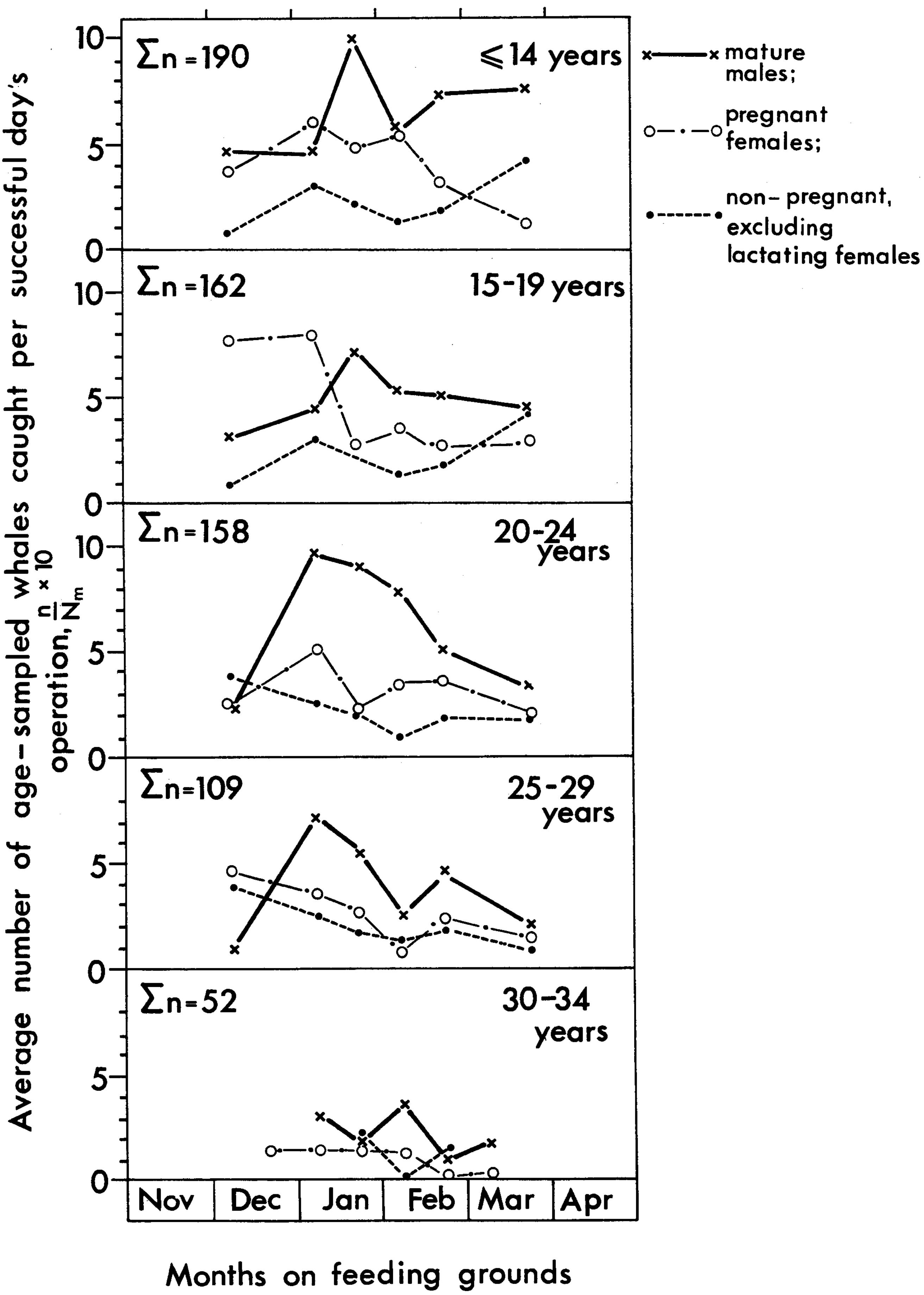

Fig. 2. Relative daily abundance of the sexes throughout the feeding season, by age group.

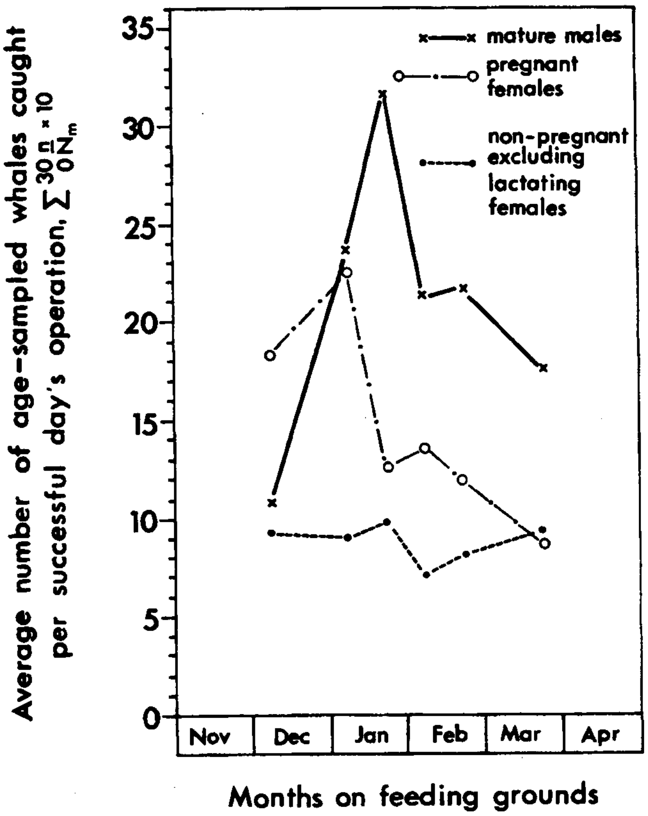

Fig. 3. Relative daily abundance of the sexes throughout the feeding season, for all age groups except whales 30 years or more in age.

for the rest of the population. Trends in abundance of pregnant whales 25 years or more in age, however, more closely resemble those of the rest of the female population (Fig. 2). The peak abundance of pregnant females does not always seem to precede that of males in this age group.

One may conclude therefore that firstly, pregnant females are more likely to be found in the earliest part of the season, because of their apparent earlier high concentrations on the feeding grounds; and, secondly, for whales 30 years or less in age, high densities of older mature males and older mature non-pregnant females generally precede the younger whales in these categories. The second point may partly explain why (as shown in the preceding section) a certain degree of aggregation of whales by age is present in the catches, though the whales are not necessarily swimming together. The overall situation is probably one where old adults precede young adults. Juveniles may arrive later, if at all, and pregnant females tend to precede males and other females.

The possible association by both age and sex for whales caught in a particular area on a particular day

This might be regarded as another way of reaching and testing the conclusions made in the preceding section. Particular examination has been made of the occasions when two whales of similar age were taken and the configuration of the reproductive classes in these catches has been analysed. Originally age groups were kept separate, but because this greatly reduced the individual sample sizes and possibly introduced biasses, ultimately all age groups (except those of 30 years or more) were combined. The frequencies of the sex ratios of the catches of whales of similar age, adjusted to allow for variations in the numbers of sample days each month, are shown in Fig. 4. The expected frequencies, calculated on the assumption that random configurations of sexes would be taken during the whaling season, are also shown in Fig. 4. The observed and expected frequencies are not always precisely similar. However, the expected frequency patterns for males only (Fig. 4d), non-pregnant females only (Fig. 4c) and pregnant females only (Fig. 4b) generally agree with the overall patterns for the corresponding groups in Fig. 3.

(1) Mature males: The comparison of observed and expected frequencies when only males were caught (Fig. 4d) indicates an observed excess in late January and a deficiency in late February. Where a male has been taken with a pregnant female of the same age (Fig. 4e) there is a corresponding deficiency observed in late January and an excess in late February. The situation in late January may arise because a massive influx of males onto the whaling grounds is occurring, see Fig. 3, so causing an apparent high degree of aggregation of males together rather than with pregnant females. However, the situation in late February tends to indicate that the reverse situation is happening, with males aggregating with pregnant females to a greater extent than anticipated, perhaps even preferentially. The non-pregnant females (Fig. 4f) do not seem to aggregate particularly with the males except perhaps in early January. The purely male catches in Fig. 4d show no observed deviation from the expected frequency in early January, so that this excess of catches of males and non-pregnant females together may not be significant.

(2) Non-pregnant females: In December, the non-pregnant females appear to aggregate together preferentially (Fig. 4c) when compared with observed deficiencies in associations with both pregnant females (Fig. 4a) and males (Fig. 4f). In early January, the close agreement of observed and expected frequencies in Fig. 4c suggests that the observed excess of male – non-pregnant female catches (Fig. 4f) may not be because of preferential association, but more probably due to the influx of pregnant whales at this time (Fig. 3). During February, a comparison of observed and expected frequencies indicates that resting females are associating together rather than with other whales (Figs. 4c, a and f).

(3) Pregnant females: The observed frequencies of pregnant whales only (Fig. 4b) show that between December and February, association is far higher than anticipated, perhaps because of early arrival. Pregnant whales are not found associating particularly with non-pregnant whales at this time, nor in fact at any time (Fig. 4a). The opposite occurs in male – pregnant female configurations (Fig. 4e), where the observed excess in February has already been discussed. Pregnant female and pregnant – non-pregnant female associations are relatively infrequent at this time (Fig. 4b and a), and also suggest that the male – pregnant female associations may be significant.

Sex configurations in the total seasons' age samples

In Table 1, all the actual numbers of daily samples throughout the season are combined. All the observed sex configurations in the catches of one to five whales of the same age are shown in Table 1 alongside the expected ones for comparison. The expected distribution figures were assumed to follow a binomial expansion, $N(p + q)^n$, where

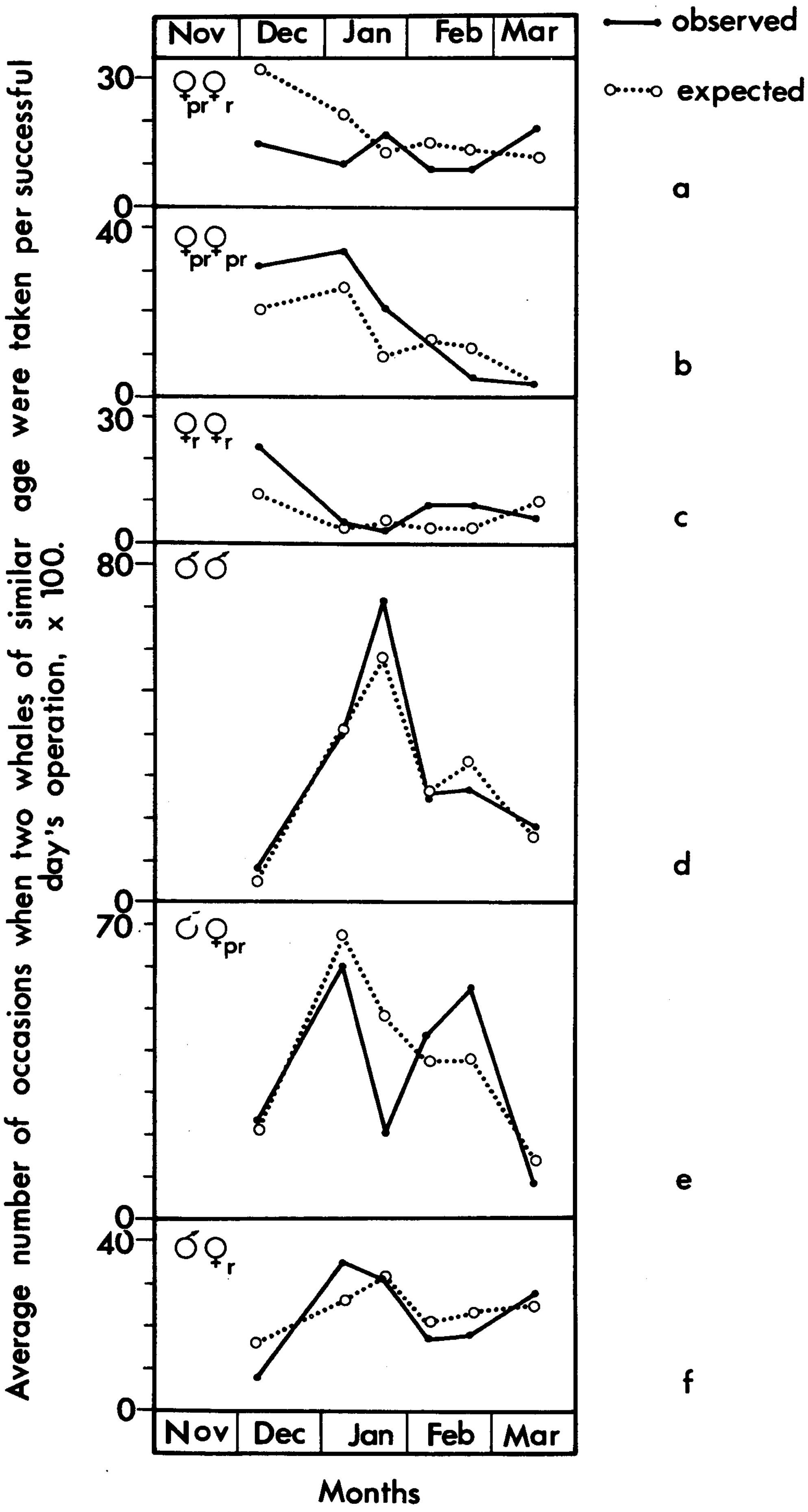

Fig. 4. Relative daily frequencies of different sex configurations in the catches throughout the feeding season, when two whales of the same age were taken (pr = pregnant, r = non-pregnant). Observed and expected frequencies are shown.

p and q are the proportions of males and females in the total sample, 732, and are therefore 0.514 and 0.486 respectively (Table 1). The term, n, refers to the number of whales, male and/or female, in a particular configuration between n = 1 and 5 in Table 1. The term N represents the overall number of configurations possible from the sample size available shown for each value of n in Table 1. It is clear that the overall result indicates random dispersion of the sexes, in spite of the fact that monthly categories give a different result.

The conclusions are therefore that whales of different reproductive status tend to migrate separately into latitudes greater than 50°S, but mingle with other whales whilst on these feeding grounds; perhaps preferentially in the case of males and pregnant females. The appearance over the whole season however, is that all sex configurations appear to be randomly represented.

These conclusions differ from the findings of Nemoto (1964), where the sex configurations were not random. For fin whales Nemoto observed that all male, and male/female configurations were unexpectedly more numerous than all female ones. This also appeared partly to be indicated for sei whales. However, these data were recorded for sei whales in the North Pacific on the main feeding grounds. The sex configurations Nemoto gave were also for actual schools taken, and therefore his results are not comparable to the findings here.

The actual group size observed swimming together prior to capture

Some information is available on the number of whales swimming together before capture. Unfortunately it is difficult to assess whether the group size recorded was always the original one, or whether it had already been diminished by catching. Any analysis of groupings is therefore likely to be misleading. However, referring to Fig. 5 where group size frequencies are plotted, it is probably safe to say that sei whales swim alone or in groups up to 10 in size. The most frequently observed numbers of whales swimming together were one to four.

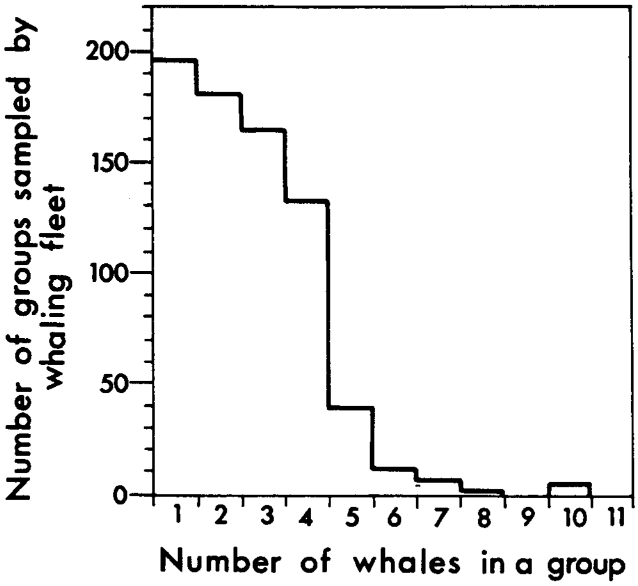

Fig. 5. Frequency distribution of the group sizes of sei whales sampled by the whaling fleet.

SUMMARY OF CONCLUSIONS AND COMMENTS

These results confirm those already published for sei whales in the Antarctic (Gambell, 1968a), i.e. that different reproductive classes migrate separately. Older adults tend to arrive before young adults, so that aggregation of whales by age and sex is not surprising. It might be worthwhile to examine further the total possible combinations by age, using more complex analyses, to see whether certain mixed

Table 1

Incidence of capture of one or more whales of similar age at any one time, by sex configuration, for all months (mid-November to April) and seasons combined.

Number of whales of similar ages taken in a day's operation, n		Actual total number of incidences for whales of similar age by observation and from random expectation					Total number of whales	Total/n = N
		♂	♀					
1	Observed	158	147	–	–	–	305	305
	Expected	156.77	148.23	–	–	–	–	–
		♂♂	♂♀	♀♀				
2	Observed	40	73	38	–	–	302	151
	Expected	39.86	75.50	35.64	–	–	–	–
		♂♂♂	♂♂♀	♂♀♀	♀♀♀			
3	Observed	3	13	12	4	–	96	32
	Expected	4.35	12.32	11.65	3.68	–	–	–
		♂♂♂♂	♂♂♂♀	♂♂♀♀	♂♀♀♀	♀♀♀♀		
4	Observed	2	0	2	2	0	24	6
	Expected	0.42	1.58	2.24	1.42	0.34	–	–
			♂♂♂♂♀					
5	Observed	–	1	–	–	–	5	1
	Expected	–	0.17	–	–	–	–	–
	Total						732 = 376 ♂♂ 356 ♀♀	

age associations are more common than others. The present results based on similar age associations however, indicate that a short whaling season and very small catches could yield biassed age and sex frequency distributions.

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SC/SP 74/Doc 19

The Separation of the Stock Units of Sei Whales in the North Pacific[1]

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Abstract

Separation of the stock units of North Pacific sei whales is examined by means of whale marking, catch distribution, whale sighting and baleen plates.

Combining results from these four methods, stock units of North Pacific sei whales are separated into three divided by the border lines of 175°W and 155°W.

INTRODUCTION

Whale resources must be managed rationally by each stock unit. Stock identification is therefore the basic problem in population study. Separation of the stock units of the North Pacific sei whales has been tried by means of the following methods; body length composition (Kasahara, 1950), blood typing (Fujino, 1964), catch distribution (Nishiwaki, 1967) and whale marking (Ivashin and Rovnin, 1967).

However, these studies dealt with the insufficient data available prior to 1967 when pelagic whaling began to take sei whales seriously. In the present paper, separation of the stock units of the sei whale is examined using recent biological data which were provided from whale marking, whale sighting and baleen plates.

WHALE MARKING

The data used in the present paper were the results of whale marking which have been conducted by Japan from 1949 to 1973. The number of whales marked and recaptured and the movements of recaptured whales are shown by areas in Fig. 1. As examples of long distance movement of marked sei whales, one moved from Area H to Area F, and another moved from Area E to Area C. Most of the others moved to adjacent areas, or remained in the same area as marking (Omura and Ohsumi, 1964; Ohsumi and Masaki, 1975). From these results, it may be concluded that North Pacific sei whales on the feeding ground do not make long distance movements as seen for male sperm whales and humpback whales.

Among all directions of movement of the recaptured whales, the vector of north and south is common to all stock units. The vector of east and west movement or dispersal in marked North Pacific sei whales is classified into two cases in Fig. 2; one is when both marking and recapture occurred within the same whaling season, and the other is when marked whales were recaptured in seasons subsequent to marking.

The frequency of the vector of east and west movement of recaptured whales is shown for each degree of longitude (Fig. 2). The longitudinal positions where frequency of the vector is low (corresponding to the troughs in Fig. 2) are seen at 174°W and 155°W. In other words, marked sei whales distributed either west of 174°W, between 174°W and 155°W or east of 155°W showed considerable dispersal within each area, while cases of dispersal between different areas were very few.

Omura and Ohsumi (1964) and Ohsumi and Masaki (1975) have not mentioned the separation of the stock units of whales, and only referred to the feature of movement and mixing among areas.

On the other hand, Ivashin and Rovnin (1967) recognized three local stocks of sperm whales in the tropical zone of the North Pacific: Asian, Central (Hawaiian) and American. From this fact, they made the analogy for the baleen whales (blue, fin and sei whales) of three local stocks in the tropical zone which occupy western, central and eastern parts of the North Pacific. As regards the number of stock units of the sei whale in the North Pacific, their result coincides with the present result. However, their classification was more obscure than the present one.

CATCH DISTRIBUTION

The distribution of sei whales caught by Japan in the North Pacific during the years 1952 to 1972 is shown diagramatically in Fig. 3, and the cumulative number of whales caught by each one degree longitude is also shown in Fig. 4. Four regions can be distinguished from the concentration of catch in Fig. 3. If each trough shown in Fig. 4 corresponds to the border of these regions, the four regions can be expressed as follows: (1) west of 155°E, (2) between 155°E and 175°W, (3) between 175°W and 155°W, and (4) east of 155°W.

The reasons that sei whales were not caught in the waters between 150°E and 160°E are that the eastern limit of the operating ground of Japanese coastal whaling is at most 150°E, and that Japanese pelagic whaling has been regulated in waters east of 159°E by domestic law. For these reasons, it is not valid to divide the waters west of 175°W into two regions because of the lack of catch around 155°E.

If an independent stock unit was recognized as existing in waters where relatively many whales were caught (Fig. 3), the stock units of North Pacific sei whales may be separated into three, distributed as shown above.

WHALE SIGHTING

Catch results are influenced by economic factors and many regulatory measures imposed by domestic or international laws, so that a map of catch distribution will not always

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[1] This paper is a part of the dissertation 'Biological study on the North Pacific sei whale' which was recognized by University of Tokyo in 1974.

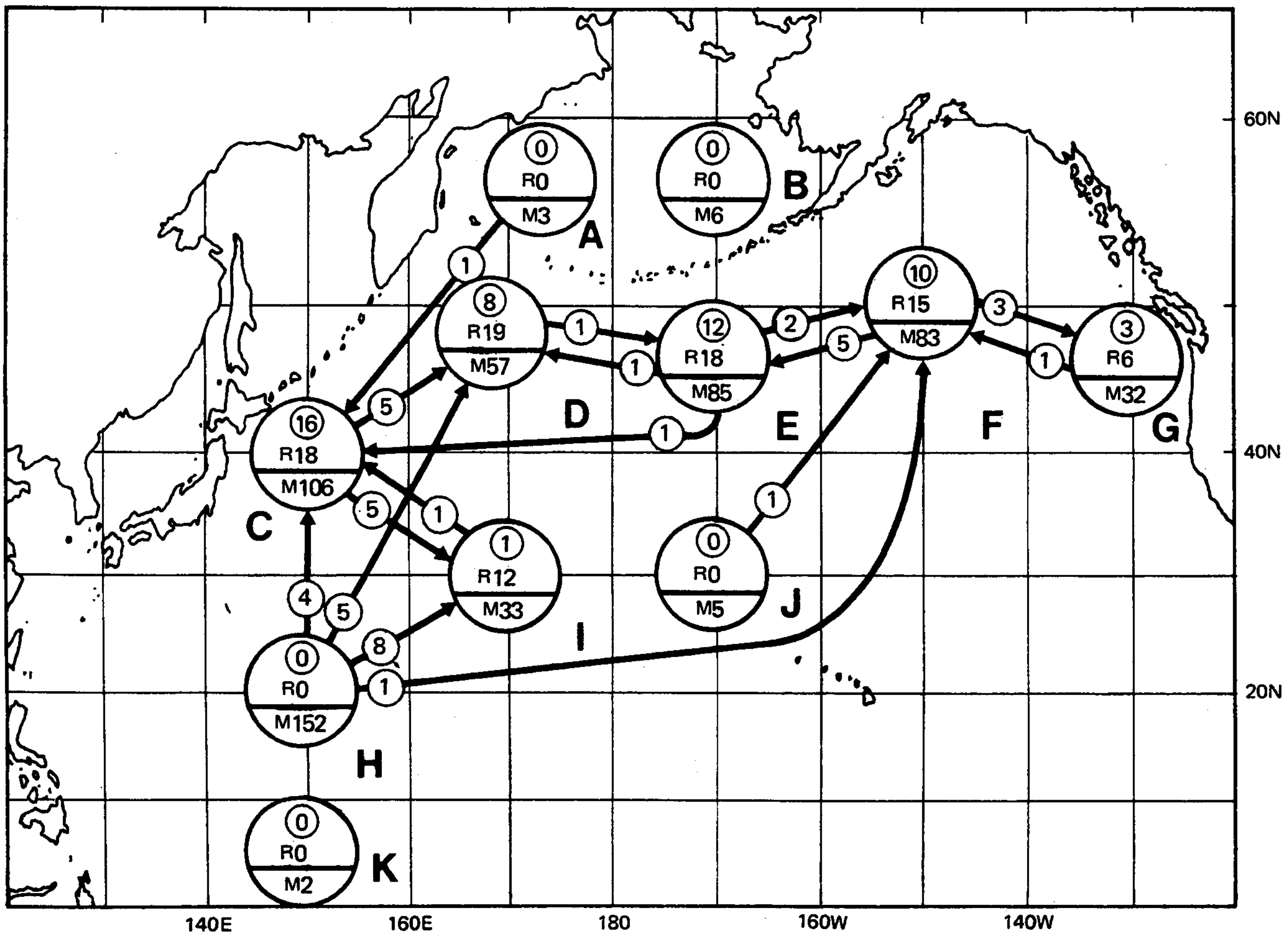

Fig. 1. Summarized result of sei whales marking by Japan in the North Pacific, and the movements of the recaptured whales during the years 1949 to 1973.

M: Number of marked whales, R: Total number of recaptured whales in each region, Number in small circle: Number of whales recaptured in the same area as marking, Number in small circle with arrow: Number of whales recaptured then had moved to different areas.

portray the real situation. The natural distribution of the sei whale will be shown by a map of the density index which is based on whale sighting rather than catch distribution.

The whale sighting data used in the present paper were obtained from the scouting boats belonging to Japanese whaling expeditions in the North Pacific during the years 1965 to 1972.

The number of whales sighted per 100 miles scouting distance was used as the density index, and the index of abundance was calculated by use of the density index and the dimension of the area concerned.

Density indices of sei whales sighted during the years 1965 to 1972 are shown diagramatically in Fig. 5. Four highly dense regions are recognized, names, (1) the waters east of 180° longitude and south of the Aleutian Islands, (2) the western side of the Bering Sea, (3) the waters between 180° and 150°W and south of the Aleutian Islands, and (4) the waters east of 150°W.

Fig. 6 shows the accumulated indices of abundance by 10 degrees of longitude. Judging from the dips in the distribution as in the case of the catch distribution, the areas of high density are divided into the following; (1) west of 180°, (2) between 150°W and 180°, and (3) east of 150°W.

The map of density distribution changes month by month. This may represent the migration of the sei whale in the North Pacific (Masaki, 1976).

The high density of sei whales in the western Bering Sea mainly in July and August may be the result of migration of the sei whales which are distributed in waters east of 180° longitude and south of the Aleutian Islands in May and June. If this is true, it is reasonable to take the view that the sei whales in both areas belong to the same stock unit.

THE SHAPE OF THE BALEEN PLATE

Using the biggest baleen plates collected from 232 sei whales caught in 1973, differences in the shape of the baleen plates in each area were examined. The length (L) and breadth (B) of each baleen plate were measured. As shown in Fig. 7, the length was measured along the outer edge of the baleen plate from the gum line to the tip of the plate. The breadth was measured in a straight line between the outer and inner edges of the gum line.

The relation between body length and the ratio of L/B is shown in Fig. 8: there is no significant relationship between these two characters. On the other hand, as differences between the mean values of L/B were recognized for both sexes by the t-test at the 5% significant level, variation in

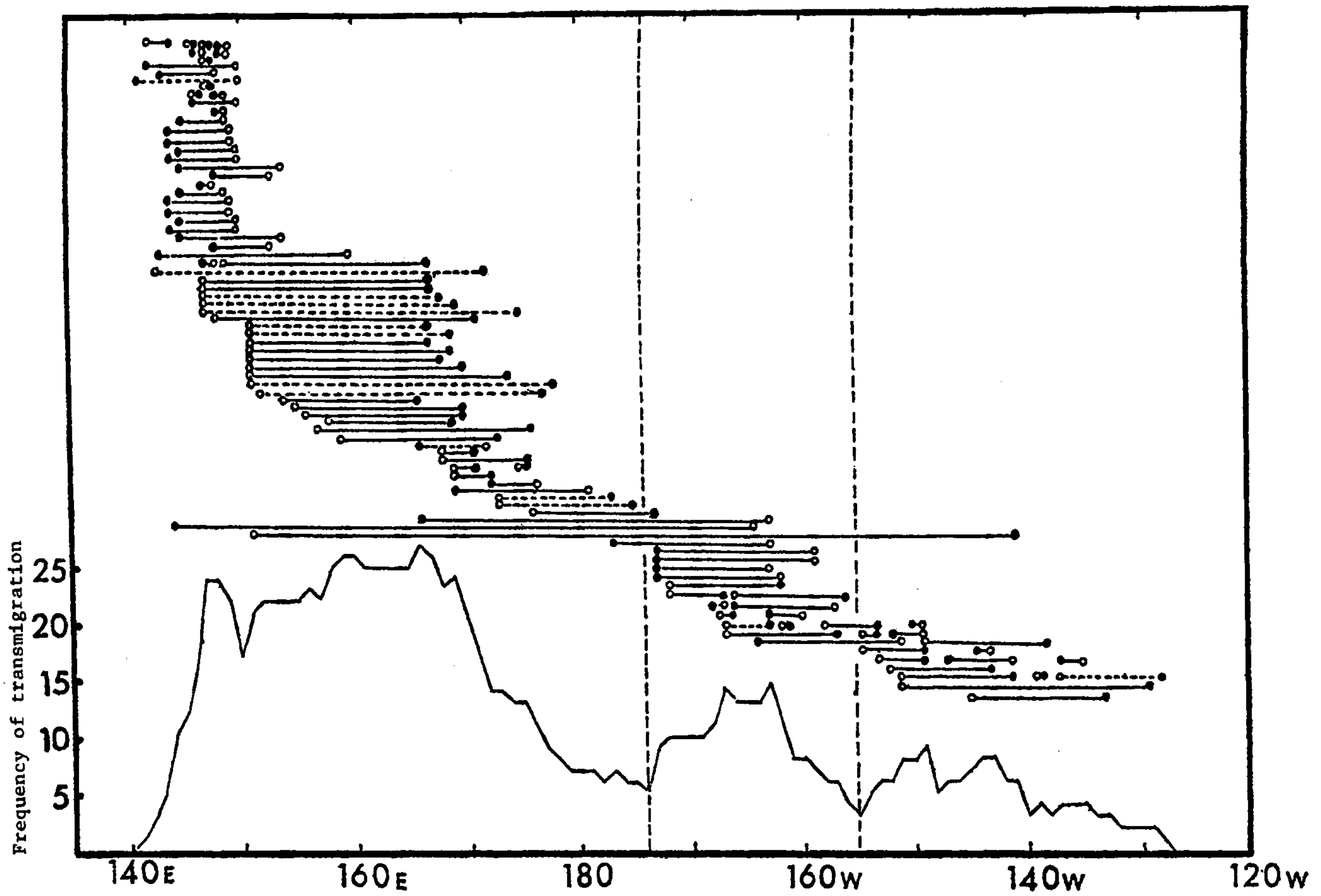

Fig. 2. Frequency distribution of movements by one degree longitude and the dispersal of Japanese marked whales in the North Pacific, 1949–73.

Open circle: Longitudinal position of mark release, Closed circle: Longitudinal position of mark recovery, Solid line: Marked and recaptured in the same whaling season, Broken line: Mark recovered in seasons subsequent to marking.

the average value of this character between the areas was examined by sexes. Examinations were made on four regions in the North Pacific; (A): between 160°E and 170°E, (B): between 170°E and 170°W, (C): between 170°W and 150°W, and (D): between 150°W and 130°W. Table 1 shows the mean value and standard error of L/B in these four regions.

Fig. 10 shows the results of the examination on the difference of the mean value of L/B between these regions. In females, there was no difference in the mean values of L/B between any two adjacent regions. A difference was recognized however between regions A and D and between B and D. In males, significant differences of the mean values of L/B were recognized between regions B and D and between B and C.

Judging from these results, it can be inferred that there are at least two stock units separated by 170°W as a border line.

The angle α is adopted as another index, indicating the degree of outward bend on the baleen plate. If the points A' and B' are fixed on the lines of OA and OB, respectively, under the condition that both lengths of OA' and OB' are 10 cm in Fig. 7, the value of angle α can be calculated by the following equation:

$$\sin \alpha/2 = A'B'/5$$

Table 1 shows the mean value and standard error of the angle in the four regions.

The relation between the angle α and body length is shown in Fig. 9: there is no significant relationship between these two characters. Fig. 10 shows the results of the examination on the difference of the mean value of α between several combinations of regions. In females, there are differences between the regions B and C and between the regions C and D. On the other hand, in males, there are also differences between the waters C and D, the waters A and D, and the waters B and D. From these results, it can be concluded that there are three stock units in these waters which are divided by 170°W and 150°W as border lines.

Combining the results for the mean values of L/B and α the North Pacific sei whale can reasonably be separated into three stock units distributed in the following regions; west of 170°W, between 170°W and 150°W and east of 150°W.

DISCUSSION AND CONCLUSION

As stated above, separation of the stock units of the North Pacific sei whales was tried by four methods, each of which contains both strengths and weaknesses. The weakness of whale marking is that it is practically difficult to get many recaptured whales in a short time. Moreover, the scarcity of marked whales on the breeding grounds makes the separation of stock units based on this method indistinct.

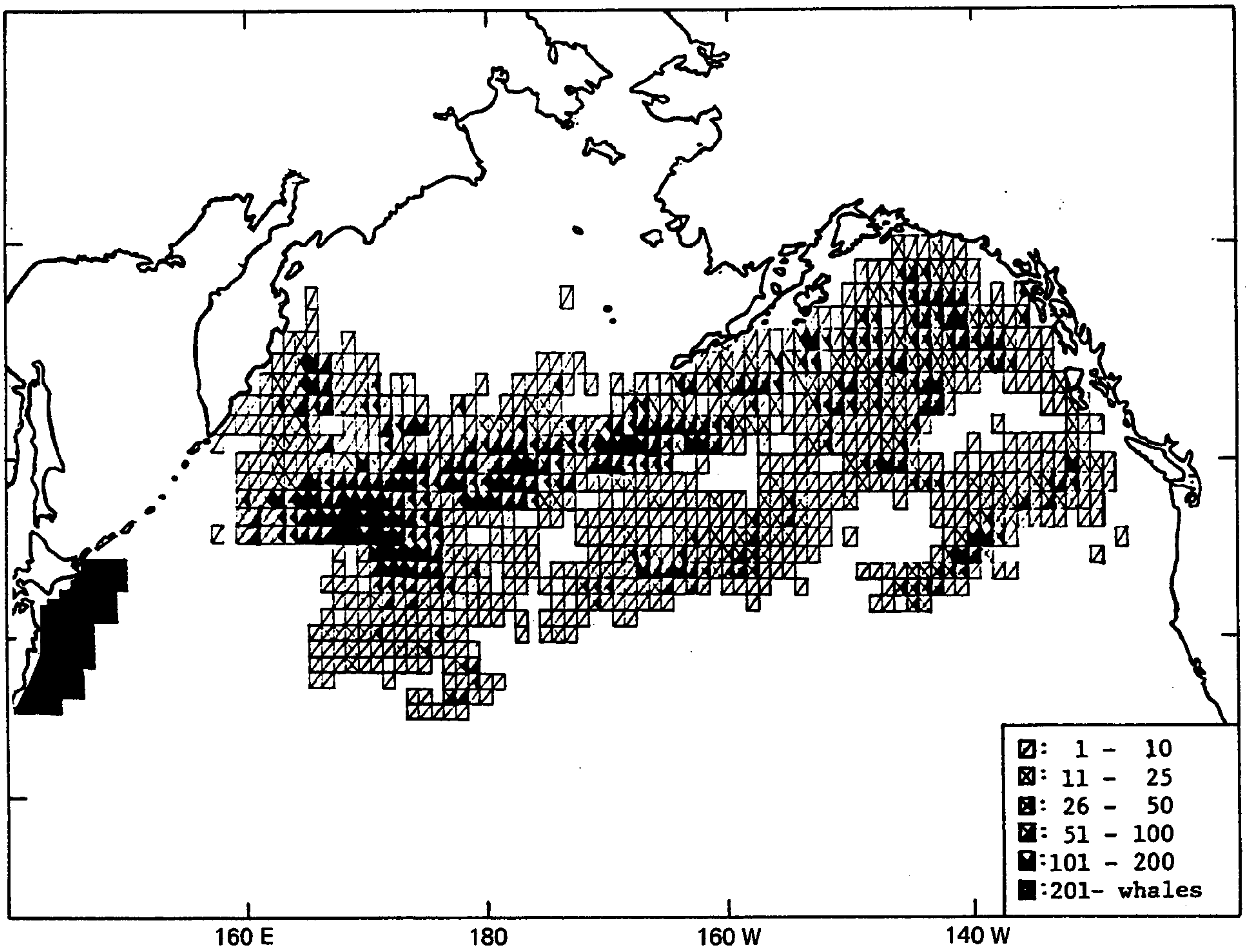

Fig. 3. Distribution of sei whales caught by Japan in the North Pacific, 1952 to 1972.

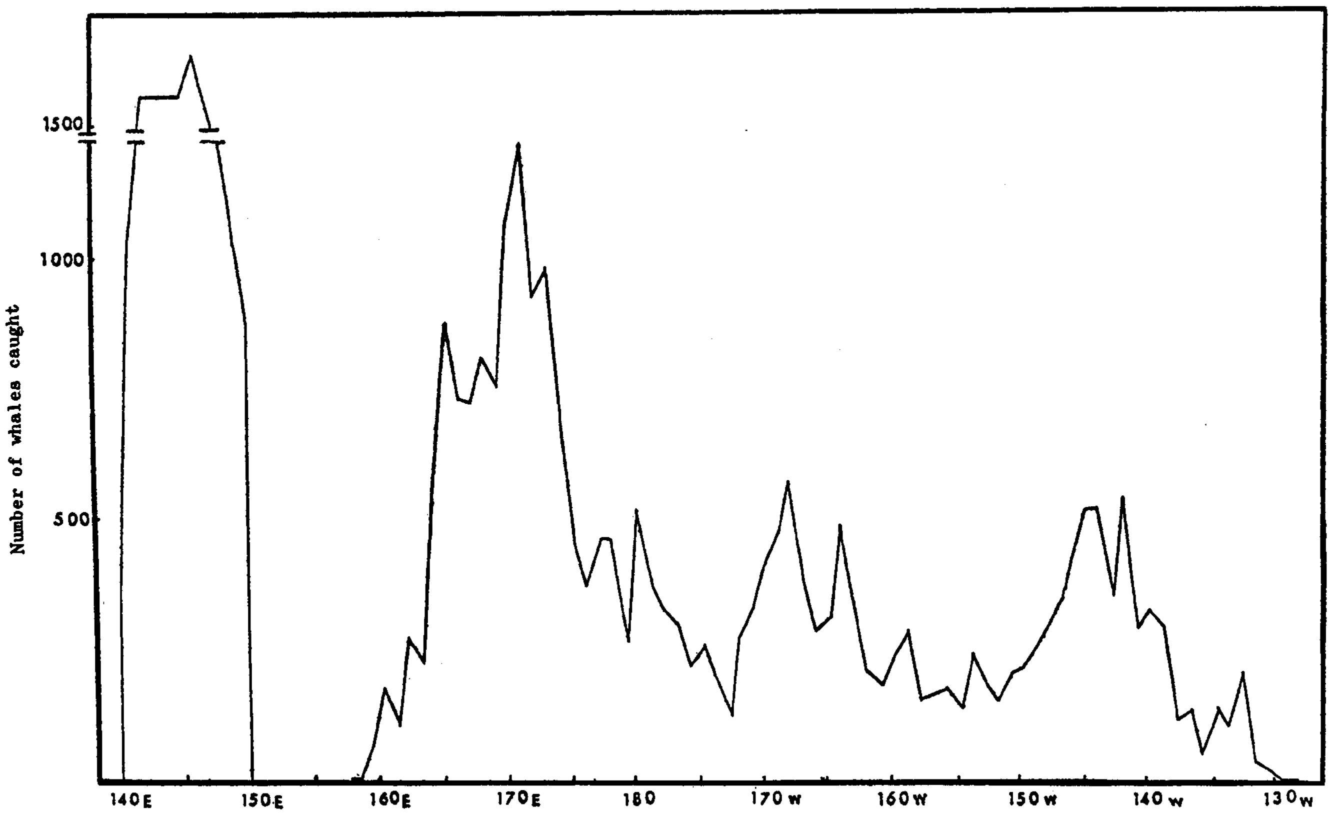

Fig. 4. Longitudinal distribution of sei whales caught by Japan in the North Pacific, 1952 to 1972.

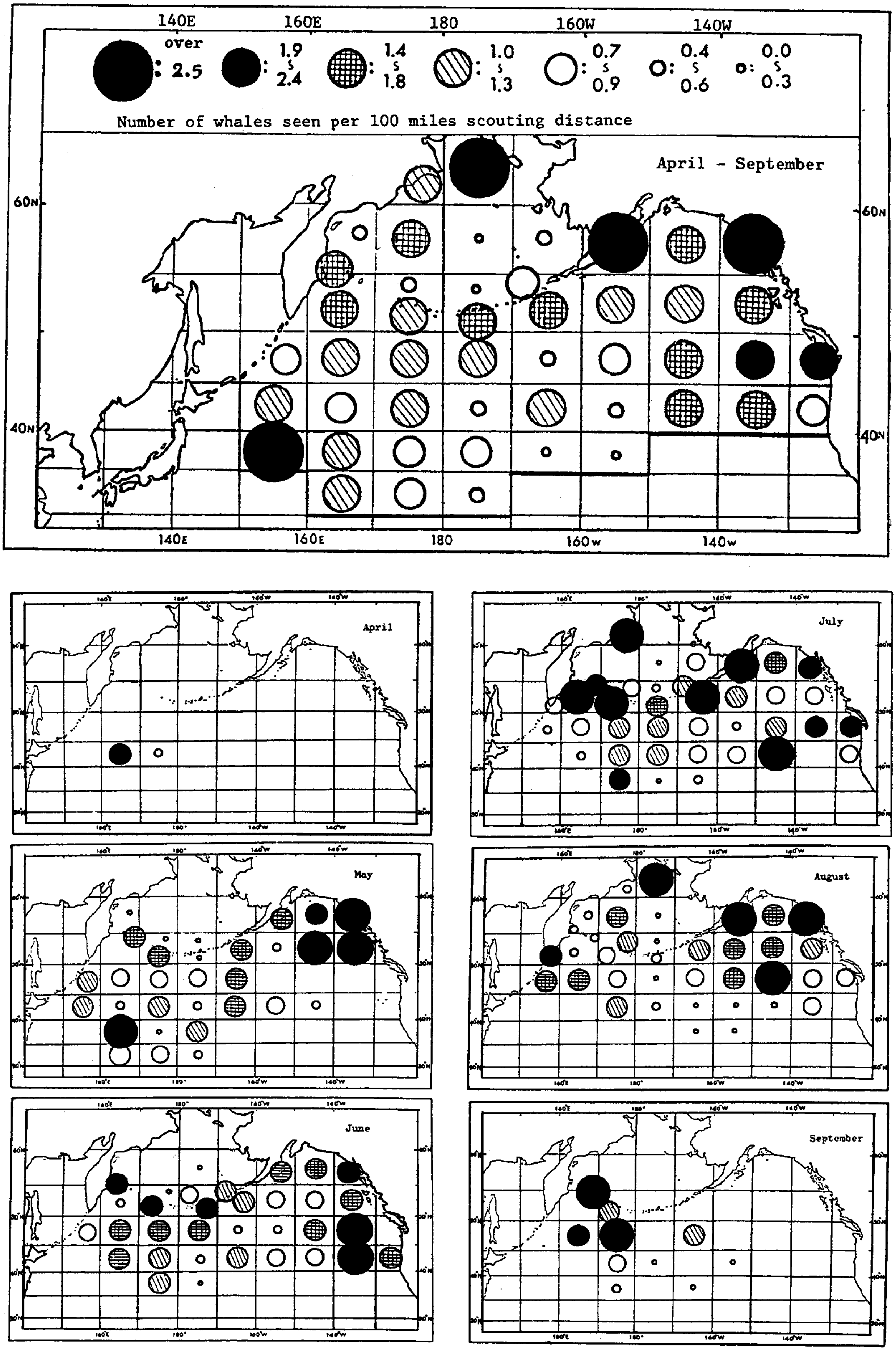

Fig. 5. Diagram of density indices of sei whales sighted by Japanese scouting boats in the North Pacific, 1965 to 1972.

Table 1

Mean value and standard error of each L/B ratio and angle α of baleen plates of the sei whales by regions in the North Pacific

Region	L/B ratio				Angle α			
	Male		Female		Male		Female	
	Mean	St. error	Mean	St. error	Mean	St. error	Mean	St. error
160°E-170°E (A)	2.45	± 0.13	2.47	± 0.22	120.4	± 5.2	123.6	± 11.4
170°E-170°W (B)	2.43	± 0.23	2.42	± 0.16	117.6	± 3.1	120.5	± 5.0
170°W-150°W (C)	2.52	± 0.45	2.52	± 0.21	121.7	± 4.2	121.0	± 3.5
150°W-130°W (D)	2.56	± 0.20	2.57	± 0.18	119.0	± 5.5	117.2	± 6.2

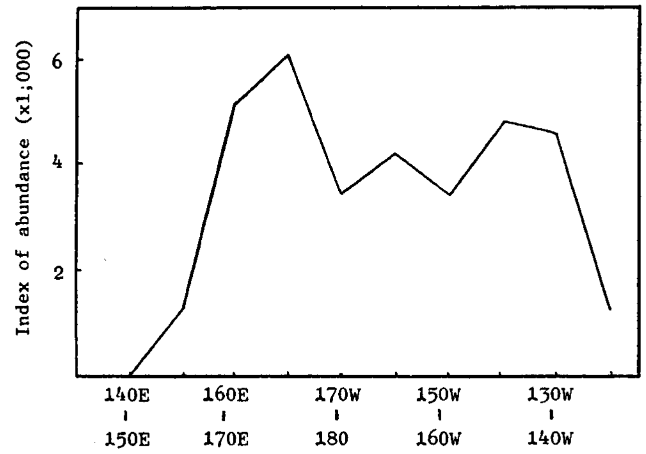

Fig. 6. The accumulated indices of abundance of North Pacific sei whales by 10 degrees of longitude.

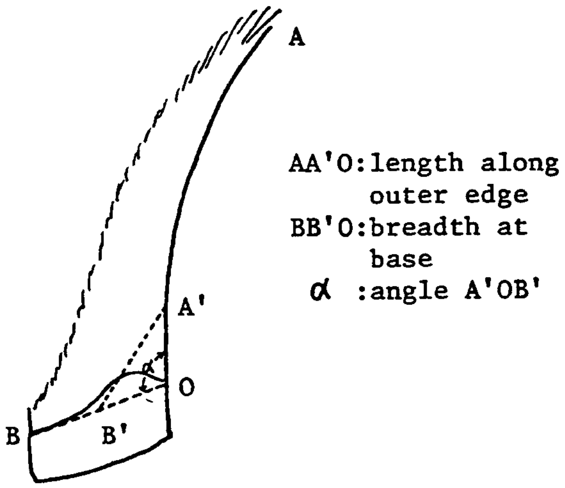

Fig. 7. Measurements of baleen plate.

Nevertheless the whale marking is a direct method which can separate stock units using the distribution or the sphere of movements of the recaptured whales, this method is superior for a definition of stock units to the other three methods treated in this paper. Therefore, the longitudes of 174°W and 155°W which were conjectured by this method as border lines of each of three stock units on the feeding grounds will be relied upon.

The methods based on the distribution of the catch and the density index from whale sightings separate the stock units fairly easily, although they do not produce a distinct separation. However, the estimated ranges of the distribution of the stock units which were obtained by these two methods provide similar results·to those obtained from whale marking.

Stock identification based on the shape of the baleen plate is a reliable method in view of its inherited character. However, as this method must treat the data as a whole, identification of the comparable areas becomes complicated. For the North Pacific sei whale, the difference in shape of the baleen plates between regions was very small and, consequently, it did not give a definite result.

Fujino (1964) showed the possibilities for identifying stock units of the sei whale using blood typing. He reported that the stock unit in the waters of the inner part of the Gulf of Alaska was different from that off Vancouver. However, the sei whales which distribute in Area E are thought to move into the inner part of the Gulf of Alaska for a short season (Masaki, 1976). Thus if Fujino's materials were composed of trespassers from Area E, the possibility stated above would be a natural conclusion from blood typing examination.

Putting all the above-mentioned results together, it is concluded that North Pacific sei whales can be separated into three stock units divided by the border lines of 175°W and 155°W.

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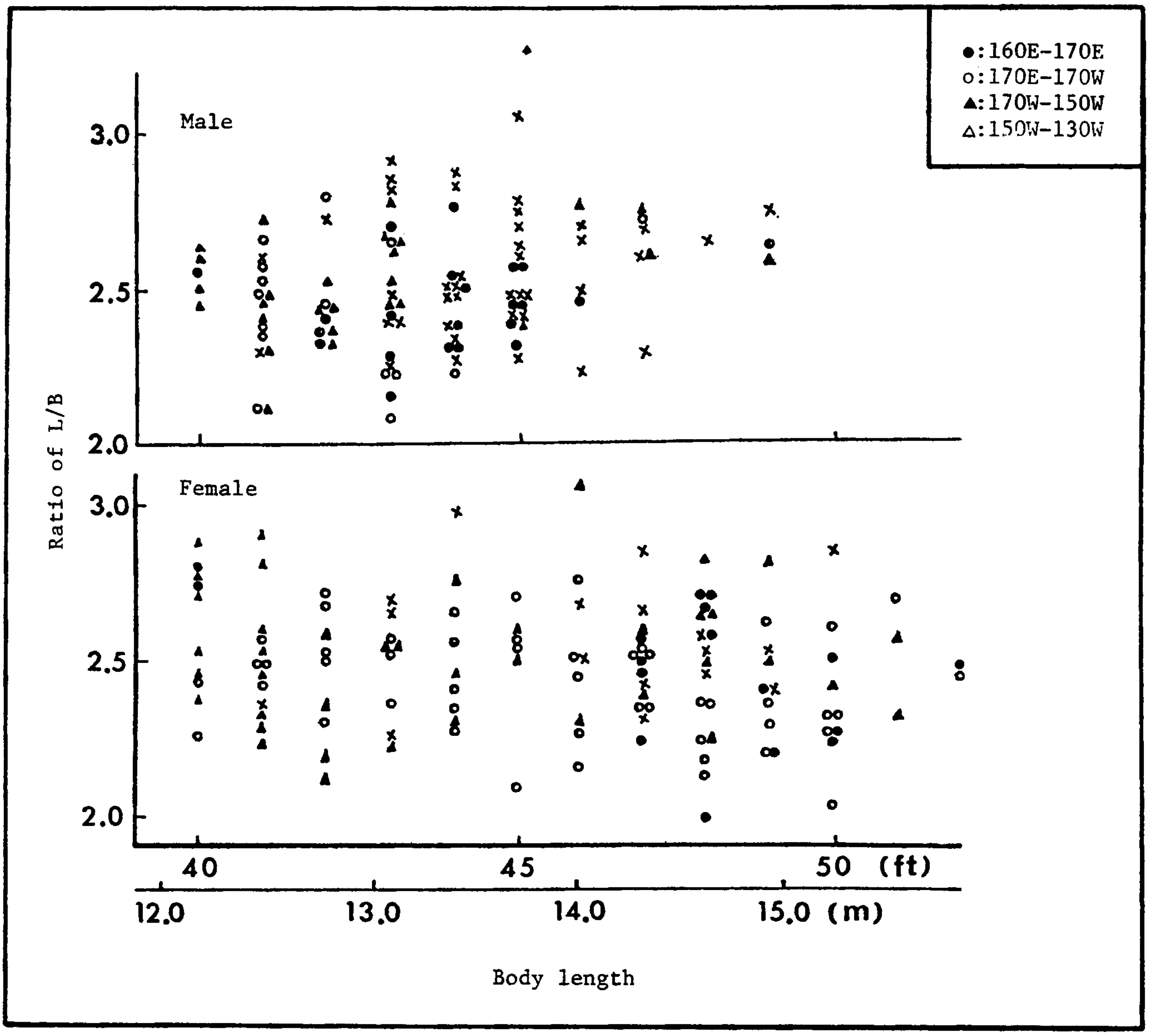

Fig. 8. Relation between body length and ratio of L/B of baleen plate in North Pacific sei whales.

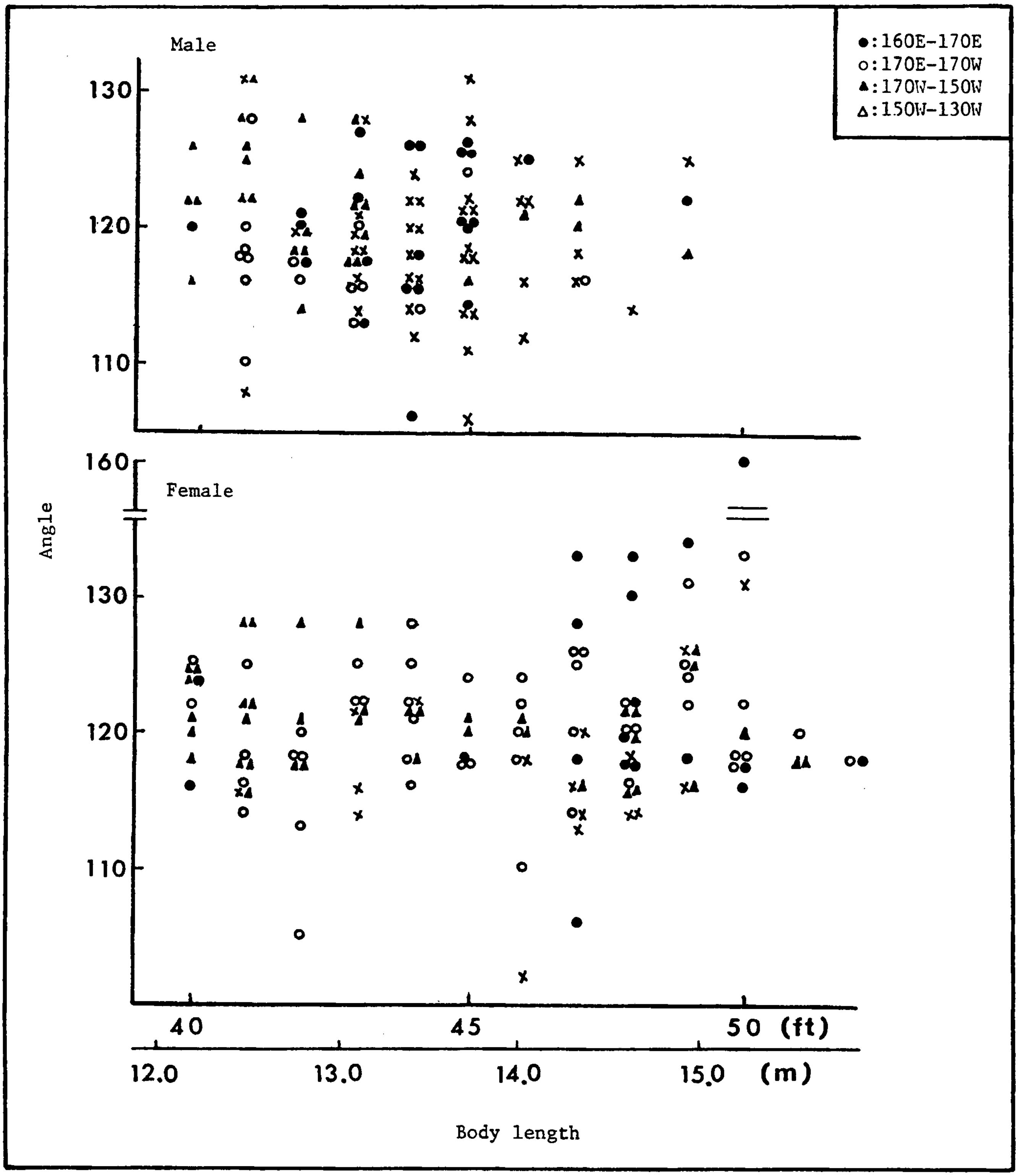

Fig. 9. Relation between body length and angle of baleen plate in North Pacific sei whales.

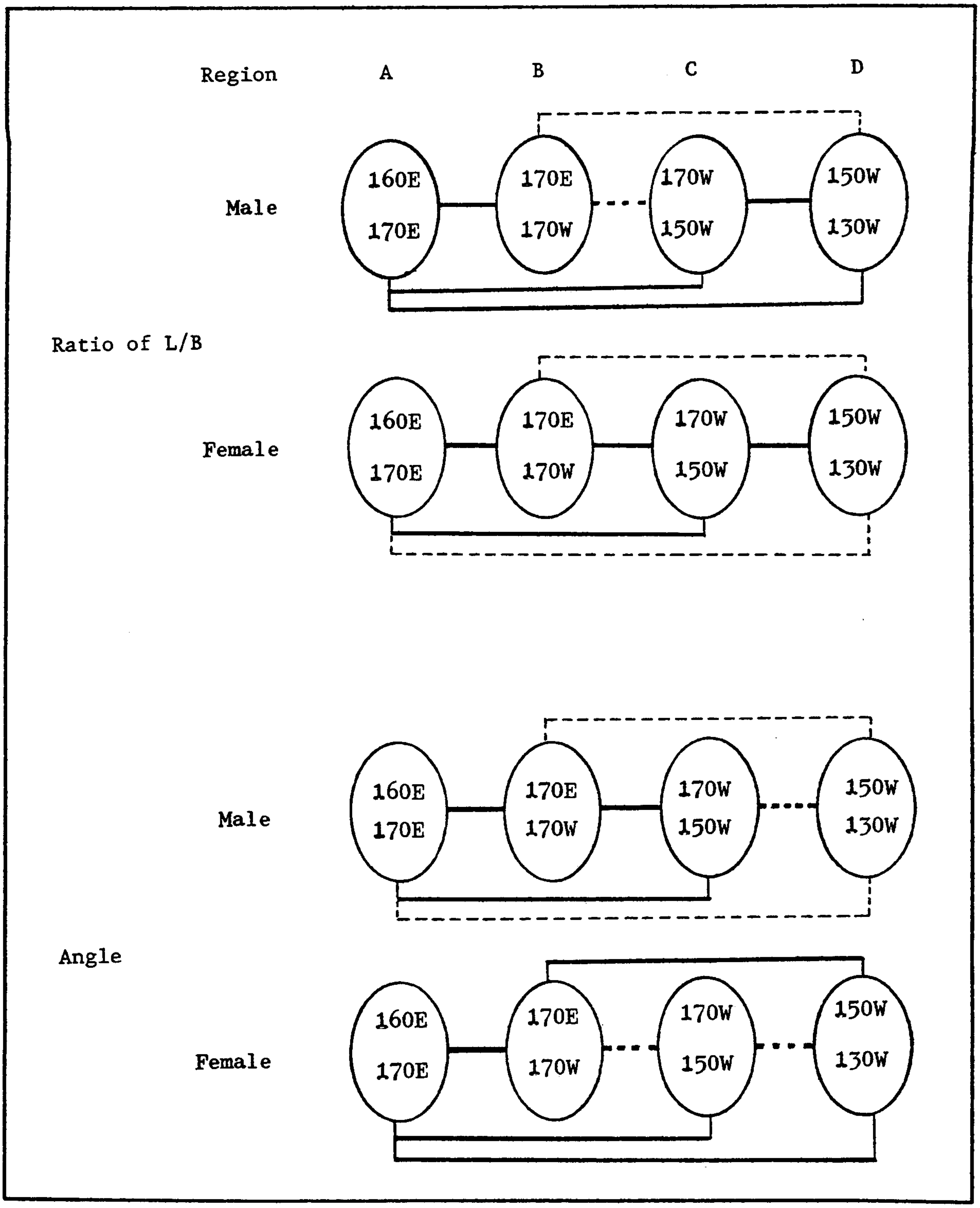

Fig. 10. The results of examination of the difference of the mean value of L/B and between regions in North Pacific sei whales.
Solid line: there is no significant difference between the two regions, Broken line: there is a significant difference between the two regions.

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Characteristics of Food Habits and Distribution of Baleen Whales with Special Reference to the Abundance of North Pacific Sei and Bryde's Whales

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Abstract

The characteristics of food and feeding of baleen whales along with their distribution are reviewed and discussed in relation to the characteristics of the trophic level of the whales' food and their population in the marine ecosystem. The preference for food species by baleen whales is very clear, and a selection order is re-emphasized. The selectivity of baleen whales is considered to be due to the characteristics of the food organisms (size, density and biomass) and the whales' preference for each food species. The trophic levels of baleen whale food also vary according to the dietary habits of different whale species. Blue and right whales undoubtedly feed primarily on species at a lower level in the food chain, but fin and sei whales feed on higher levels such as fishes and even squids.

The distribution and feeding range of baleen whales are examined. The feeding migrations and range of baleen whales are considered to be affected by the type of habitat (whether coastal waters or pelagic ocean), the biological strength of whales (number, size, age, time of migration) and inter-specific relationships. Sei whales usually do not penetrate into coastal waters and they have expanded their feeding range into higher latitudes with the depletion of the larger blue and fin whales.

Comments are made on the study of baleen whales in relation to their food and feeding as an approach for a future line of study of the population and exploitation of baleen whale stocks.

INTRODUCTION

Accumulated data and discussions on stomach contents of baleen whales form a background for consideration of the characteristics of dietary habits in baleen whales. Of the baleen whales, blue, fin and humpback whales were exploited in the earlier period of modern whaling and they have probably been better studied than any other species. The food and feeding of sei whales, however, have been studied specifically only in the last two decades, based on data accumulated from the increased catches in the Antarctic, Southern Ocean and in the North Pacific and North Atlantic. Some of these results are found in papers by Nemoto (1959; 1970), Kawamura (1973; 1974), Best (1967) and Mitchell (1975).

On the other hand, the advanced information on population studies of whales includes the concept that the status of whales as important members of an animal community should be examined so as to improve management of whale stocks. Some considerations have already been given by Gulland (1974) and discussed at the meeting of the Scientific Committee of the International Whaling Commission (Mitchell, 1975; Gambell, 1975; Chapman, 1975). In this presentation, we discuss general considerations on the food, feeding and distributions of baleen whales, and point out some characteristics of the North Pacific sei and Bryde's whales in connection with the productivity of the seas through marine food chains and the possible interaction between baleen whales.

SELECTION OF FOOD BY BALEEN WHALES

The Japanese data including recent results are given in Tables 1 and 2, in which the main items of food of baleen whales are shown in percentage figures. The selection for food by baleen whales is very clearly shown in these tables. Blue whales, for instance, feed almost exclusively on euphausiids both in the Antarctic and in the North Pacific. Other organisms such as copepods and amphipods were found in less than 3% of all blue whales examined. Fin and humpback whales also feed mainly on euphausiids, but their food species seem to be more varied in the North Pacific and North Atlantic (Mitchell, 1975). The next most important food items in the North Pacific for fin whales are copepods, and for humpback whales gregarious fishes. Sei whales commonly take copepods in the North Pacific and adjacent waters as well as in the Southern Ocean (Nemoto, 1970; Kawamura, 1974). Mitchell (1975) also refers to sei whales as copepod-feeders in the western North Atlantic.

Table 1

Stomach contents of baleen whales caught by Japanese pelagic operations from 1961 to 1966* in the Antarctic

	Whale species				
Food species	Blue	Fin	Sei	Humpback	Minke
Euphausiids	97.7%	99.4%	54.3%	100.0%	100.0%
Euphausiids and others	0.8%	0.1%	0.0%	–	–
Copepods	0.4%	–	30.5%	–	–
Amphipods	1.1%	0.1%	14.4%	–	–
Munida decapods	–	–	0.6%	–	–
Fish	–	0.5%	0.2%	–	–
Squids	–	–	0.0%	–	–
Empty	674	18,878	18,609	2	10
No. of whales examined	1,203	35,139	31,494	9	98

*Blue, Fin, Humpback and Minke whales based on data from 1961 to 1965.

Generally speaking, the dietary habits of sei whales are more complex, both in the Antarctic and in the North Pacific. Our data in the Antarctic are based on catches from 1961 to 1966, when some 20,000 sei whales were caught south of the Antarctic convergence. Copepods and amphipods are described as sei whale food from the waters around the Antarctic convergence. Data from Japanese pelagic catches of sei whales in the North Pacific also

Table 2

Stomach contents of baleen whales caught by Japanese pelagic operations from 1952 to 1971* in the North Pacific

	Whale species					
Food species	Blue	Fin	Sei	Bryde's	Humpback	Right
Euphausiids	97.6%**	64.1%**	12.6%**	88.9%	77.3%	–
Euphausiids and copepods	1.1%	3.4%	0.0%	–	0.6%	–
Euphausiids and others	–	0.3%	–	–	3.9%	–
Copepods	1.3%	25.5%	82.7%	–	0.6%	100.0%
Copepods and others	–	0.0%	0.1%	–	–	–
Fish	–	5.0%	3.4%	11.1%	17.2%	–
Fish and others	–	–	0.0%	–	–	–
Squids	–	1.7%	1.2%	–	0.3%	–
Empty	504	10,064	9,665	82	150	0
No. of whales examined	971	29,575	21,713	109	458	9

*Exclusive of data in 1966
**Including *Sergestes similis.*

suggest copepods as the main food item, but in this region even gregarious fishes are important sometimes and in some places for sei whales. If we consider data from the coastal catch of sei whales, more varied food items are found, including gregarious fishes and even squids. In the selection of food organisms, sei whales show similar first and second order of preferences as was known for right whales (Mitchell, 1975). However, the feeding method for euphausiids, a second ranked food item, may be different. Sei whales use swallowing-type behaviour for swarming euphausiids, whereas right whales may possibly use swallowing-type feeding following a rather shorter duration of skimming.

The data for Bryde's whales caught by pelagic whaling in the North Pacific are also very interesting because these whales feed almost exclusively on euphausiids and fishes. Similar results have been obtained from catches in Japanese coastal waters (Nemoto, 1959).

The selectivity of baleen whales is considered to be affected by the following main factors:

(1) Selection of food by baleen whales is correlated with their feeding apparatus and feeding behaviour as has been discussed. When various items of food are available for each whale species, selection of food organisms by taste must exist.

(2) When some whales are feeding on well-preferred food species they may also take less-preferred food species that have undoubtedly gathered to feed on the well-preferred species (as competitors).

If a baleen whale using one type of feeding has access to various forms of swarming organisms or the distribution of other food organisms in a higher trophic level, it may also take them as preferred food. This tendency may be illustrated by the following examples:

(a) Sei whales feed on copepods, and they also feed on amphipods which feed on those copepods.
(b) Fin whales feed on euphausiids, and they also feed on gregarious fishes, herring (*Clupea pallasi*) and Alaskan pollack (*Theragra chalcogramma*), which themselves are usually autophagous although the latter also feeds on euphausiids especially in the Bering Sea.
(c) Sei whales take young mackerel, saury, sardine, and anchovy in the waters adjacent to Japan and in the southern part of the northwestern North Pacific. Those fishes also feed mainly on *Calanus* copepods.

(3) Characteristics of size and density in food organisms.

Even within favourite food categories, baleen whales show particular selection for some species as their more favoured food. This tendency is clearly observed even with copepod groups such as *Calanus plumchrus* and *C. cristatus.* In this instance, fin whales prefer *C. cristatus*, whereas sei whales prefer both *C. plumchrus* and *C. cristatus.*

This tendency depends on the size-density relationship for each food species, as is shown diagrammatically in Fig. 1. This indicates that the larger the size of food, the fewer individuals but not the smaller biomass per unit volume of sea water. Each baleen whale species participates over some special range distribution according to their type of feeding.

Table 3

Main species of copepods found in sei whale stomachs

Area	Species	Source
Antarctic and southern ocean	*Calanus tonsus* *Calanus simillimus* *Drepanopus pectinatus*	Kawamura (1974)
Off the Cape Province, South Africa	*Calanus tonsus* *Calanoides carinatus* *Clausocalanus arcuicornis* f. *major* *Nannocalanus minor*	Best (1967)
North Pacific	*Calanus plumchrus* *Calanus cristatus* *Calanus pacificus*	Nemoto (1959) Kawamura (1973)
North Atlantic	*Calanus finmarchicus*	Hjort & Ruud (1929) Mitchell (1975)

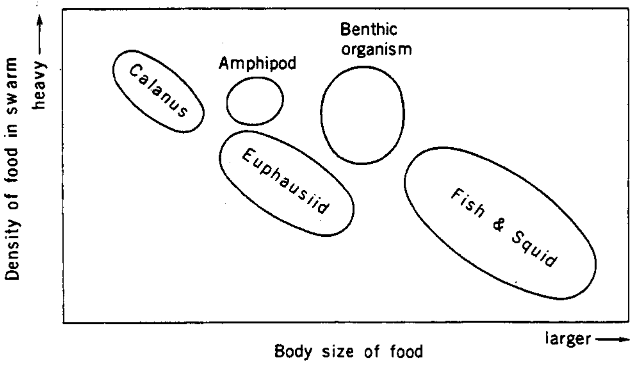

Fig. 1. Relationship between body size of food and its density (individuals per unit water volume), and the range of size-density relationship for each category of food.

It also seems that the larger-sized food of less density in sea water appears more abundantly in the stomachs of baleen whales. An example is found in the North Pacific where gregarious fishes and squids are found more abundantly in the stomachs of baleen whales than *Calanus* copepods.

(4) Distribution patterns of food organisms.

(a) Density and biomass.

The relationship between density of food (expressed as number of individuals per unit volume) and biomass of food (expressed as weight of food organisms) is shown in Fig. 2, in which the feeding range for preferred food organisms is also given. This diagram shows how the density and the biomass of food organisms affects the feeding selection of baleen whales. Sei whales in the North Pacific have the broadest range of acceptance of food organisms in these density-biomass relationships. This means sei whales feed not only on small copepods (total biomass per unit volume of water small) but they also feed on larger fishes and squids that are less densely populated when expressed as number of individuals (that is, biomass is large and the standing weight in the stomachs of whales is also large). Both fin and humpback whales show similar ranges, but humpback whales do not extend to the corner of high density and low biomass. Humpback whales extend, on the other hand, to the corner of less density and high biomass, whereas fin whales do not extend their range to this corner. The ranges of right and blue whales are monotonous in density-biomass relationships along the range of simple food categories, namely, copepods and euphausiids.

(b) Behaviour of food organisms.

The behaviour of food organisms in terms of 'fast' or 'slow' movement may be occasionally reflected in the stomach contents of whales. However it is rather difficult to clearly attribute this to the above mentioned behavioural characters of the food organisms. We are of the opinion that food preference in baleen whales is primarily due to the availability of prey in the region, and it seems unlikely that they feed on a prey simply because it moves quickly or slowly.

DISTRIBUTION OF SEI WHALES

The general distribution of sei whales in summer is well established through whaling operations, but that in winter is less well-known, especially in the North Pacific. Furthermore, there are some peculiar features in sei whale distribution, as follows:

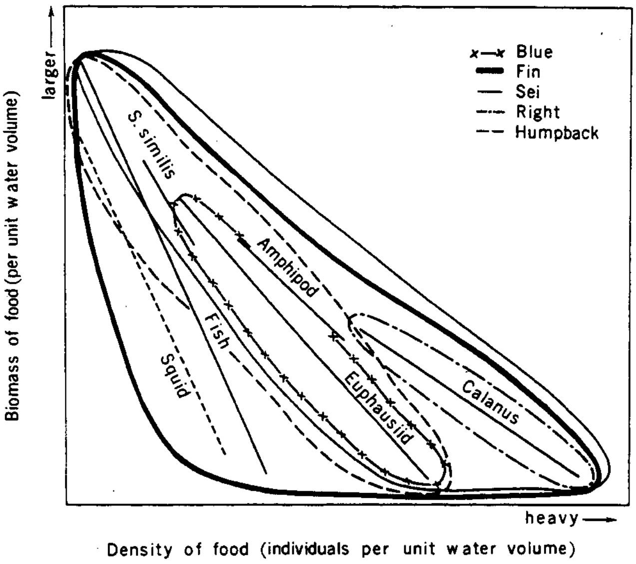

Fig. 2. Feeding ranges of baleen whales in relation to density-biomass relationships of their food in the North Pacific.

(1) Few sei whales have penetrated into marginal seas such as the Sea of Japan and the Bering Sea in the North Pacific (Nemoto, 1959), while very high primary production is found in the western side of the Sea of Japan, according to Koblentz-Mishke, Volkovinsky and Kabanova (1970). Zooplankton investigations also show that the average biomass of *Calanus plumchrus*, one of the favourite foods of sei whales, is estimated as 48 mg/m^3, which fairly substantially exceeds the figures for other food species such as *Calanus cristatus, Euphausia pacifica, Thysanoessa longipes* and *Parathemisto japonica* (Komaki, personal communication). Nakai (1942) estimated the total biomass of *Calanus plumchrus* in the southwestern part of the Sea of Japan (divided by the line between Niigata and Cape Povorothi) as about one-third of the total zooplankton. However, whaling records and sightings of whales demonstrate that few sei whales are distributed in the Sea of Japan. These facts are apparently due to the characteristic pattern of sei whale distribution. A similar case may be found in the Okhotsk Sea and the Bering Sea which few sei whales enter for feeding. As suggested by Nemoto (1959), sei whales are 'ocean denizens' and usually do not penetrate deep into marginal seas, where there may be vast volumes or biomass of their favourite food, *Calanus* copepods.

(2) Considering recent whaling grounds, the main summer distribution pattern of sei whales is found in the oceanic waters of primary production between 100–500 mg C/m^2/day.

The worldwide distribution of primary production is given by many authors (e.g. Koblentz-Mishke *et al.*, 1970). The high productivity of the sea is apparently connected to the waters of pelagic upwelling and certain shallow waters in general. The highest phytoplankton productivity in the North Pacific region is observed in the Bering Strait, Okhotsk Sea and the waters around Kamtchatka Peninsula, the Asian continental side of the Sea of Japan and the waters around Asian south-eastern archipelago. However, these areas are never favourable feeding grounds for sei whales, although considerable standing stocks of favourite copepods such as *Calanus plumchrus* and *Calanus cristatus* are found in some of these areas. The area proposed as the feeding ground of sei whales in southern waters consists largely of *Calanus tonsus* (Kawamura, 1974), and *Calanus plumchrus*, *C. cristatus* and *C. pacificus* are represented in the North Pacific (Nemoto, 1959; Kawamura, 1973). These feeding grounds, however, by no means overlap the above-mentioned areas of highest primary production, where about 500 mg C/m^2/day production is obtained as an annual average, although it may be far higher in the summer season in high latitudes. On the other hand, the feeding grounds of sei whales consisting of *Calanus* are found in areas of average primary production between 100 and 500 mg C/m^2/day, while it is clear that feeding grounds are not found in pockets of low production of less than 100 mg C/m^2/day. Areas of primary production between 100 and 500 mg C/m^2/day are situated in rather lower latitudes than the areas of highest production (except those caused by upwelling in tropical waters), where the production shows less seasonal fluctuation than the most productive waters in the high latitudes of North Pacific. This means a constant supply of food for herbivorous copepods.

(3) In a meso-scale distribution of summer feeding grounds, sei whales share the food that mainly consists of copepods with other baleen whales, especially with fin whales. As an example the North Pacific whaling grounds in terms of the catch distribution along the Aleutian Islands chain in 1960 are shown in Fig. 3. Sei, blue and fin whales were found and caught, but the food and position where these whales were spotted are quite different for each species. Sei whales took both *Calanus plumchrus* and *C. cristatus*, whereas fin whales almost confined their diet to *C. cristatus*. Blue whales, on the other hand, took only euphausiids with a small number of *Sergestes similis*, and they were spotted in different areas from the others. In fact the positions of whales found and caught usually did not overlap even when *C. plumchrus* was shared by sei and fin whales. The reasons may be; (1) 'biological strength' of baleen whales as suggested by Nemoto (1959), and (2) discrepancy of meso-scale distribution of their favourite food, namely, *C. plumchrus* and *C. cristatus*.

The main difference in distribution between right and sei whales in relation to their feeding habits is considered as follows. Both right and sei whales are considered to be primary skimmers which feed on swarms of *Calanus* copepods of low density, but sei whales to some extent also take their food by the swallowing-type feeding (Nemoto, 1970). Right whales, a true skimming-type species, have evidently a comparatively short seasonal migration (Nemoto, 1970), as shown by the catch of this species in winter and summer (Townsend, 1935). Another 'skimmer', the Greenland whale, is also confined to the waters of prevailing ice cover in the North Polar Seas and never competes for food with any other whale species. Although the substantial selectivity of food by sei whales is the same for right whales, sei whales undertake clearer seasonal migrations and the area of feeding range for sei whales may expand in parallel with the depletion of competitors of skimming and swallowing types. The food of sei whales taken by the swallowing-type of feeding is apt to consist of gregarious fish and the slightly more gregarious zooplankton species such as euphausiids rather than copepods. Sei whales, therefore, are considered to share the feeding grounds formed by poorly concentrated zooplankton with right whales, but also to penetrate into the feeding grounds of rich gregarious euphausiids south of the Antarctic convergence (Nemoto, 1962) with the depletion of other, swallowing-type baleen whales. The real skimming-type baleen whales also take gregarious euphausiids such as *Euphausia superba* in the Antarctic (Matthews, 1938a). But right whales open their mouths for a long time in order to collect sparsely-populated patches of copepods, as was clearly shown by a film taken by W. Schevill in which two right whales swam to and fro along the current rip with their mouths open in order to take a sparse patch of copepods (Schevill, pers. comm., 1962; Watkins and Schevill, 1976).

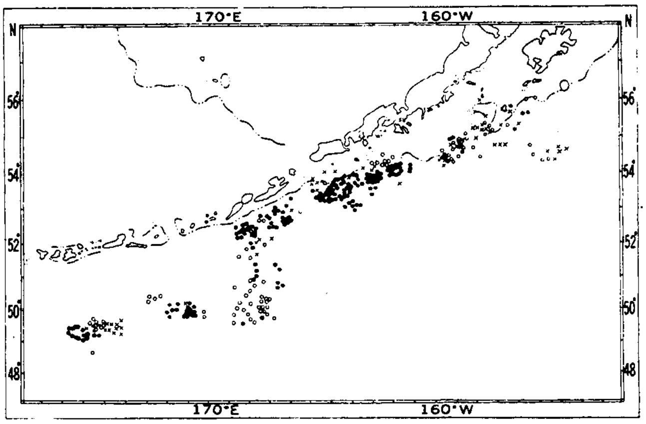

Fig. 3. Distribution of baleen whales in the North Pacific in July 1960, showing different patterns in distribution by species. Open circle: fin whales, Closed Circle: sei whales, Cross: blue whales.

TROPHIC LEVELS OF FOOD

As has been discussed, baleen whales take food of somewhat different trophic levels according to species. *Euphausia superba*, the main food in the Antarctic region, is considered as the second level in the trophic chain which feeds on a primary producer. Other copepods found as food of baleen whales are also mostly herbivorous. We can, however, find more complex trophic levels of food in fin, Bryde's, humpback and sei whales in oceanic waters. The number of trophic levels to the final (or larger) predators is also small in upwelling waters of high production (ca. 1.5) but it increases to about five in oceanic waters (Ryther, 1969).

Considering the selection order of food (Nemoto, 1970), the trophic levels of food taken by baleen whales are as listed in Table 4. This indicates that blue whales and right whales mostly feed on the secondary producer or the herbivorous plankton, although their methods of feeding are completely different. Both fin and sei whales cover much broader trophic levels than other whale species. In these two species, however, the trophic levels of their main food are different in the North Pacific and in the Southern Ocean. Generally speaking, the overall trophic levels for food of sei whales in the North Pacific are considered to be higher than in the Southern Ocean.

The nutritive conversion efficiency of baleen whales is thus comparatively high in the Antarctic and low in the North Pacific. The reduction of size in baleen whales in the Northern Hemisphere may be considered in relation to these differences in the production of food plankton and

Table 4

Trophic levels of food of baleen whales according to selection orders (North Pacific)

	Trophic levels*			
Whales species	1	2	3	4
Blue	+++	–	–	–
Fin	+++	+++	+	+
Bryde's	+++	+++	++	–
Sei	+++	++	+	+
Humpback	+++	+++	–	–
Minke	+++	+++	–	–
Right	+++	–	–	–

*1 Herbivorous euphausiids, *Calanus*, gregarious fish: anchovy
2 Amphipods, plankton feeding gregarious fish: saury, small mackerel etc., omnivorous euphausiids.
3 Gregarious fish feeding on smaller fish, mackerel etc., squids (part)
4 Squids (part).

gregarious fish, especially in oceanic waters. As the production of baleen whales apparently depends on the extent of feeding waters and the production of food, we would also suggest that differences in trophic levels significantly define the potential of population size, growth or recovery of population, feeding condition and migration of baleen whales.

The principal food organisms of baleen whales that have been found in the Antarctic region are *Calanus tonsus, C. simillimus, Clausocalanus laticeps, Euphausia vallentini, E. superba, Thysanoessa macrura*, and *Parathemisto gaudichaudii*, while those in the North Pacific are represented by *Calanus cristatus, C. plumchrus, C. pacificus, Euphausia pacifica, Thysanoessa inermis, T. spinifera, T.raschii, T. longipes, Nematoscelis difficilis, Sergestes similis, Scomber japonicus, Engraulis japonica, Sardinops melanosticta, Cololabis saira, Pseudopentaceros richardsonii*, and some gonostomatid fishes such as *Vinciguerria nimbaria* and *Maurolicus muelleri*, and even squids are included (Nemoto, 1957, 1959, 1962, 1963; Kawamura, 1970, 1973, 1974; Omori *et al.*, 1972). Of the fishes that can be added for the Antarctic region, we know only of *Vinciguerria attenuata, Scomberesox saurus* and some myctophid fishes that are relatively important foodstuffs.

Considering the food and feeding conditions of baleen whales, it is clear that the feeding grounds in the North Pacific are of somewhat complex status, being formed by a wide variety of prey organisms. In the quantitative aspects of food condition, most of the principal food organisms in the North Pacific consist of omnivorous euphausiids and carnivorous (= planktivorous) species of fishes, which may be placed in the second or third link in marine food chains as the consumer (Kawamura, 1973). Some fishes are also found which may be considered even in the third or fourth link, such as boar fish (*P.richardsonii*) (Sasaki, 1974), cod (*Gadus macrocephalus*) and Alaskan pollack (*Theragra chalcogramma*). The only herbivores among food organisms in the North Pacific would be copepods, viz., *Calanus cristatus, C. plumchrus, C. finmarchicus, C. pacificus* and *Metridia lucens*, though the latter species is of little importance (Nemoto, 1957; Minoda, 1971).

The Antarctic feeding grounds, on the other hand, are principally formed by herbivorous species of copepods and euphausiids, and only *P. gaudichaudii* can be singled out as a carnivorous species (Nemoto and Yoo, 1970). Accordingly, these two whaling (= feeding) grounds, one in the Northern Hemisphere and the other in the Southern Hemisphere, differ considerably from each other when they are compared from the viewpoint of, say, the fertility of the sea where baleen whales are placed in the centre of marine food chains. These circumstances could be expressed by two somewhat deformed schematic triangles as shown in Fig. 4. This figure shows that these feeding grounds are not substantially equivalent in their trophic structure. Since expansion in the horizontal plane is far larger in the Antarctic feeding grounds than in the North Pacific, the relative size scales of both structural triangles may determine the initial level of organic production and/or the population size of baleen whales to be yielded: that is, a very small number of whales (somewhere between 1/5 to 1/10) could be incorporated under the unit of horizontal plane (= feeding ground) in the North Pacific triangle. Actually, however, the selectivity for food organisms by whale species is one of the most important factors that has to be taken into consideration. For instance, right whales feed almost exclusively on herbivorous copepods both in the Antarctic and North Pacific (but *Euphausia superba* seems to be important in some localities of the Southern Ocean), and their potential population growth would supposedly be little different between both feeding grounds. Blue whales also are under closely related circumstances to right whales, though some minor differences in their food organisms (whether they are omnivorous or herbivorous) have to be considered in quantitative and seasonal respects.

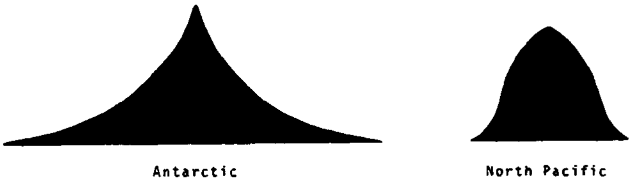

Fig. 4. Two deformed schemata for the Eltonian pyramid.

It is rather difficult to categorize whale species as either euryphagous or stenophagous, since feeding conditions vary with time, season, location and so forth. In the results actually found from the feeding of whales, there seems to be two cases, the first one is dependent on the character of the whale species itself and the second one is largely dependent on the availability of food organisms. In the latter, the sei whale even feeds on large fishes beyond its original preference for copepods (e.g. Chikini, 1970; Kawamura, 1973). However, a rather different case is known in the Nova Scotian waters where the sei whale shows a more typical stenophagous character than the fin whale (Mitchell, 1975). Even so, it is possible to some extent to classify whales in the above way when the whale species and locality are defined.

Although sei and fin whales strongly prefer copepods and euphausiids respectively, they are able to feed on such a variety of food organisms in a broad sense as even to be called euryphagous animals. Precise examinations are needed for these two species, since fin whales feed on euphausiids and sei whales on copepods and euphausiids almost exclusively in the Antarctic grounds, while in the North Pacific they feed on euphausiids, copepods, fishes and squids, or almost every gregarious organism occurring

Table 5

Order of selection of food by baleen whales (= shows equivalence and > shows the dominance to the left)*

Whale species	Food species in order of selection
Blue	Euphausiids
Fin	Euphausiids ⩾ Copepods (large) > Gregarious fish > Copepods > Squids
Bryde's	Euphausiids = Gregarious fish > Copepods
Sei	Copepods ⩾ Amphipods ⩾ Euphausiids > Gregarious fish = Squids
Humpback	Euphausiids = Gregarious fish
Minke	Euphausiids = Gregarious fish > Copepods
Right	Copepods > Euphausiids

*Modified table from Nemoto (1970).

with large biomass. Similarly, the status of Bryde's whales should be examined in relation to the fertility of the sea. In the waters off South Africa, there are two allopatric forms of Bryde's whale each of which shows different food habits, viz. kind of foodstuff and its feeding ground (Best, 1974).

AN ESTIMATION OF THE RELATIVE ABUNDANCE OF NORTH PACIFIC SEI AND BRYDE'S WHALES

We will describe here an example of estimating the relative abundance of sei versus Bryde's whales in the North Pacific feeding ground being based on materials which have been obtained during the past seasons.

Fig. 5 shows an approximate sea area by 5 degree squares where Japanese fleets have operated for baleen whaling in the North Pacific Ocean. The whole area shows the integrated expansion of whaling ground (and consequently, assumed as the feeding ground) occupied through the 23 seasons, 1952–74. The hatched areas show the whaling ground where Bryde's whale have been caught during the 1971–74 seasons. The two blocks of 5 degree squares for Bryde's whales between 40°–45°N and 170°E–180° were occupied only in the 1971 season, and those squares need some further examination in terms of determining the fertility of the region. Then it is recognized that feeding grounds for Bryde's whales are clearly restricted in the southern part of the North Pacific, and its actual northernmost latitudes would be found up to 45°N, although their southernmost limit would be extended toward the south beyond 25°N or thereabouts.

It can be seen from this figure that most of the North Pacific populations of baleen whales are likely to get their nutrition somewhere between 25°N and the Aleutian Chain. The whale species concerned here are mostly fin, sei and Bryde's whales among which the latter two are currently the more important species. Although fin and very few numbers of sei whales had been caught in the Bering Sea during those earlier days, the food organisms there were represented by *Thysanoessa* euphausiids and several kind of planktivorous and ichthiophagous fishes. That is, the fertility of the offshore waters of the Bering Sea as the feeding ground of baleen whales could be considered rather poor since food organisms found there were generally those in higher trophic levels.

However, the potential or fertility of the sea in terms of availability of whales' food in connection with whales' food habits may give us the relative abundance or size of whale stocks which may be yielded under some ecologically balanced state by sharing food between whale species. In other words, we may determine a possible yield of whales by their food habits and items by introducing reasonable indices which may suggest the fertility of the sea region. Then the sea area as feeding ground of whales by their food items is calculated by multiplying proportionally the known area according to the details found between 25°N and the Aleutian Chains.

Fig. 6 gives an approximate representation of the average percentage occurrence of food organisms in the North Pacific whaling grounds by 5 degree squares. Five groups of food items are considered here, viz. euphausiids, copepods, decapods, fishes and squids. Both euphausiids and copepods form the principal diet for baleen whales, but there are also distinct local characteristics noticeable in southern waters (Kawamura, 1974).

As mentioned before, the food organisms treated here consist of herbivores, omnivores, and carnivores. By setting their organic production or nutritive energetic efficiency through a series of trophic levels as follows, it is possible to estimate an approximate fertility of the sea region as the feeding grounds for the North Pacific baleen whales. That is,

Copepods; herbivore,	1
Euphausiids; omnivore,	0.5
Fishes, decapods, and squids; carnivore,	0.1

By using the above mentioned concepts, the fertility of the sea in terms of its relative value as a feeding ground may be assessed to indicate the productive potential to the consumer. For instance, the relative fertility of a 5 degree square where copepods constitute 100% of the food of whales could be evaluated as 1.0, and similarly, where copepods and euphausiids share the square equally, then the relative fertility may be evaluated as 0.75. This suggests that the latter can sustain 75% of the consumers which would be 100% in the first sea region. By such relative treatment of the data shown in Fig. 6, the North Pacific feeding grounds by 5 degree squares can be evaluated in proportion to the dominancy of the food organisms. The fertility of the feeding grounds calculated in this way are summarized and given in Table 6. Geographical expansion of the feeding grounds between 30°–35°N (120°–140°E) takes in an additional twenty 5 degree squares but the

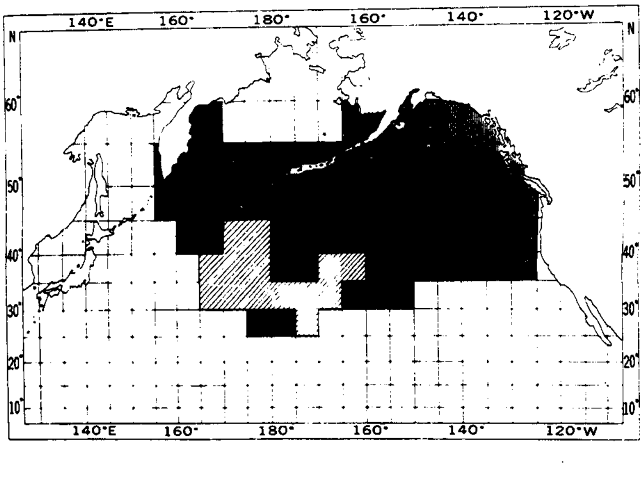

Fig. 5. Whaling grounds for sei and Bryde's whales in the North Pacific occupied by the Japanese pelagic fleets 1952–74. Bryde's whales were caught along with a small number of sei whales in the hatched squares.

Table 6

Fertility of the sea as feeding ground of baleen whales in the North Pacific by latitudinal zones.

Latitude (N)	No. of 5° squares included	Occurrence of food item in percentage[1]					(A)	(B)	(C)		(D)		(E)
		Eu.	Ca.	Fi.	Sq.	Dec.			Sei/ fin	Bryde's	Sei/ fin	Bryde's	
30°–35°	20	14	–	86	–	–	2.28	0.19	3	6	0.063	0.127	0.063
35°–40°	19	5	55	40	–	–	11.40	0.96	9	5	0.617	0.343	0.617
40°–45°	18.5	9	59	23	–	9	11.84	1.00	13	2	0.667	0.333	0.534
45°–50°	16.5	23	44	6.5	16	10.5	8.56	0.72	16	–	0.72	–	0.576
50°–55°	10	31.5	37	8.5	17	6	4.65	0.39	15	–	0.39	–	0.312

Note: (A) Actual fertility of the sea in terms of the number of 5 degree squares when the production efficiency of herbivore is taken as 1.00.
(B) Relative fertility index.
(C) Ratio between sei and Bryde's whales which occurred in the feeding ground in terms of the number of 5 degree squares.
(D) Relative fertility index by whale species.
(E) Relative fertility index of sei whales when the share of fin whales catch is taken as 20% of total catch of baleen whales in the waters north of 40°N.

[1] Eu. = euphausiids, Ca. = *Calanus* copepods, Fi. = fish, Sq. = squid and Dec. = Decapods.

actual or working ability in terms of the number of squares on an ecological efficiency basis would be reduced down 2.28 squares (see column A in Table 6). This suggests that the waters between 30° and 35°N are represented largely by fish and are consequently less fertile in sustaining the consumers of higher trophic levels.

The North Pacific Bryde's whales as far as Fig. 6 is concerned are able to take food only in the waters south of 45°N at most whilst sei whales are clearly confined to the north of 25°N. If we assume that the whaling grounds for sei and Bryde's whales as shown in Fig. 5 were separated completely from each other (i.e., no intermingling by species and/or no interspecific competition for food), the ratio of actual feeding areas expressed on a 5 degree square basis could be calculated as given in column (C) in Table 6. In this connection the total of the relative fertility indices (column D) by whale species is 2.457 for sei, and 0.803 for Bryde's whales throughout the North Pacific feeding ground. Since the catch of fin whales is included in these figures, some further corrections may be required. Fin whales were usually caught almost exclusively in waters north of 40°N. Thus if we assume a 20% share in terms of the past the overall fin whale catch against that for sei whales, the more possible figures for the fertility indices would be obtained as 2.102 (column E), that is, the ratio in fertility or productivity of the sea as feeding grounds for sei and for Bryde's whales could be considered as 2.6:1. This means that the population size or relative abundance of sei whales which feed and maintain their population in the North Pacific must be larger than approximately 2.6 times that of Bryde's whales.

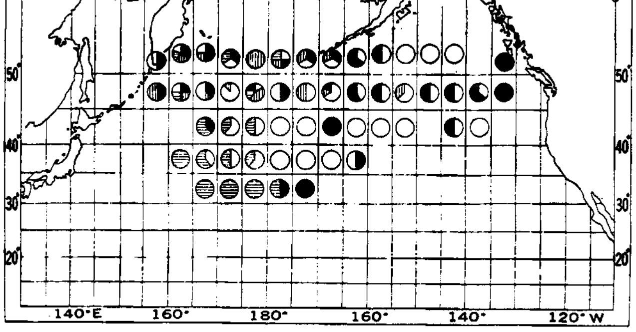

Fig. 6. Approximate occurrence of food organisms of baleen whales in terms of percentage figures.

Although this is a quite preliminary and tentative estimate, it does indicate a method of approach for considering animal populations from the stand point of production ecology or biological environment through the study of whale food. We believe that the sei whale stocks of the North Pacific and the Antarctic could be compared by a similar methodology.

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SC/SP 74/Doc 25

Review of the Occurrence of Bryde's Whale in the Northwest Pacific

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Abstract

The occurrence of the Bryde's whale in the northwest Pacific was known to science in 1952, but this species has been hunted from about two hundred years ago, by net whaling in old days and later by modern whaling. There are four major whaling grounds for this species on the coast of Japan, i.e. waters off Bonin Islands, Sanriku, Wakayama, and west Kyushu. Recent pelagic whaling operations have shown that this species is distributed widely in the North Pacific.

Two forms of the Bryde's whale may occur on the coast of Japan, but inshore form whales were only recognized from baleen plates obtained from Kyushu. Differences between *edeni* and *brydei* are discussed in relation to the shape of the rostrum.

INTRODUCTION

It was first noticed in 1952 that the external characters of the so-called sei whales in the waters off the Bonin Islands were more closely related to the Bryde's whale (*Balaenoptera edeni/brydei*) than to the sei whale (*B. borealis*) (Omura, Nishimoto and Fujino, 1952). Additional studies on external characteristics (Omura and Fujino, 1954) and skeleton (Omura, 1959) confirmed that the Bryde's whale occurs in the northwest Pacific.

The most conspicuous external characteristic of the Bryde's whale is the presence of three ridges on the head, compared with the one median ridge of the sei whale (Omura, 1962b). Other characters which separate the Bryde's whale from the sei whale are:

(1) In the sei whale, ventral grooves end at about mid-body, but in the Bryde's whale they end at or behind the umbilicus,

(2) The bristles of the baleen plates are brownish and coarse in the Bryde's whale, but white and very fine and curled in the sei whale (Omura, 1966).

The above characters are uniformly recognized on Bryde's whales from other oceans, but there still remains a question as to the shape of the baleen plates. The baleen plates of the Bryde's whale from the coast of Japan are much shorter than those of the sei whale, and the two species can be distinguished by this character alone (Omura and Fujino, 1954). Much longer baleen plates, however, were recognized in whales from South Africa (Olsen, 1913; Best, 1970) and from Brazil (Omura, 1962a). Best (1970) reported the presence of two forms of the Bryde's whale on the west coast of South Africa. These are an 'inshore form' with long baleen plates like the sei whale and an 'offshore' form with broader baleen plates.

DISTRIBUTION AND MOVEMENTS

Although the Bryde's whale was first recognized in the North Pacific in the waters off the Bonin Islands, it is also distributed on the coast of west Kyushu, off Wakayama, and Sanriku. During a period from November 1935 to July 1936 all of the so-called sei whales taken at Okochi (west Kyushu), and Oshima (Wakayama) were Bryde's whales, judging from the length of the ventral grooves (Omura and Fujino, 1954). In the four years from 1955 through 1958, only Bryde's whales were taken in these waters and no sei whales (unpublished data). It is considered, therefore, that the sei whale does not migrate to the south and west coasts of Japan and that it moves from the Bonin Islands northwards directly to Sanriku and further north (Omura, 1959).

In the old days of net whaling the Bryde's whale was called Iwashikujira or Katsuwokujira. As to the origin of these names Otsuki (1773–1850) mentions in his undated manuscript (printed later in 1925) that Iwashikujira was so named because this whale gathers and feeds on Iwashi or anchovy (*Engraulis japonica*), and Katsuwokujira because it resembles Katsuwo or skipjack (*Katsuwonus pelamis*). It is not certain why this whale resembles Katsuwo, but presumably the presence of ridges on the head of the whale would recall to fishermen the longitudinal stripes on the fish body. In any case the seas off Wakayama and Kochi were known as good grounds for skipjack.

Nemoto (1959) described that the anchovy comprises the greater part of food of the Bryde's whale off Oshima, especially in June and July, whereas the euphausiid *Euphausia similis* dominated in the stomachs of whales taken in May. He also found a good relation between the catch of the Bryde's whale and the abundance of anchovy in these waters in June 1958.

There remains a picture scroll of whales and whaling in Taiji in Wakayama, named Geirui Emaki (picture scroll of whales), which contains a picture of Katsuwokujira. In this picture the ventral grooves end behind the umbilicus of the whale body (Fig. 1), which is one of the main characters separating the Bryde's whale from the sei whale.

In the waters off Sanriku the Bryde's whale intermingles with the sei whale, but the former species lives in warmer waters of about 20°C or more, whereas the latter species prefers colder waters below this temperature and moves further north (Omura and Nemoto, 1955).

As stated already, the Japanese name Iwashikujira was originally given to the Bryde's whale, but as modern whaling shifted to Sanriku whalemen confused it with the sei whale, and now this name is only applied to the latter species. Later the Japanese name 'Nitarikujira' was proposed for the Bryde's whale (Omura, 1959), but 'Katsuwokujira' would be the right name for this species.

In 1910 Andrews visited Japan and investigated *Iwashi Kujira* (Sardine Whale) at Oshima, Kuishui (= Kii Province = Wakayama prefecture) and at Aikawa (= Ayukawa), Rikuzen (a part of Sanriku) and about 75 specimens of the *Iwashi Kujira* came under his observation (Andrews, 1916). It is possible, however, most of his observations were made at Aikawa, at least his whales nos. 19–75, judged from the

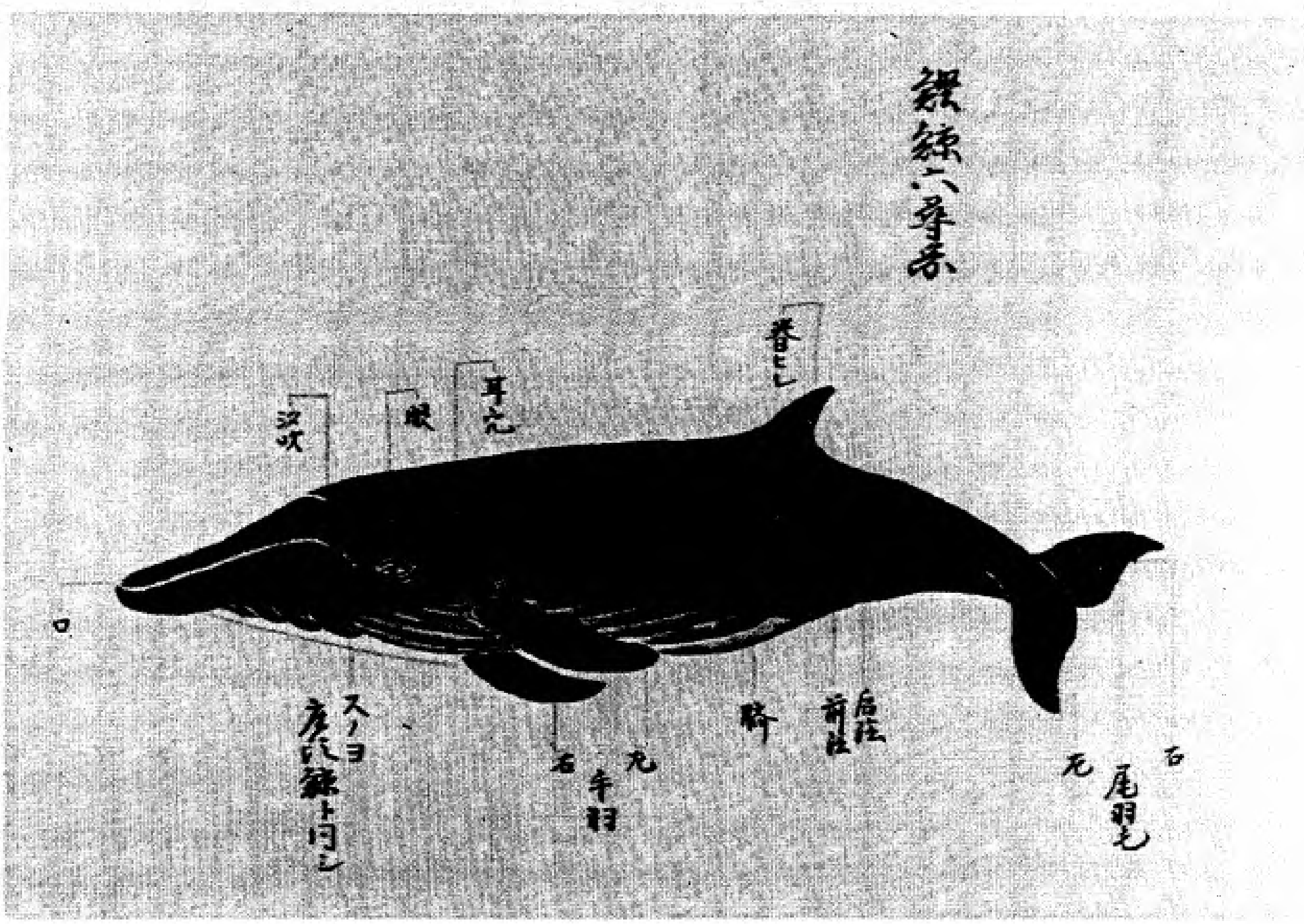

Fig. 1. Katsuwokujira in Geirui-Emaki (picture scroll of whales) by Yuboku. Note the ventral grooves extend beyond umbilicus, suggesting this whale belongs to Bryde's whale rather than sei whale.

description on pp. 338–40. He also presents many photographs of *Iwashi Kujira* processed at a landstation, but all of them were taken at Aikawa, except one i.e. Fig. 6 of Plate XXXVIII, which was taken at Oshima. This photograph is the inner view of a single baleen row after removal from a whale, presumably from a Bryde's whale rather than from a sei whale, contrary to his description (compare with Fig. 3 of the same Plate which is judged to be a sei whale).

Very little is known of the migrations of the Bryde's whale. Whale marking has shown the movement of a Bryde's whale from the Bonin Islands to Sanriku and there are grounds to suppose that whales off Sanriku and those off Oshima belong to the same population (Omura, 1962b). Since then three more whale marks have been recovered at Oshima, two marked in the Bonin waters and one in Sanriku (Ohsumi and Masaki, 1975). These suggest movements of the Bryde's whale from the Bonin Islands to Oshima and then to Sanriku or directly from the Bonin Islands to Sanriku. Both cases may occur, but recent catches of the Bryde's whale by pelagic operations have shown that the species is distributed very widely in the North Pacific, extending as far east as 150°W longitude. This suggests that Bryde's whales which come into the range of operation of catchers from landstations would be only a fraction of the whole population. But in general, the population or populations of the Bryde's whale, excepting those occurring on the west coast of Kyushu, are thought to follow seasonal migrations, though their ranges are more limited than those of the other balaenopterid whales. Practically nothing is known about movements of the Bryde's whale off west Kyushu.

CATCHES OF BRYDE'S WHALES BY NET WHALING

In the old days of net whaling, Bryde's whales were also taken off Wakayama and Kochi. Catch figures for various species of whales taken by Ukitsu whaling group in Kochi during a period from 1875 to 1896 were presented by Omura (1974). Recently catch figures of these whales in an earlier period from 1800 to 1841 by two groups in Kochi were made clear by Yoshihara (1974). His figures are based on old records of the tax charged for each whale taken. Nasu (1963) gives similar figures from 1849 to 1865 by Tsuro whaling group. Catches of whales in these three periods are compared in Table 1.

In comparing these figures it should be noted that the catch figures for the first period are the total of the two groups which operated in Kochi, but those for the second and third periods concern only one group, though two groups were in operation in this period too. Therefore average per group is shown for the first period in brackets. In the first period the main whale species hunted were the right, humpback and gray whales and the catch of fast swimming whales such as blue, fin and Bryde's whales was insignificant. But in the second and third periods the

Table 1

Catch of whales by net whaling in Kochi.

Period	Right	Humpback	Gray	Blue	Fin	Bryde's	Total
Total catch							
1800–1841[1]	346	587	225	4	–	7	1,169
1849–1865[2]	19	209	101	5	–	35	369
1875–1896[3]	21	126	64	55	23	81	370
Average per year							
1800–1841[1]	8.2	14.0	5.4	0.1	–	0.2	27.8
(Average per group	4.1	7.0	2.7	0.05	–	0.1	13.9)
1849–1865[2]	1.1	12.3	5.9	0.3	–	2.1	21.7
1875–1896[3]	1.0	5.7	2.9	2.5	1.0	3.7	16.8

[1] Total of two groups operated, Tsuro and Ukitsu.
[2] Catch figures of Tsuro whaling group.
[3] Catch figures of Ukitsu whaling group.

catches of right whales declined considerably, possibly due to a decreased stock of this species, affected by the operation of the American whale fishery in the northwest Pacific. It is possible that in order to cover the decreased catch of the right whale, fishermen gradually paid more attention to the blue, fin and Bryde's whales. Catches of humpback and gray whales increased in the second period, but in the third period they decreased to the levels of the first period.

TWO FORMS OF THE BRYDE'S WHALE

Best (1970) reported that two distinct forms of the Bryde's whale occur on the west coast of South Africa, termed 'inshore' and 'offshore' forms. A morphological difference between the two forms is in the shape of the baleen plates. Baleen plates of inshore whales are similar to those of the sei whale, but those from offshore whales are broader.

Bryde's whales from the Bonin Islands waters resemble whales of the offshore form. Whales from Sanriku and Oshima also resemble offshore whales, having broader baleen plates. But a question still remains as to the whales occuring on the west coast of Kyushu. On the west coast of South Africa the body size at sexual maturity as well as full grown size are smaller in the inshore form than in the offshore form. Food is also different between the two forms. Omura (1962b) examined the size distribution of Bryde's whales taken on the coast of Japan in the years 1955 to 1960, separating them into three groups of Sanriku, Oshima, and west Kyushu. Whales from west Kyushu were smaller by 3 to 4 ft than whales from other localities, suggesting they belong to a different group or population.

I accidentally obtained a baleen plate of a whale of the inshore form in December 1970. In that month I went to Taiji, Wakayama, with T. Kasuya in order to investigate skeletons of the right whale kept at the Whale Museum. On the way back to Tokyo we had a rest at a restaurant in Katsuura, a nearby city of Taiji and from where we returned to Tokyo by train. At the restaurant we observed a baleen plate on the wall, hanging as an ornament. The surface of the plate was polished and a few lines of a Japanese poem were written on it with paint. The shape of this baleen plate is similar to that of the sei whale, but the colour of the plate and the bristles is diagnostic of the Bryde's whale. Without doubt this baleen plate was taken from an inshore whale.

The master of the restaurant explained to us that such baleen plates were sold until some years ago at souvenir shops in Katsuura. These are not the product of the city, but they were sent from Kyushu and because whaling had stopped there, no baleen plates were sold in the city now.

Whaling on the west coast of Kyushu has not been conducted continuously. Since 1950 whaling has been carried out during the periods 1955 to 1961, 1964 to 1967, and from 1972 to the present. Catches of Bryde's whale in these periods were: first period 105 (average 15 per year), second period 32 (average 8), and total for 1972 and 1973 of 72 (average 36).

The whale from which the baleen plate in question was obtained was possibly taken in the second period. The Far Seas Fisheries Research Laboratory has collected baleen plates from Kyushu in 1973 and 1974. I had a chance to observe some of these baleen plates and noticed that both types of baleen plates are included in the collection. The food of the Bryde's whale in these waters is dominated by anchovy and horse mackerel (Nemoto, 1959), but the problem is very complicated and future study is needed.

Best (1970) showed a list of the characteristics which separate the two forms of Bryde's whales off South Africa. There are good reasons for separating the two forms on morphological, physiological, and environmental grounds, in addition to baleen plate shape. Soot-Ryen (1961) found more pronounced differences in various ratios of the cranium between *brydei* and *edeni* than between the two and *borealis*, and concluded that until the external characters and the baleen plates of *edeni* are described, there are reasons to keep the two nominal taxa separate. But his grouping of the specimens into *brydei* and *edeni* is arbitrary and needs further consideration, and the baleen plates of *edeni* have already been described by Anderson (1879).

In connection with the difference of baleen plates between the two forms of the Bryde's whale, however, the shape of the rostrum of the skull should be considered. One of the main differences between the skull of the sei and Bryde's whales is in the downward curving rostrum of the sei whale, compared with the flat rostrum of the Bryde's whale. Omura (1962a) gives a figure showing a cross section of the rostrum of these two species. It is clear from this figure that the inferior surface of the right and left maxillaries is more concave in the sei whale than in the Bryde's whale. This fact coincides with the long and narrow baleen plates of the former and the short and broad baleen plates of the latter species. It is possible, therefore, that the inshore form of the Bryde's whale has a curved rostrum, similar to that of the sei whale.

Most skulls of the Bryde's whale hitherto reported have a flat rostrum, but Junge (1950) reports that in the specimen in the British Museum the rostrum is more curved to the rostral side. The specimen of *Balaenoptera edeni* stranded at Thaybyoo Choung, Burma, had a much less downward shelving rostrum (Anderson, 1878). It had short baleen plates about 12 inches in length and a maximum breadth at the base of 6 inches, suggesting that this whale belonged to the offshore form.

In the Pulu Sugi specimen of Junge (1950) the rostrum was flat, though no baleen plate has been preserved. Berry, Wells and Ng (1973) have reported on a Bryde's whale from Malaysian seas. This whale was washed into the mangroves at Kampong Sungei Layang, five miles south of Morib, in May 1972. They presented two photographs in their report, one showing the head of the whale which wedged among mangrove trees and the other a baleen plate cut from the whale by a villager. It is clear that this whale has a flat rostrum and three ridges on the head. The baleen plate is short and broad and very similar to those obtained from the Bonin Islands. Berry *et al.* also mentioned that there were four more strandings of Bryde's whales in Malaysian seas in the past, including the Pulu Sugi specimen of Junge (1950). It is possible, therefore, that the Pulu Sugi specimen also had short and broad baleen plates, and presumably ridges were also present on the head. Possibly these whales are all *edeni*.

All Bryde's whales on the coast of Japan, but excluding those on the west coast of Kyushu, also belong to *edeni*, though Soot-Ryen (1961) treated some of them as *brydei*. The specimen of Lönnberg (1931) from South Africa and that of Soot-Ryen (1961) from Curacao also have flat rostrums. But Olsen (1913) reported longer baleen plates and his finding was based on whales of the inshore form, as already pointed out by Best (1970). If it should be proved in future that the two forms are subspecies, therefore, the name *edeni* should be assigned to the offshore form and *brydei* to the inshore form.

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Yuboku. Undated but probably written towards end of 17th century. *Geirui Emaki* (picture scroll of whales) (in Japanese).

SC/SP 74/Doc 26

Synopsis of Biological Data on the Sei Whale and Bryde's Whale in the Eastern North Pacific

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Abstract

Sei whales *Balaenoptera borealis* occur in the California current off central California (37° – 39° N lat) mostly during late summer and early autumn. They winter in offshore waters between 18° and 36° N lat. In summer and autumn they feed mostly on anchovies *Engraulis mordax* (57%) and krill *Euphausia pacifica* (30%). They are often heavily infested with stomach worms *Anisakis simplex* and liver flukes *Lecithodesmus spinosus*, and 7% of them are infected with a disease that causes loss of the baleen plates. Sexual maturity is attained at an average age of 10 years, at a mean body length of 13.3 m (43.5 ft) for females, 12.8 m (42.0 ft) for males. The annual ovulation rate is 0.70, and the pregnancy rate is 0.36. Calving occurs from September to March, with a peak in November, after a 12.7 month gestation period. Lactation lasts about 9 months. Estimated annual mortality after sexual maturity is 0.088 for females, 0.103 for males. Catch per unit of effort suggests a 75% decline in population from 1960 to 1970.

Bryde's whales *B. edeni* are year round residents of inshore waters of western Mexico north to 26° 12'N lat.

INTRODUCTION

This report is a synopsis of selected portions of a manuscript in preparation on the biology of the rorquals in the California Current region of the eastern North Pacific.

This study is based on data derived from four sources: (1) examination of 284 sei whales processed by the shore whaling stations of the Del Monte and Golden Gate fishing companies of Richmond, California from 1959 through 1970 (Table 1); (2) observations on the distribution and numbers of sei whales and Bryde's whales during whale marking cruises, totalling 17 months, off Mexico and California between 18° and 38° N. Lat., from 1962 through 1971; (3) results of whale marking; and (4) analysis of the Californian catch statistics, from 1956 through 1971.

THE SEI WHALE

Distribution and movements

During the winter (December to March) I have found sei whales sparsely but widely scattered from 35°30'N, off Point Piedras Blancas, California, south to 18°30'N, 600 km. offshore in the vicinity of the Islas Revillagigedo.

During the summer (May to October) sei whales frequently range south as far as 32°47'N, in the area immediately west of the Channel Islands off southern California. A group of four was sighted on 13 June 1965 at 27°13'N, 114°31'W, off Baja California.

Off central California, sei whales are present only during the late summer and early autumn (Table 2). In some years a few arrive in late May or June, but in most years they do not show up until early July. They may be common through August and September, but they all leave by the middle of October.

We effectively marked only 10 sei whales. Two were recovered:

Marked	*Recovered*
35°30'N, 122°00'W 13 November 1962	49°56'N, 128°10'W 28 August 1966
33°14'N, 120°09'W 22 June 1965	47°43'N, 140°15'W 25 July 1969

The occurrence of different species of the parasite *Pennella* on sei whales in the western and eastern North Pacific (see *Parasites and Diseases*) suggests that the stocks on either side of the ocean do not intermingle.

Food

From June through August the dominant food of sei whales off California is northern anchovies *Engraulis mordax*. During September and October their main food is krill *Euphausia pacifica*. About 90% of the euphausiids eaten by sei whales are 0-year-class individuals, 5 to 10 mm long, hatched in the early summer, rather than the adult 1-year-class individuals which are 20 to 25 mm. long.

Table 1

Number of sei whales examined, California.

Year	Males	Females	Total
1959	4	15	19
1960	13	11	24
1961	12	14	26
1962	3	16	19
1963	30	60	90
1964	4	8	12
1965	2	9	11
1966	21	33	54
1967	1	1	2
1968	4	9	13
1969	5	5	10
1970	2	2	4
Total	101	183	284

Sei whales are more euryphagous than the other large rorquals in Californian waters (Table 3). Their extremely fine baleen fringe permits them to feed on smaller food species than the other rorquals do, such as copepods. However they also feed on larger fishes such as sauries, *Cololabis saira*, and jack mackerel, *Trachurus symmetricus*, that the other species never feed on.

The differences in food habits among the larger species of rorquals imply that the sei whale should be able to respond to a decrease in abundance of the other species by increasing and occupying most of the vacant feeding niche, but that the other species – particularly the extremely

Table 2

Catch of sei whales by 10-day periods, 1956–77.

10-day period beginning	Catch
16 May	1
26 May	0
5 June	5
15 June	16
25 June	39
5 July	51
15 July	13
25 July	40
4 August	37
14 August	34
24 August	43
3 September	28
13 September	37
23 September	21
3 October	19
13 October	2

stenophagous blue whale – would respond very little to a decrease in abundance of sei whales.

Parasites and diseases

Ectoparasites and epizoites are scarce on sei whales. The following five species were found at the indicated frequencies of infestation:

Cocconeis ceticola – scarce.

None of the whales bore a heavy diatom film.

Pennella sp. – 8.1%

The species of *Pennella* found on Californian sei whales differs from *P. balaenopterae* found on local fin whales, and differs markedly from *P. antarctica* found on Japanese sei whales (Andrews, 1916).

Table 3

Stomach contents of rorquals (Tr. = trace (<0.5%)).

Food Species	Frequency of occurrence (per cent).			
	Sei	Fin	Blue	Humpback
Engraulis mordax (northern anchovy)	57	7	–	60
Euphausia pacifica (krill)	30	86	95	40
Cololabis saira (Pacific saury)	9	Tr.	–	–
*Sebastes jordani** (rockfish)	3	Tr.	–	–
Calanus pacificus (copepod)	2	–	–	–
Sardinops sagax (Pacific sardine)	1	–	–	–
Trachurus symmetricus (jack mackerel)	1	–	–	–
Thysanoessa spinifera (krill)	–	9	5	Tr.
Clupea harengus (herring)	–	–	–	1
Total number of stomachs containing food	230	481	19	215

*All immature individuals which, unlike adults, school in offshore waters.

Coronula reginae – 0.4%

Conchoderma virgatum – 0.4%

Xenobalanus globicipitis – 9.0%

Lampetra tridentata – 100.0% (scars only)

All except the youngest sei whales were very heavily scarred by the characteristic bites of the Pacific lamprey (Pike, 1951).

Remora australis – 0.8%

On the baleen plates the minute copepod *Balaenophilus unisetus* is often abundant.

Endoparasites are much more frequent and abundant in sei whales than in other species of large whales in Californian waters. Three of the eight species produce obvious pathogenic effects. I found the following frequency of occurrence of each species in sei whales:

Anisakis simplex – 59% (stomach)

This roundworm is often abundant; in one stomach I estimated over 100,000 individuals! In one whale these nematodes had invaded the liver, which had undergone pathological degeneration to such an extent that it might have ultimately caused death.

Crassicauda ?crassicauda – 8.9% (kidneys)

These nematodes sometimes occlude the main urinary duct in the kidney and may cause calcification of the surrounding tissue.

Phyllobothrium delphini – 22.7% (blubber)

Diplogonoporus balaenopterae – 5.3% (intestine)

Tetrabothrius affinis – 1.8% (intestine)

Bolbosoma turbinella – 40.2% (intestine)

Bolbosoma balaenae – 0.5% (intestine)

Lecithodesmus spinosus – 37.9% (liver)

Infestations of this large fluke are usually accompanied by hardening of the tips of the liver lobes.

A disease of the baleen plates afflicted 7% of the sei whales taken off central California (Rice, 1961). This unique disease results in the progressive shedding of the baleen plates and their replacement by an abnormal papilloma-like growth. In one case all normal baleen plates were missing. The epidemiology and etiology of this disease are unknown. Histological studies revealed the presence of tiny granular structures that resemble bedsonia (*Chlamydia* sp.). Attempts to isolate and culture the causative agent were unsuccessful. None of the diseased animals appeared emaciated. Most of them had fish in their stomachs, but none had euphausiids or copepods. Because of its high incidence and severity, this disease might cause significant mortality. This disease has never been reported in sei whales elsewhere in the world, nor in any other species of whale, with the possible exception of an Antarctic fin whale (Tomilin and Smyshlyaev, 1968).

Age and growth

Because they are small and fragile, the ear plugs of sei whales are difficult to extract, section, and read. Therefore counts of ear plug growth layers are available for only 80% of the males and 72% of the females examined. Errors in counting may amount to plus or minus 20%. Mean ages based on growth layer counts are probably fairly reliable, but extremes have little significance. In the absence of direct evidence, I have assumed as a working hypothesis that two layers are formed the first year, one each year thereafter.

Fitting a growth curve to the body length/age data

(Table 4) is rather meaningless because of gunner selection against the smaller, younger animals.

The criterion for sexual maturity in females was the presence of a corpus luteum or corpus albicans in the ovaries. In males it was a combined testis weight exceeding 2.5 kg, a figure established by histological examination of a subsample. Both sexes attain sexual maturity at a mean age of 10 years (11 growth layers), at a mean length of 43.5 ft. (13.3 m) for females and 42.0 ft (12. 8 m) for males.

Most of the animals of both sexes with 25 or more ear-plug layers were physically mature, as shown by their completely ankylosed vertebral epiphyses. At this stage, females average 49.3 ft (15. 0 m) in length and males averaged 44. 9 ft (13. 7 m) in length.

The female reproductive cycle

Ovulation. The overall mean frequency of ovulation in sexually mature females may be estimated by comparing the number of corpora lutea and corpora albicantia in the ovaries with the number of growth layers in the ear plug (Table 5). The simplest way to do this is with the formula

$$R = \frac{(\Sigma Y)-N}{(\Sigma X)-AN}$$

where R = ovulation rate
Y = number of corpora
X = number of ear plug layers
A = mean value of X when Y equals one
N = sample size.

This result is an overall estimate of 0. 70 ovulations per year. The data (Table 5) further suggest that the rate may be slightly higher than 0.70 in females with 25 or fewer ear plug layers, and considerably less in females with more than 25 layers.

This estimate is in close agreement with the estimate of 0.69 per year for Southern Hemisphere sei whales which Gambell (1968) made by using a different method.

The sample, collected from June to October, included no females that had recently ovulated.

Pregnancy. The sample of foetuses represents only four months during mid-pregnancy. The monthly means of the body lengths (Table 6) agree closely with the curve fitted by Laws (1959) to Mizue and Jimbo's (1950) data on North Pacific sei whales. This growth curve, which accelerates in late pregnancy, would intercept the estimated mean length at birth (4.4 m) on 10 November.

Gambell (1968) fitted a straight line to the monthly mean lengths of Southern Hemisphere sei whale foetuses during mid and late pregnancy. His line, if applied to my data, would result in a projected mean birth data about a month later than that projected from Laws' curve. Gambell's line does not accurately depict foetal growth, however, because he did not allow for the fact that during late pregnancy the monthly means become increasingly biased towards the smaller foetuses as an increasing number of the larger ones are born.

Examination of the monthly modal lengths (Gambell, 1968) reveals that Southern Hemisphere sei whales also show accelerated foetal growth in late pregnancy.

The projected birth dates for all the California foetuses show that the calving season is prolonged, extending from September to March (Table 7).

Laws (1959) estimated the total gestation period as 12.0 months. I have previously (Rice and Wolman, 1971) pointed out the error in Laws' estimate of the duration of the period of early embryonic growth, which he termed t_0, following Huggett and Widdas (1951). A reasonable extrapolation of the latter authors' data yields an estimate of roughly 60 days for t_0, rather than Law's estimate of 39 days. I therefore estimate the total gestation period as about 12.7 months.

Lactation. Although International Whaling Commission regulations prohibit killing females accompanied by calves, moderate numbers of lactating females were taken from June through August, whereas only one was taken during September and October (Table 8). Since the majority of calves are born by the end of November (Table 7), these data suggest that lactation lasts at least nine months, after which the females either cease lactating or move out of the study area.

The resting period. Since we have estimates of the duration of pregnancy and lactation, the duration of the resting period can be estimated from the annual pregnancy rate.

The observed pregnancy rate (Table 8) will be higher than the true rate because of the bias against lactating females. To estimate the true rate, I have assumed that the number of lactating females in the population equals the number of pregnant females until August, after which lactation apparently ends. The resulting estimate of the annual pregnancy rate is 0.36.

This indicates that the great majority of females become pregnant only once every three years, and that very few conceive two years after their previous conception. The lack of any females that were simultaneously pregnant and lactating indicates that females rarely if ever conceive again after only a one year interval. Of course on frequent occasions the interval between successive conceptions may be more than three years. However, the reproductive cycle of the majority of sei whales off California appears to be as follows:

Pregnancy	12.7 months
Lactation	9.0 months
Resting	14.3 months
Total	36.0 months

The male reproductive cycle

From June through October, sexually mature males showed no significant changes either in the weight of both testes ($\bar{x}$ = 6.4 kg) or in the mean diameter of their seminiferous tubules ($\bar{x}$ = 149 micra). Increases in both parameters are suggested by the October data–9.8 kg (N = 4) and 201 micra (N = 1)–but they are too few to be conclusive.

Mortality rates

I used Chapman and Robson's (1960) formula to calculate mortality rates for the frequency distribution of ear plug layer counts (Table 4). Since there is selection against the smaller animals, I calculated the rate only for those animals with ear plug layer counts of at least eleven–the mean number at sexual maturity. The resulting estimates of the annual total mortality rate are 0.088 for females and 0.103 for males.

Population trends

The Californian whalers made no real effort to take sei whales until 1959, after the depletion of the humpback

Table 4

Body length versus number of layers in ear plugs of sei whales.

Body length (ft.)	Number of layers in ear plug																																											
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Females (N = 131)																																												
52																1				1																								
51																1			1						1	1																		
50								1							1						1	2			1			1					1	1			1							1
49								1					1	1	1		1	1	3		1		1		1		1	1	1	1	1					1								1
48							2			3			1	2	1	1	1	1	3	1			1				1				1													
47										4	1	1	2	1	1	1		2		3				1			1		2															
46				1			1	3		1		1	2		1		1		1																									
45			1		3		1	1		1	1	2	1	1										1																				
44						1	1	1		1																																		
43				2	1	1			1	1	1			1				1																										
42			1			1	1	1	2																																			
41				1	1																																							
40				2	1	1		1																																				
39				1																																								
38		2			1																																							
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35																																												
34		1																																										
Total		3	2	7	7	4	6	9	3	11	3	4	7	6	5	4	3	5	8	5	2	2	2	2	3	1	3	2	3	1	2		1	1		1	1							2
Males (N = 81)																																												
47																1	1								1		1												1					
46				1				1						1	1		2			2				1							1													
45						1	1		4	1		2			2					1			3	1		1						1			1									
44						1	2	2	3	2		3				1			2	1			1		1												1							
43			2	1				1	1					1	1				1			1																						
42	1			1			1	1	1	1		1																																
41					1	1	2	2																																				
40																																												
39		1	1					1																																				
38		1																																										
37												1																																
Total	1	2	3	3	1	3	6	8	9	4		7		2	4	2	3		3	4		1	4	2	2	1	1				1	1			1		1		1					

Table 5

Number of corpora lutea and corpora albicantia in ovaries versus number of layers in ear plugs of sei whales

No. of corpora	Number of layers in ear plug																																			
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
17																								1												
16																												1								
15															1									1												
14																		1							1				1							1
13															1		1											1		1		1				
12																	1																1			
11																																				
10														1					1									1		1						
9									1									2	1			1	1			1									1	
8							1						2				1	1	2		1			1			1									
7												1		1	1			1		2						1	1									
6							1		1		1	1						3			1															
5									1			1	1			1			1			1	1													
4									2					1	1		1																			
3				1		2	2		2	1	2	1	1	1		1																				
2				1		1	1		2		1	2				1										1										
1					1	2	3		1	2		1	1																							
0	3	2	7	5	3	1	1	3	1																											

Table 6

Mean body length, by month, of sei whale foetuses.

Mean date	Mean length (m.)	No.
24 June	1.31	4
14 July	1.67	25
15 August	2.09	9
16 September	2.93	20

Table 7

Projected birth dates of sei whale foetuses.

Month	Number	%
September	2	3
October	22	38
November	22	38
December	6	10
January	5	9
February	–	–
March	1	2
Total	58	100

Table 8

Reproductive status of sexually mature female sei whales.

	Number			
Month	Pregnant	Lactating	Resting	Total
May	–	–	1	1
June	3	1	4	8
July	22	8	14	44
August	9	8	16	33
September	19	1	13	33
October	–	–	12	12
Total	53	18	60	131

Table 9

Sei whale catch per unit of effort (C/E).

Year	Catch	Effort*	C/E
1956	–	–	–
1957	1	294	0.003
1958	2	443	0.005
1959	37	610	0.061
1960	47	765	0.061
1961	51	685	0.074
1962	22	685	0.032
1963	96	685	0.140
1964	13	685	0.019
1965	22	650	0.034
1966	61**	567	0.106
1967	3	411	0.007
1968	14	411	0.034
1969	10	411	0.024
1970	4	274	0.015
1971	2	274	0.007

*Gross number of catcher's day's work, June to October only.
**Excluding one whale taken in May.

whales which were larger and easier to catch. The catch of sei whales per unit of effort (Table 9) declined about 75% between 1960 and 1970, but because of large year to year fluctuations, little confidence can be placed in the calculated rate of decline.

THE BRYDE'S WHALE

Distribution and movements

Bryde's whales are year-round residents of the inshore waters from 26°12'N on the west coast of Baja California south at least as far as the Islas Tres Marias (21°N). They range all across the southern end of the Gulf of California, and I have received reports of them in the northern part of the gulf. There is one record from La Jolla, California (Morejohn and Rice, 1973).

Food

Off southern Baja California I have observed Bryde's whales feeding on the red crab, *Pleuroncodes planipes,* an anomuran crustacean that often lives in dense shoals at the surface. I have also seen them apparently feeding on schools of anchovies (presumably *Engraulis mordax*).

Population trends

A few Bryde's whales were taken by floating factories between Bahia San Juanico, Baja California, and the Islas Tres Marias from 1924–25 to 1928–29, and again in 1935. Since then this stock has not been exploited, and is presumably stable at the carrying capacity of its range.

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Estimates of Population Size for the North Pacific Sei Whale

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Abstract

Annual recruitment rates were estimated for the North Pacific sei whale, *Balaenoptera borealis* Lesson, using Allen's (1966) method of analyzing age composition data. Recruitment into the population apparently did not respond in a density-dependent manner following the onset of heavy exploitation in 1963. Given this result, estimates of abundance were obtained from catch per unit effort statistics and sighting indices using a variety of assessment models. Averaging the several results gave composite estimates of initial and current levels of abundance: $N_{63} = 42{,}000$ and $N_{74} = 8{,}600$. These values indicate that the North Pacific sei whale apparently has undergone a considerable decline due to exploitation.

INTRODUCTION

According to Rice (1974), the onset of heavy exploitation of whales in the North Pacific coincided with the introduction of additional floating factories beginning in 1962. However, in their review of Japanese whale research in the North Pacific, Omura and Ohsumi (1974) commented that the North Pacific sei whale, *Balaenoptera borealis* Lesson, was not significantly exploited by pelagic operations until 1963.

The effects of heavy exploitation upon this population were first assessed by means of Ohsumi's (1970) complex life history model. However, in a recent review of population estimates for this species, Ohsumi and Fukuda (1975) indicated that Ohsumi's model contained inherent difficulties involving the assumptions of the dependence of natural mortality and reproductive parameters upon population size. Because of these problems, they concluded that past applications of this model had led to overestimates of population size.

Consequently, following the example of Chapman (1974a), they applied the modified DeLury equation to catch, effort, and sighting data for the North Pacific sei whale and developed population estimates which seemed to account for exploitation in a reasonable manner. In a recent unpublished extension of their analysis, Tillman (1974) subsequently concluded that this North Pacific population had suffered a considerable decline in numbers since the onset of exploitation in 1963.

However, new biological evidence presented at the Special Meeting of the IWC Scientific Committee in La Jolla, 3–13 December 1974 (IWC, 1976), indicated that the assumption of constant recruitment inherent in the above modified DeLury analyses may not have been applicable to the North Pacific sei whale. In particular, the mean age at recruitment of this population apparently had decreased in some statistical areas. As a result, it was felt that the possibility of density-dependent changes in recruitment should be accounted for when making future assessments of the size of this population.

Thus the purpose of this paper was to estimate annual recruitment rates and ascertain if they had increased during the later years of exploitation. These results were then used to prepare new estimates of initial and current North Pacific sei whale abundance and thereby measure the decline attributable to exploitation.

ESTIMATION OF RECRUITMENT RATES

Annual recruitment rates were estimated from age composition data using Allen's (1966, 1968, 1969) method of determining the proportion of new recruits in the catch each year. His method essentially compares the ratio of the proportion in the catch of a partially recruited year class to the proportion of all fully recruited year classes with the same ratio of proportions one year later. If f is the age at full recruitment, the appropriate comparison of ratios is defined as

$$B_{a,i} = \frac{P_{a+1,i+1}/Q_{f+1,i+1}}{P_{a,i}\ /Q_{f,i}}$$

$P_{a,i}$ = proportion in the catch of the ath partially recruited age-group in year i
$Q_{f,i}$ = proportion in the catch of all fully recruited age groups from f up in year i
$P_{a+1,i+1}$ = proportion in the catch of the a+1th age group in year i + 1
$Q_{f+1,i+1}$ = proportion in the catch of all age groups from from f + 1 up in year i + 1.

The proportion of new recruits in the recruited part of the a + 1th age group in year i + 1 is then defined as

$$p_{a+1,i+1} = \frac{B_{a,i} - T}{B_{a,i}}$$

where T is the ratio between the survival rate of the recruited part of the younger age-groups and that of older (fully recruited) ages. According to Allen (1969) T is usually taken to be 1.0. The total proportion of new recruits in the exploited stock for any year i (the annual recruitment rate r_i) is finally determined as

$$r_i = \sum_{a=0}^{f-1} p_{a,i} P_{a,i}$$

It should be emphasized that this method of computation does not depend upon estimates of other parameters.

We do not have a breakdown of sei whale catches by age but we do have length data since 1963 (Table 1) and age-length keys. Two series of pelagic keys were available: pre-1967 and post-1967. The pre-1967 keys were obtained

Table 1

Length frequencies of North Pacific sei whales, obtained from NP_3 data sheets.

Year	Sex	Lengths in feet																	Total
		<39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	≥55	
1963	M	51	19	39	32	75	105	140	152	135	72	44	19	4	3	–	–	–	890
	F	57	27	30	42	40	47	54	90	64	74	62	52	32	17	12	–	–	700
1964	M	1	19	47	49	94	132	192	190	143	47	20	4	1	–	–	–	–	939
	F	1	6	22	14	24	36	50	80	92	88	81	66	23	10	1	–	–	594
1965	M	35	78	80	110	128	162	233	218	180	103	48	27	15	5	12	7	8	1,449
	F	17	63	84	68	76	79	89	114	127	104	114	95	55	24	19	10	6	1,144
1966	M	20	152	192	159	196	210	252	329	243	153	91	16	14	6	11	9	9	2,062
	F	35	147	147	81	155	140	142	229	168	214	183	119	78	33	36	7	14	1,928
1967	M	37	116	226	227	372	415	509	538	290	189	82	54	51	47	20	3	8	3,184
	F	50	127	153	174	192	204	211	310	301	289	277	182	122	122	47	10	15	2,786
1968	M	65	147	231	269	406	496	478	519	317	165	61	17	5	3	1	2	–	3,182
	F	71	119	172	141	193	203	265	287	265	275	237	166	90	39	13	3	2	2,541
1969	M	22	240	239	221	321	379	418	395	291	124	51	20	10	3	6	6	–	2,746
	F	17	169	185	153	192	162	225	222	255	277	245	158	95	31	6	5	4	2,401
1970	M	48	160	175	188	252	280	378	339	213	128	57	20	8	8	3	2	1	2,260
	F	54	136	157	168	225	205	210	177	198	237	191	131	84	42	14	9	1	2,239
1971	M	26	152	182	147	156	190	207	179	107	76	27	8	1	–	–	–	–	1,458
	F	25	138	148	117	128	118	136	93	162	152	132	94	58	27	4	–	1	1,533
1972	M	53	94	139	113	141	161	146	144	88	41	25	7	3	–	–	–	1	1,156
	F	33	85	126	89	114	88	98	107	106	105	82	60	43	26	1	1	1	1,165
1973	M	11	62	119	117	116	133	122	103	102	63	26	9	1	1	1	–	–	986
	F	14	102	98	64	59	69	68	83	89	79	60	55	15	15	2	–	–	872
1974	M	16	63	91	75	93	73	78	71	28	17	7	2	–	–	–	–	–	614
	F	15	54	89	56	53	66	61	46	51	59	56	29	21	8	1	–	–	665

from Dr H. Omura of the Whales Research Institute and the post-1967 keys from Dr S. Ohsumi of the Far Seas Fisheries Research Laboratory. From these, a key was formulated for each sex and period and used to assign an age to all sei whales of legal size for pelagic fleets (40 feet and larger). Table 2 gives the age frequency distributions obtained when the results for the two sexes are combined.

Doi and Ohsumi (1970) reported that the age at full recruitment for North Pacific sei whales was 16. The major modes of the above age frequency distributions also occurred consistently at age 16, which subsequently was used to define the age at full recruitment of this population. However, it should be noted that the proportion of catches comprised by partially recruited age-groups (Table 3) has increased over the years, which is likely to have caused the mean age at recruitment to decrease, particularly in recent years.

Table 2

Age frequency distributions of North Pacific sei whales 40 feet or greater in length, males and females combined

Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
2	5	3	11	19	24	25	28	23	19	14	13	9
3	14	10	28	47	65	63	67	63	47	34	27	22
4	27	22	56	105	130	132	136	123	97	73	61	45
5	20	19	39	67	92	96	91	80	60	46	38	28
6	22	21	42	74	98	101	95	83	63	52	40	31
7	32	29	61	104	137	139	141	125	88	68	49	40
8	37	39	70	112	162	171	161	137	97	74	58	43
9	44	41	80	132	183	185	177	156	112	85	69	51
10	38	40	64	101	157	155	141	125	86	66	51	38
11	38	40	68	110	181	161	152	132	87	68	55	40
12	54	55	95	149	216	212	194	168	114	87	72	50
13	55	55	96	156	220	222	207	179	123	95	76	56
14	42	45	74	115	215	171	161	141	91	68	57	39
15	42	45	74	106	153	144	130	109	70	53	43	28
16	67	69	113	176	265	263	236	208	135	104	81	60
17	61	64	105	170	238	233	219	181	130	97	79	54
18	59	62	104	165	239	233	215	190	131	97	80	55
19	57	64	98	150	238	224	198	168	113	86	70	48
20	46	46	79	114	162	148	135	115	75	55	46	29
21	49	52	80	120	179	169	151	126	82	62	50	33
22	55	59	96	143	209	197	177	148	99	76	62	40
23	57	62	93	145	211	208	188	158	102	77	64	41
24	56	58	92	138	245	196	179	151	94	72	62	37
25	48	48	81	121	171	165	150	128	82	64	52	34
⩾26	457	483	742	1,096	1,693	1,574	1,379	1,180	743	562	478	297
Total	1,482	1,531	2,541	3,935	5,883	5,587	5,108	4,397	2,940	2,235	1,833	1,248

The results of applying Allen's method to the age frequency distributions of Table 2 are given in Table 4. Except for a very low value in 1964 and a very high one in 1974, a clear pattern of increasing recruitment rates is not readily evident. Moreover, the great difference between beginning and ending values might just as well be due to random variation as to some density-dependent mechanism. Apparently, then, annual recruitment rates have not yet increased in response to decreased population abundance. Consequently, until additional data become available, one might assume as a working hypothesis that a constant rate applies.

Table 3

Proportion of sei whale catches not fully recruited, assuming age at full recruitment is 16 years.

Year	Percent	Year	Percent
1963	31.7	1969	36.8
1964	30.3	1970	37.4
1965	33.8	1971	39.3
1966	35.5	1972	39.5
1967	34.6	1973	40.3
1968	35.4	1974	41.7

POPULATION ESTIMATES USING CPUE DATA

Developing an appropriate CPUE statistic

The North Pacific catches of fin, sei and Bryde's whale are given by year and 10° statistical zone in Table 5. North Pacific statistical zones are defined by the following latitudes: Zone L (20°N–30°N), Zone M (30°N–40°N), Zone N (40°N–50°N), Zone P (50°N–60°N), Zone Q (60°N–70°N). These catch statistics indicate that the emphasis of North Pacific whaling apparently shifted from fin whales taken mainly in Zone P onto sei whales taken in Zone N. This shift seems to have occurred in 1967 and to have continued on until the 1974 season when Bryde's whales in Zone M seemed to be on an equal footing with sei whales in Zone N.

Table 5 also gives the proportions that Zone N catches comprised of pelagic and total North Pacific catches of sei whales. These proportions indicate that Zone N catches have been consistently large from 1967 to 1974. Table 6 indicates that Japanese pelagic effort for baleen whales has

Table 4

Estimates of North Pacific sei whale recruitment rates, r_i, utilizing Allen's (1966) method for analyzing age frequency data.

Year	r_i	Year	r_i
1963	–	1969	0.10641
1964	0.05783	1970	0.10241
1965	0.11792	1971	0.12355
1966	0.10878	1972	0.11062
1967	0.07171	1973	0.09190
1968	0.10015	1974	0.15170

Table 5

Catch statistics for North Pacific fin, sei, and Bryde's whale.

Year	Species	Pelagic catch by zone					Pelagic catch	Total catch	Proportion Zone N	
		L	M	N	P	Q			pelagic	total
1963[1]	Fin	–	–	–	–	–	2,105	2,503	–	–
	Sei	–	–	–	–	–	1,468	2,590	–	–
	Bryde's	–	–	–	–	–	–	–	–	–
1964[1]	Fin	–	–	–	–	–	3,507	3,991	–	–
	Sei	–	–	–	–	–	2,128	3,642	–	–
	Bryde's	–	–	–	–	–	–	–	–	–
1965[2]	Fin	–	–	464	2,414	20	2,898	3,165	–	–
	Sei	–	–	382	1,696	10	2,088	3,172	0.18	0.12
	Bryde's	–	–	–	–	–	–	8	–	–
1966	Fin	–	–	167	2,095	343	2,605	2,885	–	–
	Sei	–	–	573	2,906	263	3,742	4,406	0.15	0.13
	Bryde's	–	–	–	–	–	–	63	–	–
1967	Fin	–	–	791	1,205	35	2,031	2,272	–	–
	Sei	–	–	3,501	1,966	–	5,467	6,053	0.64	0.58
	Bryde's	–	–	–	–	–	–	63	–	–
1968	Fin	–	–	526	1,260	65	1,851	1,942	–	–
	Sei	–	59	4,089	772	–	4,920	5,740	0.83	0.71
	Bryde's	–	–	–	–	–	–	171	–	–
1969	Fin	–	–	890	279	–	1,169	1,276	–	–
	Sei	–	–	4,126	304	251	4,681	5,157	0.88	0.80
	Bryde's	–	–	–	–	–	–	89	–	–
1970	Fin	–	–	698	232	–	930	1,012	–	–
	Sei	–	–	3,852	163	–	4,015	4,503	0.96	0.86
	Bryde's	–	–	66	–	–	66	139	–	–
1971	Fin	–	–	525	207	–	732	802	–	–
	Sei	–	15	2,568	132	–	2,715	2,993	0.95	0.86
	Bryde's	–	638	109	–	–	747	919	–	–
1972	Fin	–	10	455	211	–	676	758	–	–
	Sei	–	828	1,265	19	–	2,112	2,327	0.60	0.54
	Bryde's	–	76	–	–	–	76	201	–	–
1973	Fin	–	5	350	62	–	417	455	–	–
	Sei	–	635	1,170	8	–	1,813	1,856	0.65	0.63
	Bryde's	526	127	–	–	–	653	724	–	–
1974	Fin	–	32	257	100	–	389	413	–	–
	Sei	–	359	862	10	–	1,231	1,280	0.70	0.67
	Bryde's	351	825	–	–	–	1,176	1,363	–	–

[1] 1963 and 1964 statistics obtained from Doi & Ohsumi (1968).
[2] 1965–1974 statistics obtained from NPI data sheets.

also occurred at consistently high levels in Zone N during the same period. Thus it was assumed that during the 1967–74 period, Zone N catch and effort data would not be biased by the shifting of emphasis from one species to another. This assumption is analogous to that made for catch and effort data of Antarctic sei whales obtained from statistical series D (Tillman and Breiwick, 1977).

Effort statistics for Japanese pelagic operations are given in Table 6. Following Holt and Gulland (1964) catching power was taken as proportional to average catcher tonnage, and the number of catcher days whaling in each season was multiplied by the average vessel size to give the corrected effort for each season.

Japanese pelagic catches from Zone N are given in the first column of Table 7. These were divided by the corrected Zone N effort for each season from Table 6. The resulting pelagic CPUE figures for Zone N are given in the second column of Table 7 and indicate that a continuing decline in sei whale abundance has occurred since 1967. Table 7 also gives the level of effort, in terms of corrected pelagic Japanese effort, required to take the total sei whale catch and was estimated as

$$X_i = C_{\text{Total},\,i}/\text{CPUE}_{N,\,i}$$

Allen's least squares method

Allen (1966, 1969) developed a computerized method for estimating population sizes which minimizes the sums of squares of the differences between actual and expected catches. Given the approximate recursion formula

$$N_i = (N_{i-1} - C_{i-1})\, e^{-M} + r_i N_i \qquad (1)$$

$$\text{or } N_i = \frac{(N_{i-1} - C_{i-1})\, e^{-M}}{1 - r_i} \qquad (2)$$

where N_i = population in numbers at start of season i
C_i = catch in numbers during season i
r_i = proportion of new recruits entering at start of season i,
M = instantaneous natural mortality rate

Table 6

Japanese pelagic effort statistics for North Pacific sei whales, obtained from NP2 data sheets.

Year	Catcher days whaling		Proportion Zone N	Average vessel size (Tons)	Corrected effort Zone N (Catcher – Ton days/10^3)
	Total	Zone N			
1965	1,554	109	0.07	656	71.5
1966[1]	1,723	183	0.11	652	119.3
1967	1,869	839	0.45	664	557.1
1968	1,876	1,454	0.78	673	978.5
1969	2,167	1,954	0.90	677	1,322.9
1970	2,903	2,273	0.78	688	1,563.8
1971	2,687	2,183	0.81	706	1,541.2
1972	2,397	1,511	0.63	712	1,075.8
1973	1,896	1,186	0.63	737	874.1
1974	2,100	1,106	0.53	745	824.0

[1] 1966 Baleen effort estimated from total Japanese pelagic effort (baleen and sperm) multiplied by the average ratio of baleen to total from 1965 and 1967 (0.5980).

the sum of the squares of differences between actual and expected catches for years 1 to T is estimated by

$$d^2 = \sum_{i=1}^{T} (C_i - qX_i\bar{N}_i)^2$$

where $\bar{N}_i = N_i - \frac{1}{2}C_i$

X_i = total effort in season i
q = coefficient of catchability.

Given estimates of r_i and M, Allen's computer routine solves for the N_1 and q which minimize d^2 and, utilizing (2), also determines the population sizes in subsequent years. This method was applied to the North Pacific sei whale data for 1967 to 1974, using values of r_i from Table 4, total catches from Table 5, and Zone N CPUE data from Table 7. As decided at the Special Meeting in La Jolla, it was assumed that the overall adult natural mortality rate M was 0.06 (IWC, 1976). Results of applying the method are given in Table 8.

As seen from the differences between actual and expected catches, the fit of the model seems quite good. The results are disturbing, however, in that they indicate a considerable decline in numbers. Equation (1) and estimates of r_i for 1964 to 1967 were used to extrapolate backwards and gave an estimate of N_{63} = 39,705. This suggests that over an 80% decline in numbers has occurred since the start of heavy exploitation of this population in 1963. The low estimates are in part due to the low M value used, but even for M = 0.075, as used by Ohsumi and Fukuda (1975), the relative decline is nearly the same:

$$N_{63} = 43{,}167 \text{ versus } N_{74} = 7{,}511$$

Quite obviously the above estimates derived by Allen's Least Squares Method should be verified by using a variety of other estimation techniques and data bases.

Chapman's modified DeLury method

Since recruitment rates apparently have not behaved in a density-dependent manner, Chapman's (1974a) Modified

Table 8

Population estimates obtained using Allen's (1966) Least Squares Method

Year	Estimated population size	Actual catch	Expected catch	Difference
1967	30,424	6,053	6,114	–61
1968	25,506	5,740	5,640	100
1969	20,832	5,157	5,082	75
1970	16,446	4,503	4,491	12
1971	12,833	2,993	3,155	–162
1972	10,420	2,327	2,619	–292
1973	8,393	1,856	1,534	322
1974	7,257	1,280	1,151	130

Table 7

Japanese Zone N pelagic catches and catches per unit effort and estimated total effort for North Pacific sei whales.

Year	Zone N		Total effort (Catcher-ton days/10^3)
	Catch	CPUE	
1965	65	(0.91)[1]	–
1966	455	(3.81)[1]	–
1967	2,085	3.74	1618.4
1968	3,110	3.18	1805.0
1969	3,381	2.56	2014.5
1970	3,071	1.96	2297.4
1971	2,287	1.48	2022.3
1972	1,221	1.13	2059.3
1973	1,089	1.25	1484.8
1974	837	1.02	1254.9

[1] Insufficient effort to calculate a reliable index.

Delury Method was adopted as one verification method. This model relates CPUE to catch removals and constant recruitments as follows:

$$U_i = qN_0 - q\,f(M, C_j, j = 1, \dots, i) \qquad (3)$$

where U_i = CPUE in season i

$$f(M, C_j, j = 1, \dots, i) = \sum_{j=1}^{i-1} C_j(1 - M)^{j-i} + \frac{1}{2} C_i$$

(the latter being called the 'adjusted cumulative catch').

If M is known, adjusted cumulative catches can be calculated and q and N_0 estimated from (3) using regression procedures. Population sizes in subsequent years can then be determined from the approximate recursion formula

$$N_i = (N_{i-1} - C_{i-1})(1 - M) + R. \qquad (4)$$

A major assumption in this model is that R, the recruitment at the beginning of each season, is constant and approximated by MN_0. For a more complete discussion of the assumptions inherent in this assessment technique, one should consult Tillman and Breiwick's (1977) review of population estimates for the Antarctic sei whale.

The results of fitting (3) to Zone N CPUE data since 1967 are given in Table 9. These estimates are somewhat larger than those for the Least Squares Method but still indicate a considerable decline in numbers. Assuming R = MN_{63} and using (4) to extrapolate backwards gave N_{63} = 45,408, which again suggests that a decline of over 80% has occurred since the start of heavy exploitation.

Table 9

Adjusted cumulative catches and population estimates obtained from Chapman's (1974) Modified DeLury Method

Year	Adjusted cumulative catch for M = 0.06 (10^3)	Population estimates R = MN_{67}
1967	3.027	30,050
1968	8.560	24,360
1969	13.323	19,306
1970	17.198	15,103
1971	19.779	11,767
1972	21.163	10,051
1973	21.915	9,064
1974	22.112	8,579

Allen's modified DeLury method

Another verification method, due to Allen (1966), utilizes estimates of M and r_i to obtain a series of modified DeLury estimates of $\bar{N}_1$. His generalized formula is given as

$$\bar{N}_1 = \frac{\sum_{i=1}^{t-1} C_i}{1 - Y_i - M \sum_{i=1}^{t-1} Y_i + \sum_{i=2}^{t} r_i Y_i} \qquad (5)$$

where average catch, $C_i = \frac{1}{2}(C_i + C_{i+1})$ and normalized CPUE, $Y_i = U_i/U_1$. The series of estimates is generated by using increasing values of t up to the maximum available. The final estimate is then obtained as the mean of the series.

The average catches and normalized Zone N CPUE data since 1967, as well as the series of $\bar{N}_{67}$ estimates obtained by this method, are given in Table 10. Population size at the start of 1967 was estimated by adding one-half the season's catch to the average value of Table 10, giving N_{67} = 33,960. Population sizes in 1963 and 1974 were then extrapolated using equation (2) and the r_i values from Table 4, giving N_{63} = 42,795 and N_{74} = 12,618. These estimates are somewhat larger than those for Allen's Least Squares Method but suggest that a 70% decline in numbers has occurred in the sei whale population since 1963.

Table 10

Input data and mean population estimates obtained from Allen's (1966) Modified DeLury Method

Year (i)	Ending period (t)	Average catch (C_i)	Normalized CPUE (Y_i)	Estimates of $\bar{N}_{67}$
1967	–	5,896.5	1.000	–
1968	2	5,448.5	0.850	33,675
1969	3	4,830.0	0.684	31,262
1970	4	3,748.0	0.524	30,202
1971	5	2,660.0	0.396	29,255
1972	6	2,091.5	0.302	28,781
1973	7	1,568.0	0.334	32,325
1974	8	–	0.273	31,031
Average				30,933

The q method

Direct estimates of mean population size during season i can be obtained using estimates of q, the catchability coefficient, and the appropriate Zone N CPUE:

$$\bar{N}_i = U_i/q. \qquad (6)$$

Estimates of q were available from two sources, Allen's Least Squares Method and Chapman's Modified DeLury Method. Table 11 gives these two estimates, which are very similar, and shows the 1967 and 1974 population sizes estimated for each, assuming size at the start of the season is equivalent to adding one-half the season's catch to the estimated mean population size. It was not possible to estimate N_{63} in this manner, but the values obtained for 1967 and 1974 are very similar to those obtained by previous methods and again suggest that a rather large decline has taken place.

Table 11

Population estimates using CPUE and the q Method

Source of q value	$\hat{q}$ (10^{-3})	$\bar{N}_{67}$	$\bar{N}_{74}$	$\hat{N}_{67}$	$\hat{N}_{74}$
Allen's Least Squares Method	0.13797	27,107	7,393	30,130	8,033
Chapman's DeLury Method	0.14401	25,970	7,083	29,000	7,723

Age and CPUE data method

Chapman (1974b) described another method of determining q if catches, and subsequently, CPUE data could be classified into age groups. This could readily be done since the age distributions of Table 2 were available.

The first step in this method was to estimate Z_i, the instantaneous rate of total mortality, from the logarithm of the ratio of the CPUE of whales aged f and older in year i to the CPUE of those aged f + 1 and older in year i + 1, where f is the age at full recruitment and is 16 for North Pacific sei whales. Table 12 gives the basic data used, and

Table 12

Catches and CPUEs of North Pacific sei whales aged 16 or older and 17 or older

	Proportion of catches		Zone N Japanese pelagic catches		Zone N CPUE	
Year	⩾16	⩾17	⩾16	⩾17	⩾16	⩾17
1967	.645	.609	1344.8	1269.8	2.414	2.279
1968	.646	.599	2009.1	1862.9	2.053	1.904
1969	.632	.586	2136.8	1981.3	1.615	1.494
1970	.626	.579	1922.4	1778.1	1.229	1.137
1971	.607	.562	1388.2	1285.3	0.901	0.834
1972	.605	.558	738.7	681.3	0.687	0.633
1973	.597	.554	650.1	603.3	0.744	0.690
1974	.583	.535	488.0	447.0	0.592	0.543

the first column of Table 13 gives the estimated Z_i values. (The negative value for 1972 was excluded from further analysis).

Since $Z_i = M + F_i$ the second step was to estimate F_i, the instantaneous rate of fishing mortality, by subtracting $M = 0.06$ from each Z_i (the second column of Table 13). A separate estimate of q was then determined by dividing F_i by the appropriate total effort from Table 7. An average q was then determined as shown in the third column of Table 13. Since $Z_i = M + qX_i$, it was also possible to obtain a regression estimate for q. The above regression method also provides the estimate $M = 0.067$, which suggests that the assumed value of 0.06 may be too low.

Table 13

Estimates of Z_i, F_i, and q obtained from the Age and CPUE Data Method

Year	$\hat{Z}_i$	$\hat{F}_i$	$\hat{q}$ (10^{-3})
1967	0.2513	0.1913	0.11820
1968	0.3152	0.2552	0.14139
1969	0.3509	0.2909	0.14440
1970	0.3877	0.3277	0.14264
1971	0.3530	0.2930	0.14488
1972	(–0.0044)	–	–
1973	0.3149	0.2549	0.17167
Average			0.14386

The two q values obtained are shown in Table 14. They are very similar to previously estimated values and yield similar estimates of population abundance for 1967 and 1974. Once again it is implied that a rather significant decline in sei whale abundance has occurred.

Table 14

Population estimates using the Age and CPUE Data Method

Estimation Method	q (10^{-3})	$\hat{N}_{67}$	$\hat{N}_{74}$
Average (q_A)	0.14386	29,000	7,730
Regression (q_R)	0.13865	30,000	8,000

POPULATION ESTIMATES USING SIGHTING DATA

Wada (1975) provided indices of abundance, derived from Japanese data for whale sightings from 1965 to 1973, which have been used to verify results obtained from Zone N CPUE data. According to Figs 1 and 2 in his data review, the research area for whale sightings remained constant while the area of pelagic harvest expanded considerably after 1971. Consequently, sighting indices should not have been biased by the recent shift in Japanese operations in the North Pacific and should be an appropriate basis for estimating sei whale abundance using Chapman's Modified DeLury Method.

Chapman's equation requires a set of linearly related stock indices and adjusted cumulative catch data. The data for 1965 to 1973 are plotted in Fig. 1 and reveal that a downward linear trend apparently occurs from 1968 to 1973. Thus 1968 was chosen as the starting year for fitting equation (3), resulting in the set of input data given in Table 15.

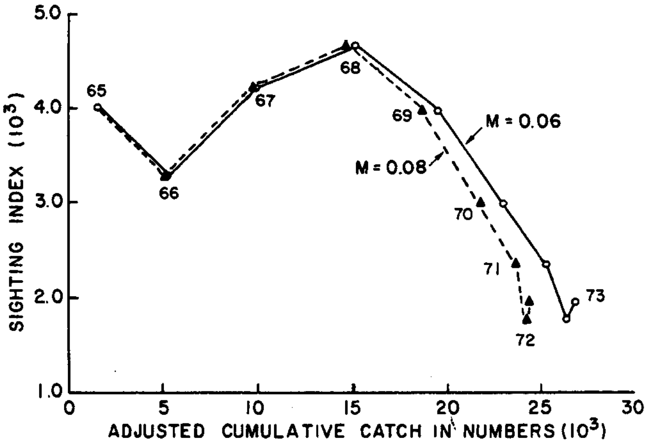

Fig. 1. Relationships between sighting index and adjusted cumulative catch for two values of M, assuming one large population of sei whales in the North Pacific.

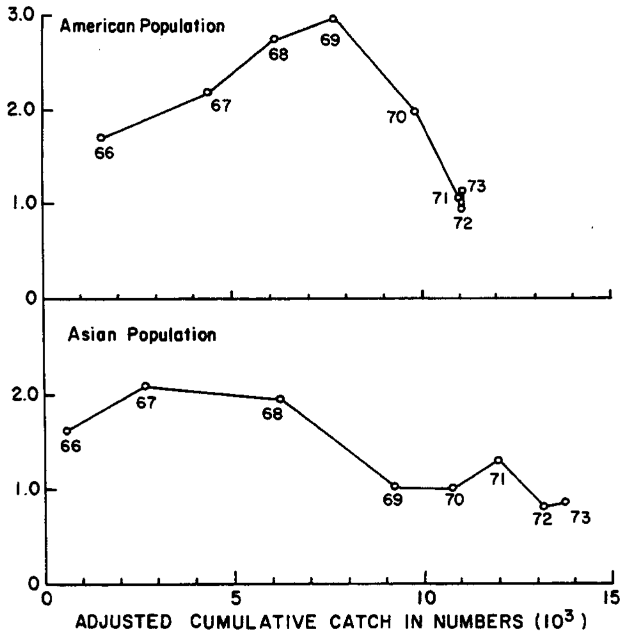

Fig. 2. Relationships between sighting index and adjusted cumulative catch, assuming M = 0.06 and two populations of sei whales in the North Pacific.

For stock assessment purposes it has sometimes been assumed that two distinct stocks of sei whales, arbitrarily divided at longitude 180°, reside in the North Pacific

Table 15

Sighting indices and adjusted cumulative catches of North Pacific sie whales, assuming one population and M = 0.06.

Year	Sighting index (10^3)	Adjusted cumulative catch (10^3)
1968	4.654	2.876
1969	3.975	7.986
1970	2.971	12.187
1971	2.341	15.074
1972	1.762	16.740
1973	1.931	17.757

(Ohsumi, Shimadzu, and Doi, 1971; Omura and Ohsumi, 1974; Rice, 1974). A secondary analysis was made using this alternative hypothesis (versus a single large stock) to determine how sensitive the results would be to population structure. Fortunately, catch data since 1966 have been reported according to major statistical area in the North Pacific. This facilitated the allocation of pelagic and coastal catches occurring west of longitude 180° to the Asian stock and those occurring east, to the American stock. Further, it was assumed that the sum of Wada's (1975) sighting indices for statistical areas II, III, and IV provided a stock index for the American side and the sum for areas V and VI, an index for the Asian side. A weakness of the above sighting indices is that they do not account for the area of coastal whaling on either side of the North Pacific. This should not preclude their use, however, as indices (rather than as direct measures) of abundance in the arbitrary stock areas chosen.

As in the single stock model, sighting indices and adjusted cumulative catches since 1966 were plotted for the two stock case (Fig. 2). A general downward trend seems to occur from 1967 to 1973 for the Asian side and from 1969 to 1973 for the American side. Thus 1967 was chosen as the starting year for fitting the Asian data and 1969 as that for the American data. Table 16 gives the input data reflecting these facts for the two assumed stocks.

Table 16

Sighting indices and adjusted cumulative catches of sei whales from the North Pacific, assuming two populations and M = 0.06.

Population	Year	Sighting index (10^3)	Adjusted cumulative catch (10^3)
Asian	1967	2.072	1.668
	1968	1.940	5.282
	1969	1.019	8.270
	1970	0.998	9.893
	1971	1.278	11.203
	1972	0.800	12.390
	1973	0.829	13.005
American	1969	2.956	1.293
	1970	1.973	3.776
	1971	1.063	5.264
	1972	0.962	5.659
	1973	1.102	5.982

Applying Chapman's equation to the above sighting data gave estimates of 1968 sei whale abundance of 26,735 for one stock, and 26,190 for two stocks. (To make estimates for the two stock case comparable to the 1968 single stock estimate, the 1967 Asian stock size was forward calculated one year and the 1969 American stock size stock was back calculated using equation (4) and determining the annual recruitment R as MN_{67} for the Asian side and as MN_{69} for the American.) Since the two estimates are very similar, application of this technique does not seem to be very sensitive to assumptions about population structure.

Since Chapman's Modified DeLury Method also estimates q, which for sighting data is defined to be a constant of proportionality rather than the coefficient of catchability, estimates of abundance were also obtained using the q Method. Given $q = 0.20087 \times 10^{-3}$ in the single stock case, population sizes estimated for the start of the 1968 and 1973 seasons were respectively 26,039 and 10,541 sei whales. The 1968 value agrees closely with the two previous modified DeLury estimates.

For purposes of comparison with the above estimates, all previously discussed techniques were used to estimate the 1968 and 1973 population sizes from Zone N CPUE data. A summary of the estimates obtained from all data sources and methods of analysis are listed in Table 17.

The estimates based upon sighting indices are remarkably similar to those obtained from Zone N CPUE data. All of the estimates within each year are quite consistent and average values were obtained for the purpose of extrapolation. Using the r_i values of Table 4 and equation (2), the 1968 value gave N_{63} = 40,110 and the 1973 value yielded N_{74} = 9,110. These estimates again intimate that a considerable decline in sei whale abundance has occurred.

Table 17

Estimates for N_{68} and N_{73} using different data and methods of analysis

Data source and method of analysis	$\hat{N}_{68}$	$\hat{N}_{73}$
Sighting data		
Chapman's DeLury		
Assuming 1 stock	26,740	–
Assuming 2 stocks	26,190	–
q Method	26,040	10,540
Japanese Zone N CPUE		
Allen's Least Squares	25,510	8,390
Chapman's DeLury	24,360	9,060
Allen's DeLury	29,210	13,220
q Method		
Using Chapman's q	24,950	9,610
Using Allen's q	25,920	9,990
Age and CPUE Data		
q_A	25,210	9,710
q_R	25,810	9,940
Average	25,990	10,060

DISCUSSION

Table 18 recapitulates all of the sei whale population estimates obtained in this paper. Within each year the estimates are quite similar, particularly the 1967 values, and averages have been obtained to give composite estimates of the initial and current levels of abundance: N_{63} = 42,000 and N_{74} = 8,600. These values indicate that the North Pacific sei whale apparently has declined to about 20% of its level prior to the onset of heavy exploitation. Assuming that the MSY level of this population occurs at about 56–58% of its initial level (Ohsumi, 1970), then the 1974 level is some 63–65% below the MSY level. Surely this evidence of a substantial decline should urge that Protection Stock status be imposed upon this population.

This conclusion might be tempered somewhat by realizing the limitations of the foregoing analysis. First, it

Table 18

Summary of all North Pacific sei whale population estimates obtained in this analysis

Method	$\hat{N}_{63}$	$\hat{N}_{67}$	$\hat{N}_{74}$	Percent comparison 1963 & 1974
Allen's Least Squares	39,710	30,420	7,260	18.3
Chapman's DeLury	45,410	30,050	8,580	18.9
Allen's DeLury	42,800	33,960	12,620	29.5
q Method				
Allen	–	29,000	7,720	–
Chapman	–	30,130	8,030	–
Age & CPUE Data				
q_A	–	29,300	7,810	–
q_R	–	30,000	8,000	–
Extrapolated from sighting data analysis	40,110	30,890	9,110	22.7
Average	42,000	30,500	8,600	20.5

did not consider the long history of Japanese coastal whaling, which between 1910 and the late 1950's accounted for an annual catch of 500 to 600 sei whales (Ohsumi *et al.*, 1971). Consequently one should not consider the 1963 population to be at its virgin level of abundance, although a modest catch sustained over a long period should have resulted in the population being at another equilibrium level somewhat below the virgin level.

Additionally, most of the estimates used in this analysis assumed that a single large stock of sei whales resides in the North Pacific. However, the sighting data analysis did examine the alternative of two North Pacific stocks, and the similarity of the estimates obtained indicates that stock structure may not be a very sensitive issue. Also, in the foregoing treatment we neglected the possibility of density-dependent changes in natural mortality, although the most commonly used hypothesis is that density-dependent effects are usually expressed through changes in reproductive parameters (Gambell, 1975). Finally no attempt was made to take into consideration possible interactions between species of whales. However, one might speculate, as Gambell has for Antarctic sei whales, that the apparent lack of a recent increase in recruitment rates could be due to the occurrence, prior to exploitation, of decreased inter-specific competition.

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Estimates of Stock Size for the Antarctic Sei Whale

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Abstract

A method for estimating stock size was developed based upon Chapman's (1974) modified DeLury method. Estimated stock sizes for the Antarctic sei whale, *Balaenoptera borealis*, were obtained from this model using three different indices of stock abundance: total catch per unit effort in series D, Japanese catch per unit effort in series D, and sei whale sighting indices. Model results were extrapolated backward to 1961/62 and forward to 1974/75 to estimate respectively stock size prior to exploitation and current stock size. Comparison of these estimates provided a measure of the decline due to exploitation which occurred within each stock. Reliable results were obtained only for the presumed stock in statistical Area III and indicated that it is now only 49 to 53% of its abundance prior to exploitation. Such a decline should at least urge that considerable restraint be employed when setting quotas for this area.

INTRODUCTION

According to the 'New Management Procedure' adopted in 1974 at the Twenty-sixth Meeting of the International Whaling Commission, Protection Stock status should be imposed whenever stock size declines below those levels providing either the Maximum Sustainable Yield (MSY) or the optimum yield. Unfortunately for many species of whales, definitive estimates of the stock size providing these yields are not yet available. Such is the case for the several stocks of Antarctic sei whale, *Balaenoptera borealis.*

However, some speculation does exist concerning 'safe' minimum stock yield levels. In a theoretical comparison of symmetrical and skewed yield curves, Gulland (1969) noted that no direct data exists which supports either curve form and concluded that, until such data were obtained, it may be unwise to allow stocks to decrease below 60–70% of unfished abundance. Moreover, Chapman (1974) suggested that, for Antarctic sei whales, 60% of the total initial stock seemed a safe level as an initial management guide.

Antarctic statistical areas are defined by the following longitudes: Area I (120°W – 60°W), Area II (60°W – 0°), Area III (0° – 70°E), Area IV (70°E – 130°E), Area V (130°E –170°W), Area VI (170°W – 120°W). If Antarctic statistical areas are treated as defining stock areas, then Chapman's (1974) results indicate that two stocks may have declined below the advised 60% level. Comparison of his estimates of initial (1961/62) and current (1973/74) stock sizes reveal that stocks in Areas II and III have declined, respectively, to 58 and 46% of their 1961/62 levels of abundance. Stocks in Areas IV and V apparently remain in good condition, having declined, respectively, to only 62 and 67% of their levels prior to extensive exploitation.

The purpose of this study has been to utilize new data made available after Chapman's (1974) analysis and to independently measure for each stock, but particularly for Areas II and III, the decline attributable to exploitation.

MODEL DEVELOPMENT

Annual Recruitment

Heavy exploitation of Antarctic sei whales did not begin until the 1961/62 season. During the 13 year period between the onset of exploitation and the start of the 1974/75 season, annual recruitment should have occurred at the equilibrium level produced by stocks in an unexploited state. This assumption can be made since the average age at recruitment, estimated to be 15 years by Nasu and Masaki (1970), exceeds the period of exploitation (Chapman, 1974).

In an equilibrium state, the annual instantaneous rate of recruitment could be considered equal to the annual instantaneous rate of natural mortality, M. Moreover, it could be assumed that M is constant, although changes in other sei whale parameters might have occurred prior to 1961/62 while fin and blue whale stocks were declining (Gambell, 1975). Using these assumptions, Chapman (1974) approximated the equilibrium level of recruitment as

$$R = MN_0$$

where R = annual recruitment to a stock
M = instantaneous annual rate of natural mortality
N_0 = stock size in numbers prior to heavy exploitation.

Changes in Stock Size

Allen (1966) developed the following interative model which relates successive stock sizes through removals and additions occurring during each intervening season.

t	*Population size at time t*
0	N_0
1	$N_1 = (N_0 - C_1)e^{-M} + R_1$
2	$N_2 = (N_1 - C_2)e^{-M} + R_2$
etc.	

This model is only an approximation since it assumes that catches, natural mortality, and recruitment proceed successively rather than simultaneously. Since the catching season is relatively short (about 0.3 year), successive application of mortalities does not seem too inappropriate for sei whales.

This model can be simplified by using Chapman's assumption that $R = MN_0$. Moreover, through appropriate application of the Taylor Series expansion, one could approximate e^{-M} as $(1 - M)$. Substitution of these gives equations in which N_t's can be expressed in terms of N_0:

t	N_t
0	N_0
1	$N_1 = (N_0 - C_1)(1 - M) + MN_0$ $= N_0 - C_1 (1 - M)$
2	$N_2 = (N_1 - C_2)(1 - M) + MN_0$ $= N_0 - C_1 (1 - M)^2 - C_2 (1 - M)$

and in general by

$$N_t = N_0 - \sum_{i=1}^{t} C_i (1 - M)^{t-i+1} \qquad (1)$$

where N_t = stock size at the start of time t
N_0 = stock size prior to heavy exploitation
C_i = catch during season i
M = instantaneous annual rate of natural mortality.

The average stock size between t and t + 1 (i.e. during a season) can be approximated by subtracting ½ of the season's catch from the stock size at the start of the season (Allen, 1966):

Interval	*Season*	*Average*
0–1	1	$\bar{N}_1 = N_0 - ½ C_1$
1–2	2	$\bar{N}_2 = N_1 - ½ C_2$

and in general as

$$\bar{N}_j = N_{j-1} - ½ C_j \qquad (2)$$

Expressing N_{j-1} in terms of (1) and substituting into (2) then gives the average stock size during season j as

$$\bar{N}_j = N_0 - \sum_{i=1}^{j-1} C_i (1 - M)^{j-i} - ½ C_j. \qquad (3)$$

Assessment Model

Indices of abundance during season j can be related deterministically to average stock size as $I_j = k \bar{N}_j$. Substituting for $\bar{N}_j$ with (3) then yields the modified DeLury equation used by Chapman (1974) and by Ohsumi and Fukuda (1975) to assess Antarctic sei whales:

$$I_j = kN_0 - k\left(\sum_{i=1}^{j-1} C_i (1-M)^{j-i} + ½ C_j\right) \qquad (4)$$

where I_j = index of stock abundance during season j
k = proportionality constant
C_j = catch in season j

and other terms are as previously defined. The summation term for catches is called the 'adjusted cumulative catch' for season j.

If M is known and a suitable series of stock index and catch data is available, then N_0 can be estimated from (4) using linear regression methods:

$$Y_i = a + bX_i$$

where Y_i = stock index for season i
X_i = adjusted cumulative catch for season i
a = $(k\hat{N}_0)$
b = k.

The desired estimate becomes $\hat{N}_0 = a/b$. In this case, $\hat{N}_0$ refers to the stock size at the start of the first season of data.

This estimate may be statistically biased. However, Seber (1973) provides a technique, based upon the Taylor Series expansion, for approximating a bias correction factor. Application of this technique gives the following estimate:

$$\hat{\text{Bias}} = -\bar{Y}S^2_{y/x} \Big/ \left(b^3 \sum_{i=1}^{n} (X_i - \bar{X})^2\right)$$

where $\bar{Y}$ = mean value of stock indices
$S^2_{y/x}$ = variance about linear regression
b = regression coefficient
n = number of years of data
$\bar{X}$ = mean value of adjusted cumulative catches.

As suggested by Seber, if the bias term exceeds 10% of the magnitude of the standard deviation of $\hat{N}_0$, it has been subtracted from the estimate of $\hat{N}_0$.

The variance of $\hat{N}_0$ and an approximate 95% confidence interval can be estimated from the above regression coefficients and their variances, using the so-called 'delta method' (Seber, 1973):

$$\hat{N}_0 \pm t\sqrt{\hat{\text{Var}}}\ (N_0)$$

where t is the 95% upper tail value of the t distribution having n – 2 degrees of freedom.

The estimated variance is

$$\hat{\text{Var}}(N_0) = (1/b^2)\,\hat{\text{Var}}(a) + (a^2/b^4)\,\text{Var}(b) + 2(a/b^3)\,\text{Cov}(a, b).$$

Value of M

From age frequency distributions obtained prior to the onset of heavy exploitation, Doi, Ohsumi, and Nemoto (1967) estimated the average M to be 0.065. This value has been used previously by Chapman (1974) and by Ohsumi and Fukuda (1975) and has been adopted for use in this study as well.

DATA ADJUSTMENTS

Fitting equation (4) has been done for statistical Areas II–V using three different indices of stock abundance. These are total catch per unit effort (CPUE) observed in Series D, Japanese CPUE in Series D, and the sighting index for sei whales as reported by Masaki (1973). (Series D is a subarea located between 40° and 50°S latitude within all six major statistical areas of the Antarctic whaling ground.) In general, CPUE statistics have been biased by the shifting of emphasis from fin to sei whales. However, in Series D, sei whale catches have been consistently large over the period of concern while fin whale catches have, generally, been quite small. Thus, bias from this source should not be a major concern.

Table 1 lists the indices used along with the starting points chosen for application of the regression procedure. Different starting points were necessitated by the facts that intensive exploitation began later in some Areas than in others and that, within Areas, collection of different statistics began at different times. In one case, that of total CPUE values for Area V, two different starting points seemed equally likely, and both were used.

Catches of sei whales are indicated by season and Area in Table 2. Assuming M = 0.065, adjusted cumulative catches were calculated from these data as indicated in equation (4). The use of different starting seasons for an Area required the recalculation of adjusted cumulative catches. For

Table 1

Indices of abundance for Antarctic sei whales by Area and season

Area	Season	Series D Total CPUE[1]	 Japanese CPUE[1]	Sighting index[2]
II	1965/66	2.378*	–	754*
	66/67	1.654	–	527
	67/68	–	–	–
	68/69	1.176	–	–
	69/70	1.619	–	195
	70/71	1.076	–	–
	71/72	0.556	–	–
	72/73	0.236	–	–
III	1965/66	1.592	1.592	636
	66/67	1.802*	2.150*	1,744
	67/68	1.161	2.171	885
	68/69	0.788	0.665	499
	69/70	0.594	0.601	236
	70/71	0.368	0.399	233
	71/72	0.376	0.502	143
	72/73	0.377	0.557	–
	73/74	0.384	0.384	–
IV	1965/66	–	–	686
	66/67	–	–	825*
	67/68	1.664	–	971
	68/69	0.875	–	482
	69/70	1.817	2.707*	878
	70/71	1.973*	2.128	761
	71/72	1.760	1.925	382
	72/73	1.604	1.777	–
	73/74	1.264	1.342	–
V	1966/67	–	–	1,503*
	67/68	2.281*	–	841
	68/69	2.029	–	656
	69/70	0.108	–	955
	70/71	0.332	–	477
	71/72	1.596*	2.539*	1,302
	72/73	1.127	2.178	–
	73/74	0.794	1.482	–

*Indicates starting points for applying modified DeLury relationship.

[1] Catch per catcher days' work, uncorrected.

[2] See Doi (1974).

example, Table 3 shows the three different sets of input values required by the three starting points used in Area IV.

RESULTS

Regression Estimates

Table 4 gives the results of applying the modified DeLury equation to the data for Areas II to V. Using the criteria of smallest confidence interval, best linear correlation, and least bias, the regression estimates for Area III apparently have the best statistical reliability. This is a fortunate result since, due to Chapman's (1974) analysis, we were primarily interested in Area III and would like to draw reliable inferences about the current status of this presumed stock. Unfortunately, the regression results for Area II, another region of potential concern, were not quite as reliable.

Examining the results of Table 4 in detail, the two estimates of N_0 for Area II are not too disparate and bracket Chapman's (1974) estimated values of 17,700 to 18,500. Both were used in the next section to extrapolate initial and current stock sizes for this Area.

For Area III, the two estimates based on CPUE are essentially the same as Chapman's estimate of 13,200. The estimates based on sightings is lower than Chapman's (15,900), but this difference is not too great, considering that our estimate uses a starting point one year later and that 2,724 sei whales were caught during the intervening season. The regression results for this Area probably provide the most reliable extrapolations.

Although the two estimates based on CPUE for Area IV are identical, we would expect some slight difference between them, owing to their different starting points. However, both are more reasonable than Chapman's estimate of 70,100. Our sightings estimate is less than Chapman's (24,100), and the difference probably cannot be accounted for by the one season difference in starting points. Despite these problems, all three estimates were used for purposes of extrapolation.

The estimate based on sightings for Area V was rejected outright as not only did it lack statistical reliability but it was also considerably lower than Chapman's estimate of 16,600. The three CPUE estimates are of the same magnitude as Chapman's (7,900), although he has discarded that value as being unreasonable. Nevertheless, our extrapolations for this Area were based upon these three low values.

Estimates of Exploited Components

To estimate initial and current sizes of exploited stock components, the estimates of stock size given in Table 4 were extrapolated backward to the start of the 1961/62 season and then forward to the start of 1974/75, thus:

$$\hat{N}_{61} = \hat{N}_{0,t} + \sum_{i=61}^{t-1} C_i/(1-M)^{i-61}$$

$$\hat{N}_{74} = \hat{N}_{61} - \sum_{i=61}^{73} C_i\,(1-M)^{73-i+1}$$

where $N_{0,t}$ is the regression estimate for starting point t given in Table 4.

Table 5 gives some results of these extrapolations which can be compared directly to Chapman's (1974) estimates of the exploited component of each stock. Considering stocks individually, our estimates of exploited components for Areas III and V seem most comparable to Chapman's values, while those for Area IV appear to be least comparable.

To obtain estimates of total exploited population size, we followed the suggestion of Chapman (1974) and added 10% of the sums for Areas II to V to account for Areas I and VI. In general, our totals for 1961/62 are very close to the range reported by Ohsumi and Fukuda (1975): 131,800 to 134,500 sei whales. However, our 1973/74 totals tend to be higher than theirs (51,900 to 54,000). Most of this discrepancy is probably due to the generally high estimates we obtained for Area IV.

Initial and Current Stock Sizes

The results of previous back and forward extrapolations were next adjusted to account for the fact that the sei whale population has an unexploited component north of 40°S., i.e. north of the Antarctic whaling ground. According to Chapman (1974), the size of this unexploited component is roughly 38.4% of the initial size of the exploited component. This amount has been added to the exploited component estimates to give the total initial (1961/62) and current (1974/75) stock sizes (Table 6).

Table 2

Catch (in numbers) of Antarctic sei whales by statistical Area

Season	II	III	Statistical Area IV	V	I & VI	Total
1961/62	1,696	427	633	406	2,031	5,196
62/63	1,812	1,457	631	430	1,173	5,503
63/64	4,459	1,984	274	1,820	158	8,695
64/65	16,076	443	1,564	2,207	90	20,380
65/66	12,722	2,724	436	1,014	691	17,587
66/67	1,540	6,865	2,826	717	420	12,368
67/68	195	2,352	2,271	3,327	2,212	10,357
68/69	188	1,771	1,030	2,156	631	5,776
69/70	1,278	1,997	1,925	474	183	5,857
70/71	640	1,065	3,967	285	196	6,153
71/72	266	1,172	2,605	1,384	22	5,449
72/73	98	600	1,685	943	538	3,864
73/74	3	391	1,537	519	1,942	4,392

Comparison of these initial and current stock sizes provided a measure of the decline due to exploitation within each Area. Consistent results have been obtained only for Area III. This stock has apparently declined considerably and is now 49 to 53% of its level prior to heavy exploitation. Some of the estimates for Area IV and V are also disturbing. For the most part, however, these two Areas, as well as Area II, seem to be in good condition, being well above the advised 60% level.

Table 3

Adjusted cumulative catches of Antarctic sei whales from Area IV, assuming different starting points and M = 0.065.

	Adjusted cumulative catches for		
Season	Sighting Index	Japanese CPUE	Total CPUE
1966/67	1,413	–	–
1967/68	3,778	–	–
1968/69	5,109	–	–
1969/70	6,221	963	–
1970/71	8,700	3,783	1,984
1971/72	11,292	6,695	5,012
1972/73	–	8,320	6,746
1973/74	–	9,335	7,864

The reasonableness of these results depends in part upon how well the model's projections of total stock size between 1961/62 and 1974/75 compared with observed trends in indices of abundance. Table 7 gives a general comparison between model results and the trends observed in stock indices (from Table 1). A good fit between the two occurs in all Areas except Area II. Thus, the model's finding that Area III has declined considerably does seem reasonable. However, it does not seem reasonable to conclude from the model that Area II is in good condition unless the stock indices for that Area are in error.

DISCUSSION

Considering all of the elements necessary to derive our results, we apparently can make reliable inferences about current stock status only for Area III. Here the presumed stock has almost certainly declined below the advised 60% level. In fact our results indicate that it may have declined below 50% of its abundance prior to exploitation. Such evidence should, at least, urge that considerable restraint be exercised in the setting of quotas for this particular Area. At most, it might suggest that sei whales in this Area should be designated a 'protected stock.'

Considering the other Areas analyzed, our results were

Table 4

Results for fitting modified DeLury relationship to data for different Areas, using different indices of abundance and starting points and assuming M = 0.065.

Area	Index	Starting season	$\hat{N}_0$ (10^3)	Confidence interval (± %)	Correlation coefficient	Bias (%)
II	CPUE (T)	65/66	14.6	49	0.59	9
	Sightings	65/66	19.0	71	0.66	12
III	CPUE (T)	66/67	13.5	3	0.996*	0
	CPUE (J)	66/67	13.2	18	0.89*	1
	Sightings	66/67	11.9	5	0.99*	0
IV	CPUE (T)	70/71	19.5	86	0.94	5
	CPUE (J)	69/70	19.5	37	0.97*	2
	Sightings	66/67	16.2	+	0.60	33
V	CPUE (T)	67/68	7.6	83	0.61	15
		71/72	4.1	56	0.998*	0
	CPUE (J)	71/72	4.6	+	0.94	9
	Sightings	66/67	5.5	+	0.47	67

\+ Indicates confidence interval exceeds ± 100%

* Indicates significant correlation ($p = 0.05$).

Table 5

Estimates (in thousands) of the size of the exploited component of the Antarctic sei whale population in 1961/62 and 1973/74.

Season	Area	Extrapolated population sizes			Chapman's (1974) estimates
		CPUE (T)	CPUE (J)	Sightings	
1961/62	II	43.0	(45.2)[1]	47.4	40
	III	21.9	21.5	20.3	25
	IV	35.9	32.6	20.3	27
	V	21.8	22.3	(22.1)	22
		122.6	121.6	110.1	114
	I & VI	12.3	12.2	11.0	
	Total	134.9	133.8	121.1	
1973/74	II	19.9	(22.1)	24.2	17.0
	III	7.0	6.7	5.4	6.4
	IV	21.5	18.2	5.8	12.9
	V	11.8	12.3	(12.1)	12.0
		60.2	59.3	47.5	48.3
	I & VI	6.0	5.9	4.8	
	Total	66.2	65.2	52.3	

[1] Values in parentheses are Area means used in place of missing observations.

Table 6

Initial (1961/62) and current (1974/75) stock estimates (in thousands) for Antarctic sei whales.

Area	Index	Exploited component		Unexploited component	Total		% comparison 1974/75 and 1961/62
		1961/62	1974/75		1961/62	1974/75	
II	CPUE (T)	43.0	21.4	16.5	59.5	37.9	64
	Sightings	47.4	25.7	18.2	65.6	43.9	67
III	CPUE (T)	21.9	7.6	8.4	30.3	16.0	53
	CPUE (J)	21.5	7.3	8.3	29.8	15.6	52
	Sightings	20.3	6.0	7.8	28.1	13.8	49
IV	CPUE (T)	35.9	21.0	13.8	49.7	34.8	70
	CPUE (J)	32.6	17.7	12.5	45.1	30.2	67
	Sightings	20.3	5.3	7.8	28.1	13.1	47
V	CPUE (T)						
	1967/68*	15.6	5.8	6.0	21.6	11.8	55
	1971/72	21.8	12.0	8.4	30.2	20.4	68
	CPUE (J)	22.3	12.5	8.6	30.9	21.1	68

*Estimates for different starting points.

Table 7

Comparison of model results with trends observed in indices of abundance for Antarctic sei whales.

Area	Model results	Trends in indices of abundance	Level of agreement
II	Decline to below 50% in 1966/67 with significant recovery for 8 years thereafter.	Decline until end of data in 1972/73; no recovery	Very poor
III	Decline to below 50% in 1972/73 with slight recovery thereafter.	Decline until 1971/72 or 1972/73 with little or no recovery thereafter.	Good
IV	Decline continues to 1974/75.	Decline until end of data in 1973/74.	Very good
V	Decline until 1973/74 with slight recovery in 1974/75.	Decline until end of data in 1973/74.	Good

tainted by one or more of the following problems: regression estimates were not statistically reliable; extrapolations were not consistent within an Area nor in agreement with previous analyses; projections of the model were not in agreement with observed trends in stock indices. Consequently, we find it difficult to make any substantive conclusions for Areas II, IV, and V or for the Antarctic sei whale population as a whole. However, some of the results obtained for these Areas were disturbing, and this should urge that new models or indices be developed which would have greater reliability and sensitivity than the methods currently used.

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Records of Sei and Bryde's Whales from the Atlantic coast of the United States, the Gulf of Mexico, and the Caribbean

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INTRODUCTION

The distribution of sei (*Balaenoptera borealis*) and Bryde's (*B. edeni*) whales in the temperate and tropical waters of the western North Atlantic has been poorly understood as a result of several factors. There has been no modern whaling of appreciable extent in these waters, so the distribution of these species is known only from strandings and rare sightings of animals at sea. Neither of these species appears to be particularly abundant in coastal waters in these areas, resulting in a paucity of records. This can be readily appreciated by examining the two major works on the large whales of these waters by True (1904) and Allen (1916). Both of these contain abundant records and data for the other species of *Balaenoptera,* but only one record for *B. borealis* (Allen, 1916). The problem has been further compounded by a lack of expertise in distinguishing *B. borealis* from *B. edeni,* and, in fact, distinguishing them from the other species of *Balaenoptera.* Since the usefulness of the data depends entirely on the validity of the identifications, and since there are relatively few records of these species, they are discussed below, giving some idea of the information available, the circumstances of the data, and the reliability of the identification.

METHODS

As noted above, one of the fundamental problems has been identifying these species. I have found the following characteristics useful in the case of stranded animals, and the identifications given in this paper are based upon them.

Balaenoptera borealis is most readily distinguished from all other *Balaenoptera* species by the very fine bristles of its baleen (about 0.1 mm in diameter at the base of the bristle, as opposed to about 0.3 mm or greater for the other species). *B. borealis* is distinguished from all the other species except *B. acutorostrata* by its relatively short ventral grooves. In these two species the ventral grooves reach a point about midway between the flipper and the umbilicus, while they reach the umbilicus in the other species. *B. borealis* is readily distinguished from *B. acutorostrata* on the basis of size, pigmentation, and the colour and texture of the baleen.

Balaenoptera edeni is most easily distinguished from *B. borealis* by its baleen, as noted above. Some baleen plates from *B. edeni,* however, are difficult to distinguish from some plates of other *Balaenoptera* species. If the dorsal surface of the head is examined, the lateral rostral grooves of *B. edeni* separate it from all other species.

The above are the critical characters used to identify the specimens listed below. I have not relied upon skeletal characters, as several of these specimens appear to be either intermediate or contradictory in some of the characters generally used to separate *B. borealis* from *B. edeni,* particularly the shape of the nasal bones. Much of the comparative work which has been done on these species has relied upon works such as Miller's (1924, 1925), in which the material described was misidentified.

INDIVIDUAL RECORDS

Balaenoptera borealis,
Eastham, Massachusetts and Corolla, North Carolina.

On 21 July, 1974, a whale stranded alive in a small boat harbour at Eastham, Massachusetts. The Coast Guard placed a line around the tail and towed the animal into deep water, where it became active and the tow line was cut. The length of the animal was estimated to be between 12 and 13 m, and a photograph received from the Eastham police department showed a high, falcate dorsal fin, suggestive of *B. borealis.* The photograph also showed a small notch in the posterior edge of the dorsal fin. On 5 April, 1975 a large balaenopterid (USNM 504244) washed ashore dead just north of the Currituck light, Corolla, North Carolina. This proved to be a 14.5 m male *B. borealis,* with a notch in the dorsal fin and about 10 m of heavy nylon line attached to the tail. The type of line and the manner in which it was tied were checked with the Coast Guard, verifying that this was the same whale that had stranded in Eastham.

Balaenoptera borealis,
Chatham, Massachusetts.

Allen (1916) recorded this specimen, which stranded in August, 1910. Local fishermen indicated that it was probably part of a school of 'finbacks' which had been seen offshore near that locality. There was a report of another specimen stranded at about the same place and time, but Allen was unable to confirm this. His photograph shows a medium sized *Balaenoptera* with a relatively large dorsal fin. The remains of this specimen were deposited in the Boston Society of Natural History and appear to have been lost, but the Museum of Comparative Zoology at Harvard possesses some baleen from this specimen, which confirms its identification as *B. borealis.* (MCZ 8031).

Balaenoptera borealis,
Cape Island, South Carolina.

In December, 1972, the United States National Museum collected the skeleton and baleen of a 13.8 m female of this species from Cape Island (USNM 486174). This specimen had probably been dead for a week or so, but the length of the ventral grooves and the very fine baleen bristles clearly indicated that it was *B. borealis.*

Balaenoptera borealis,
Gulfport, Mississippi.

Gunter and Christmas (1973) described a whale which entered Gulfport Harbour on 7 April, 1972, and stranded on Ship Island the next day. They identified it as *B. physalus* on the basis of the white underside of the flippers and flukes. Their photographs, however, clearly show an animal far too large to be a *B. acutorostrata* and with short ventral grooves. The apparent light pigmentation of the underside of the flippers and flukes is due to sloughing of skin as a result of decomposition. This record was repeated by Lowery (1974). and corrected by Gunter and Overstreet (1974).

Balaenoptera borealis,
Fort Bayou, Louisiana.

Negus and Chipman (1956) reported an 11.4 m male *Balaenoptera* which stranded near the mouth of Fort Bayou in April, 1956. They identified this specimen as *B. acutorostrata,* without providing any particular reasons, and noted that it may represent the largest one on record. Lowery (1974), however, identified this individual as *B. borealis,* on the basis of the total length of the carcass and the relative length of the ventral grooves as given by Negus and Chipman (1956), a conclusion with which I concur. The skull and other elements are in the Tulane University collection (no. 4172).

Balaenoptera borealis,
La Costa de Buen Hombre, Dominican Republic.

I recently examined a baleen plate from an animal that stranded on the northern coast of the Dominican Republic on 12 July, 1974. The very fine baleen bristles left no doubt as to its identity. The entire skeleton is preserved in the Museo Nacional de Historia Natural in Santo Domingo, as Division of Mammals no. M 121.

Balaenoptera cf. *borealis,*
Campeche, Mexico.

Miller (1928) identified a series of photographs of a skeletal characters. Photographs of the carcase, which show have examined the photographs, which are largely oblique views of a partially disarticulated skull, and am unable to confirm this diagnosis. Miller's account mentions two specimens (nos. 257 and 289), but was in error here, as the numbers refer to the exhibit case on which the specimen was lying. The photos leave no question that there was only one specimen.

Balaenoptera edeni,
Walnut Point, Virginia.

A juvenile male (8 m) of this species was described by Miller (1927) as *B. borealis,* apparently on the basis of skeletal characters. Photographs of the carcase, which show long ventral grooves and lateral ridges on the rostrum, as well as the baleen bristles, which are far too coarse for this species, indicate that it is actually *B. edeni*. These materials are catalogued in the United States National Museum as number 230307. This stranding has been cited a number of times as *B. borealis* (Kellogg, 1928; Handley and Patton, 1947), and Kellogg's figure of the skull has been copied in a number of later works.

Balaenoptera edeni,
Pablo Beach, Florida.

On 14 May, 1919, a 13.7 m male *Balaenoptera* stranded at Pablo Beach (now Jacksonville Beach), Florida. The skeleton was prepared and exhibited for some time, then sold along with a few baleen plates to the United States National Museum, where it resides as number 236680. Miller (1924) identified this specimen as *B. borealis* on the basis of skeletal characters, and Moore (1953) followed Miller's determination in a compilation of records from Florida. A single external photograph (oblique dorsolateral view of the left side) in the United States National Museum files provided no further information, but Miller's (1924) illustration of the baleen suggested that this might not be a sei whale. This was confirmed by an examination of the baleen, which is clearly that of *B. edeni.*

Balaenoptera edeni,
Panacea, Florida.

Rice (1965) reported a newspaper account of an 11.6 m animal which stranded alive at Panacea on 2 April, 1965, and was subsequently towed off and released by the Coast Guard. The news photo clearly shows the lateral ridges on the rostrum characteristic of *B. edeni.*

Balaenoptera edeni,
Anclote Key, Florida.

On 29 May, 1974, an immature male of this species stranded alive on Anclote Key. It had a length of polypropylene rope wrapped around the head, resulting in blindness in one eye, and probably interfering with proper functioning of the jaw.

Based on preliminary information, this animal was identified as *B. borealis,* and was reported as such by the Center for Short-Lived Phenomena of the Smithsonian Institution (event 76–74). This report was subsequently cited by Gunter and Overstreet (1974). Photographs of the specimen, however, show the lateral ridges on the rostrum characteristic of *B. edeni.* The baleen plates are dark grey with coarse white bristles, further substantiating the diagnosis. This specimen has been catalogued in the US National Museum as number 504074. The skeleton is presently buried in Florida, awaiting recovery.

Balaenoptera edeni,
Venice Louisiana.

Shane and Schmidly (1975) reported an 8.4 m male of this species which stranded near Venice, Louisiana on 11 January, 1975. The presence of three ridges on the rostrum, the texture and colour of the baleen, and the length of the ventral grooves confirmed the identification of this specimen.

Balaenoptera cf. *edeni,*
Chandeleur Island, Louisiana.

Lowery (1974) reported a skull which was recovered from Chandeleur Island in June, 1954. As this was apparently a clean skull when found, there is no indication of when the animal might have stranded, or what its external configuration was. F. C. Fraser (*in litt.* to Lowery) identified this as *B. edeni.* Although this is certainly a reasonable identification, I am hesitant to believe that the cranial characters of these species are adequately defined, particularly in view of the large number of misidentified specimens which have been used as the basis for comparisons.

Balaenoptera cf. *edeni*, Ensenada de Mora, Cuba.

Varona (1965) identified as *Balaenoptera borealis* a specimen which was captured by fishermen on 3 January, 1963, at Ensenada de Mora on the southern coast of Cuba, just east of Cabo Cruz. The total length of the specimen was given as 10.28 m, although there was some question whether this was a straight line measurement or over the curve of the body. In either case it would be a young animal, as noted by Varona (1965). The baleen plates were described as uniformly black, and the bristles as cream to white and very fine. I have examined some of the bristles (which were sent to me by Dr. Varona) and find that their diameter ranges between 0.4 and 0.5 mm, which is too coarse for *B. borealis*, but appropriate for either *B. edeni* or *B. physalus*. Dr. Varona (*in litt.* 1975) informed me that no ridges were seen on the dorsal surface of the rostrum.

The above combination of characters does not permit a definitive identification. The description of the baleen, particularly the uniform dark colour of the plates, is more suggestive of *B. edeni* than *B. physalus*. The ridges on the dorsal surface of the rostrum are sometimes faint, so their apparent lack does not preclude this species, and I am assigning this record to *B.* cf. *edeni*.

Balaenoptera cf. *edeni*, Grenada, Windward Islands.

Harmer (1928) reported one individual of this species taken in 1926, and two taken the previous year at a shore station operating on Grenada. Owing to the common confusion of this species and *B. borealis*, however, he was sceptical as to the exact identity of these.

Balaenoptera cf. *edeni*, Wacao, Curacao.

Soot-Ryen (1961) described a specimen of *Balaenoptera* which drifted ashore on 12 July, 1959 in the bay of Wacao on the northeast side of the island of Curacao. The specimen was evidently an adult, as indicated both by his length estimate (13.5 m), and the apparent fusion of the vertebral epiphyses in his Figure 14. Unfortunately the specimen was in an advanced state of decomposition and neither photographs of the exterior nor baleen were recovered. Soot-Ryen (1961) identified this specimen as a *member of the B. edeni-brydei group on the basis of* skeletal characters, particularly the shape of the nasal bones. As noted earlier in this paper, these characters are unreliable with the limited sample of specimens available. Accordingly I have listed this specimen as *B.* cf. *edeni*.

I have been unable to locate the locality given by Soot-Ryen (1961), and am using approximate coordinates for the northeast side of Curacao in Table 1.

In addition to the above records, Villa-Ramirez (1969) identified a whale stranded at Tecolutla, Veracruz, Mexico (20°15'N, 96°47'W) as *Balaenoptera borealis*. This stranding recieved considerable attention from the popular press as a sea monster, and as a result came to the attention of numerous biologists. Robert Brownell (*in litt.* 1969) examined photographs of the specimen and identified it as a sperm whale, *Physeter catodon*. This is confirmed by an examination of the illustrations given by Villa-Ramirez (1969), which clearly show the remains of the skull of a sperm whale.

DISCUSSION

Although the data are sparse, they shed some light on the distribution of these species. It must be borne in mind, however, that stranded individuals are in many ways unlikely to be representative of the population as a whole, and may have strayed considerable distances from their normal range.

Balaenoptera borealis is commonly known to frequent the waters of the northwestern Atlantic, where it has been taken as part of the whaling catch in recent years. The summer records from Cape Cod fit what is already known of its distribution in this area, and offer nothing unusual. The December record of this species from South Carolina

Table 1

Records of sei and Bryde's whales from the northwest Atlantic

Species	Number	Length (m)	Locality	Geographical coordinates	Date	Source
			NORTH ATLANTIC			
*B. borealis**	1	14.5	Eastham	41°50'N, 69°58'W	21 VII 74	USNM files
B. borealis	1	12	Chatham	41°40'N, 69°57'W	VIII 10	Allen, 1916
*B. borealis**	1	14.5	Corolla	36°26'N, 75°50'W	5 IV 75	USNM 504244
B. borealis	1	13.8	Cape Island	33°04'N, 79°20'W	XII 72	USNM 486174
B. edeni	1	8	Walnut Point	37°59'N, 76°28'W	18 III 23	Miller, 1927
B. edeni	1	13.8	Pablo Beach	30°17'N, 81°23'W	14 V 19	Miller, 1924
			GULF OF MEXICO AND CARIBBEAN			
B. borealis	1	13.7	Gulfport	30°19'N, 89°18'W	7 IV 72	Gunter & Christmas, 1973
B. borealis	1	11.4	Fort Bayou	29°22'N, 89°21'W	IV 56	Negus & Chipman, 1956
B. borealis	1	–	Buen Hombre	19°51'N, 71°22'W	12 VII 74	Museo Nacional
B. cf. *borealis*	1	–	Campeche	19°50'N, 90°32'W	pre–1915	Miller, 1928
B. edeni	1	11.6	Panacea	30°02'N, 84°22'W	2 IV 65	Rice, 1965
B. edeni	1	10	Anclote Key	28°10'N, 82°51'W	29 V 74	USNM 504074
B. edeni	1	8.4	Venice	29°07'N, 89°24'W	11 I 75	Shane & Schmidly, 1975
B. cf. *edeni*	1	–	Chandeleur Is.	29°50'N, 88°50'W	pre–1954	Lowery, 1974
B. cf. *edeni*	3	–	Grenada	12°05'N, 61°40'W	1925–27	Harmer, 1928
B. cf. *edeni*	1	13.5	Wacao	12°15'N, 69°00'W	12 VII 59	Soot-Ryen, 1961

*Same animal – see text.

Table 2

External measurements of two sei whales and one Bryde's whale in the USNM collection.

	B. borealis				*B. edeni*[1]	
	486174		504244		504074	
Measurement	cm	(%)	cm	(%)	cm	(%)
total length	1,375	(100)	1,450	(100)	1,001	(100)
snout to centre of blowhole	260	(19)	250	(17)	163	(15)
snout to centre of eye	295	(21)	305	(21)	203	(20)
snout to angle of mouth	–	(–)	315	(22)	221	(22)
snout to flipper (anterior origin)	440	(32)	450	(31)	320	(32)
snout to umbilicus	735	(53)	775	(53)	533	(53)
snout to end of ventral grooves	680	(49)	720	(50)	–	(–)
snout to centre of genital slit	975	(71)	950	(66)	646	(65)
snout to anus	–	(–)	–	(–)	723	(72)
snout to tip of dorsal fin	950	(69)	1,050	(72)	719	(72)
fluke notch to anus	333	(24)	–	(–)	257	(26)
fluke notch to genital slit	394	(29)	460	(32)	–	(–)
girth at axilla	–	(–)	–	(–)	396	(40)
girth at anus	–	(–)	–	(–)	193	(19)
centre of eye to ear	84	(6)	85	(5.9)	–	(–)
eye to centre of blowhole	137	(10)	115	(7.9)	76	(7.6)
length of blowhole	50	(3.6)	50	(3.4)	28	(2.8)
width of blowhole	10	(.73)	12	(0.83)	–	(–)
flipper length, anterior	189	(14)	170	(12)	121	(12)
flipper length, posterior	135	(9.8)	120	(8.3)	108	(11)
flipper width, maximum	42	(3.1)	40	(2.8)	26	(2.6)
genital slit length	–	(–)	80	(5.5)	24	(2.4)
anal slit length	–	(–)	23	(1.6)	15	(1.5)
perineal length (males)	–	(–)	135	(9.3)	51	(5.1)
fluke width (tip to tip)	280	(20)	370	(26)	221	(22)
fluke depth (notch to anterior edge)	87	(6.3)	88	(6.0)	66	(6.6)
dorsal fin height	–	(–)	80	(5.5)	23	(2.3)

[1] measurements taken in feet and inches and converted to metric units.

may have come from a southward migration of this same population during the winter months.

The Eastham-Corolla record, which was essentially a tagged animal, provides further substantiation for a southward winter migration of this species along the Atlantic coast of the United States.

The *B. edeni* record from well within Chesapeake Bay (Walnut Point) in March is more of a problem. It may either be a stray, or it may indicate some actual overlap of the winter ranges of these two species. The *B. edeni* recorded from Pablo Beach, Florida in May is more consistent with the common interpretation of this species as an inhabitant of tropical waters.

The distribution of these species in the Gulf of Mexico and the Caribbean is more problematic. *B. edeni* may be resident in this area and the strandings of this species on the Atlantic coast may represent strays. The number of *B. borealis* strandings is probably too large for them to have merely strayed into this area. The stranding on the Dominican Republic in July suggests that the *B. borealis* in the Caribbean may well be a separate population from those which appear farther north at about this time.

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Preliminary Assessment of Stocks of Northwest Atlantic Sei Whales (*Balaenoptera borealis*)

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Abstract

A fishery off Nova Scotia took 825 sei whales between 1966 and 1972. The stock fished may be discrete from a Labrador Sea stock. Nine whales were tagged in the Nova Scotia area during the whaling season (May to November), with three returns in years 4 and 5. Four whales were tagged in winter months, and one in September possibly at the eastern edge of the stock. Tagging data indicates a stock of 1,393, 2,075 or 2,248 animals on the Nova Scotia shelf in summer, depending on assumptions regarding stock identity and migration. A minimum estimate from census data is 870.

INTRODUCTION

Whaling in the northwest Atlantic since the late 1890's has been concentrated around Iceland, in Davis Strait and on the coasts of Newfoundland. Generally sei whales (*Balaenoptera borealis*) have not been the preferred species in these fisheries. In Newfoundland, catches of sei whales have been low, on the order of 10 or 20 per month during the periods of heaviest catch. Whaling in Newfoundland has been episodic, with periods of inactivity. The most recent episode began in 1966 and ended in 1972, with a total catch of only 16 sei whales.

A small fishery of short duration took no sei whales in the Gulf of St. Lawrence in the early part of this century.

However, a fishery beginning in 1966 off the east coast of Nova Scotia took a substantial catch of sei whales on the Nova Scotia shelf. It is with this fishery and the stock fished that this paper is mainly concerned.

The fishery off Nova Scotia was confined to a single land station at Blandford, near Chester, approximately 40 miles southwest of Halifax. The only other whaling activity in Nova Scotia in this recent episode was a small operation that worked for only one year near Comeau, on the Gulf of Maine coast, and it did not land any sei whales as far as is known. The Blandford operation grew from a small scale fishery for bottlenose whales (*Hyperoodon ampullatus*), with an experimental catch of fin whales (*B. physalus*) first taken in 1965. Sei whales were first taken in 1966, with a catch of at least eleven. Between 1966 and 1972, when commercial whaling was terminated in Canada, 825 sei whales were landed and virtually all were examined by technicians of the Fisheries Research Board of Canada.

Statistical and other data have been presented on this Nova Scotian fishery elsewhere (Mitchell, 1972, 1974a, 1974b; Mitchell and Kozicki, 1974). Data are summarized below only as necessary to identify separate stocks and estimate their size.

STOCK IDENTITY

A number of lines of evidence indicate that two stocks of sei whales occur in the Northwest Atlantic, one with its centre of abundance off eastern Nova Scotia and another centered in the Labrador Sea (Fig. 1).

Evidence from the seasonal distribution of this species indicates that sei whales occur in the Labrador Sea as early as the first week of June, where a few were seen on the May–June cruise of the *Polarstar.* At the same time, a group of sei whales moves along the continental slope off the eastern United States, arriving in the area of Georges Bank, the Northeast Channel and Browns Bank by mid to late June (Mitchell and Kozicki, 1974).

The whales in the Labrador Sea apparently represent the stock fished in earlier years by land stations in Labrador (especially Hawke Harbour) and in northeast Newfoundland (especially Williamsport and South Dildo, see Mitchell, 1974a for locations of stations, catcher range and history of fishing). It is probable that records of sei whales seen or taken in West Greenland waters represent the same stock, and less likely but entirely possible that the Labrador Sea stock is the same as is fished by Icelandic whalers in Denmark Strait (Jónsson, 1965). Catches by the Labrador and northeast Newfoundland stations would then be samples from the periphery of the stock.

The whales on the Nova Scotia shelf apparently migrate along the continental slope in June and July in an early season, northward 'run,' then return from mid September to mid November through the same area in a late season, southward 'run.' Occurrences on the south coast of Newfoundland in August and September apparently represent the northernmost migration of at least a part of the Nova Scotian stock (Mitchell and Kozicki, 1974).

Other data on the seasonal distribution of sei whales in summer and fall months must be treated with caution. For example concentrations of sei whales observed on the cruise of the *William S* on 29 September 1966 off the north coast of Venezuela (Mitchell and Kozicki, 1974) probably represent northward migrating sei whales from a Southern Hemisphere stock during the southern winter. Recorded sightings or strandings of sei whales along the eastern United States and in the Caribbean and the Gulf of Mexico need to be re-evaluated, as many probably represent Bryde's whale (*B. edeni*) instead (Dr. J. G. Mead, *pers. comm.*, 6 December 1974).

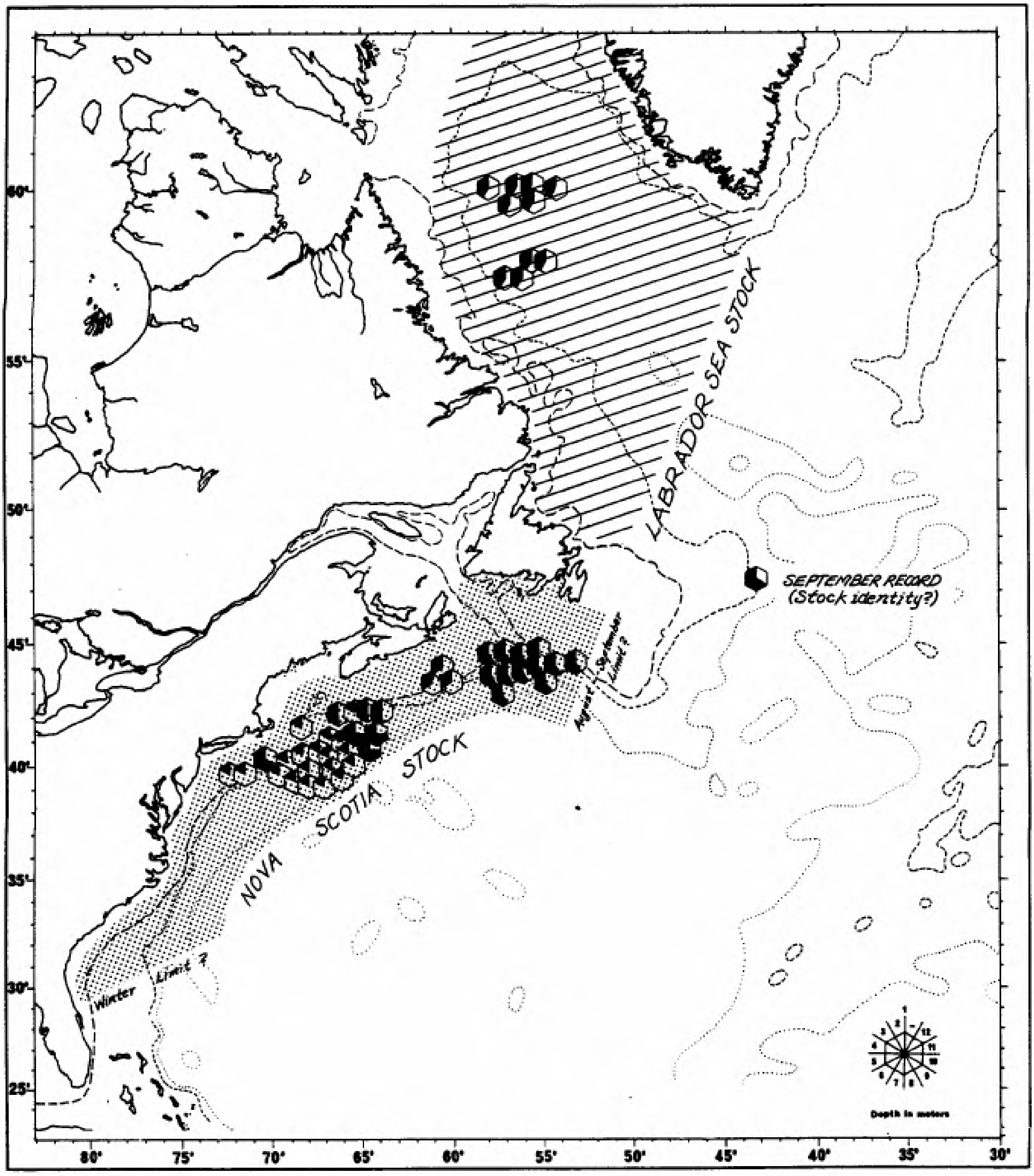

Fig. 1. Chart of northwest Atlantic, showing position of summer and winter sightings of sei whales (from Mitchell and Kozicki), 1974, with indication of migration trends and possible stock distributions.

Evidence from tagging and recapture of this species supports the hypothesis of two stocks in the northwest Atlantic. Nineteen sei whales were seen and four were tagged in the winter off the eastern United States between Cape Cod and Florida (Mitchell and Kozicki, 1974). These probably represent the Nova Scotia stock on its southward, winter migration, although none of these tags was returned in the Nova Scotia fishery.

One sei whale tagged in September off the eastern edge of the Grand Bank (Mitchell and Kozicki, 1974) may be from either the Nova Scotia or the Labrador Sea stock.

Fewer than ten whales were tagged in the Nova Scotia stock area during the season of the fishery (*e.g.* any year, months May through November). Three of these have been returned, all within the same area (Mitchell and Kozicki, 1974).

ESTIMATE OF STOCK SIZE FROM TAG–RECAPTURE

Examining the distribution of tagged whales (Mitchell and Kozicki, 1974) and taking into consideration the above evidence on distribution and possible stock identity, it is clear that some alternatives remain in calculating the size of the Nova Scotia stock from tag-recapture data. These are (1) an estimate of the population being fished on the Nova Scotia shelf, during the fishing season, using only tags shot into whales in the months of May to November in that area (*e.g.* 7 tags in 1966 with one return in 1971; 2 tags in 1967 with one return in 1971 and one in 1972);

(2) an estimate of the stock, making the assumption that winter tagging off cape Cod and southward to Florida has been on the same stock unit (*e.g.* 4 tags in February and March, 1969 and 1971, respectively, with no returns);

(3) the inclusion of one tagged whale off the eastern edge of the Grand Bank in September, assuming that it belongs to the Nova Scotia stock.

The results of these calculations are shown in Tables 1 to 3. In each case, a formula due to Chapman (1952) is used:

$$N = \frac{\Sigma M_i C_i}{(\Sigma m_i) + 1}$$

where N = population size, C_i = catch in season i, M_i = *effective number of marks present in season i, and* m_i = number of marks recaptured in season i. The winter marks were implanted before the beginning of the whaling season in that year. The effective number of marks present in each season has been calculated as the number of animals marked in previous seasons (or in the winter immediately prior to the season), less those recovered in previous seasons and with an annual survival rate for the remainder of 0.96. Marks fired or recovered during an actual season were halved to give mid-season values for that particular year.

The population estimates obtained are 1,393, 2,075 and 2,248, using the progressively more uncertain assumptions listed above.

Table 1

Nova Scotia Shelf sample only, with 9 whales tagged and 3 returns (see text for definition of symbols).

Season	M_i	C_i*	$M_i C_i$	m_i
1966	3.50	11	38.5	0
1967	7.72	56	432.3	0
1968	8.37	100	837.0	0
1969	8.04	148	1189.9	0
1970	7.71	93	717.0	0
1971	6.41	234	1499.9	2
1972	4.69	183	858.3	1
Total			5572.9	3

*actually, number examined e.g. for tags, but virtually 100% landed were examined.

Table 2

Nova Scotia shelf and winter tagging sample, with 13 whales tagged and 3 returns

Season	M_i	C_i*	$M_i C_i$	m_i
1966	3.50	11	38.5	0
1967	7.72	56	432.3	0
1968	8.37	100	837.0	0
1969	10.04	148	1485.9	0
1970	9.64	93	896.5	0
1971	11.25	234	2632.5	2
1972	10.80	183	1976.4	1
Total			8299.1	3

*number examined, approximates 100% of the catch

Table 3

Nova Scotia shelf, winter and September 1967 Grand Bank tagging sample, with 14 whales tagged and 3 returns.

Season	M_i	C_i*	$M_i C_i$	m_i
1966	3.50	11	38.5	0
1967	8.22	56	460.3	0
1968	9.33	100	933.0	0
1969	10.96	148	1622.1	0
1970	10.52	93	978.4	0
1971	12.10	234	2831.4	2
1972	11.62	183	2126.5	1
Total			8990.2	3

*number examined, approximates 100% of catch

ESTIMATES OF STOCK SIZE FROM CENSUS DATA

Another set of data is of use in estimating population abundance of sei whales in the northwestern Atlantic. Counts of all whales encountered have been made on cruises undertaken by the Fisheries Research Board of Canada (Mitchell, 1974b). Estimates have been made of the density of distribution of whales encountered, and the results have been extrapolated to the region found to be inhabited by the whales in question during summer months. The methodology and estimates for fin whales are given in Mitchell (1974a), some data on humpback whales (*Megaptera novaeangliae*) are tabulated in Mitchell (1973), and comparable data for sei whales are presented here (Table 4). The regions mentioned in the table are arbitrary statistical areas with boundaries defined in part by oceanographic features and/or suspected whale stock limits, and are discussed in detail in a paper being prepared on censuses in the North Atlantic. These preliminary compilations show that few sei whales have been observed in summer months in waters from Davis Strait to the Caribbean, from North America to Iceland, the mid Atlantic ridge and West Africa. Some of the sightings in the Caribbean possibly include Bryde's whales. There appear to be relatively few sei whales in the area of the Nova Scotia shelf on the basis of these data, while the fishery there has taken greater numbers than the census estimate gives for the total population in that region.

With these reservations in mind, and considering that some of the biases in this method give high estimates, the total population of sei in the northwest Atlantic is calculated to be 2,078 whales (Table 4). This includes an estimate of 828 for the Labrador Sea and 137 for West Greenland, probably both part of the Labrador Sea stock (total 965). Considering all other sightings outside of the Caribbean Sea region as representing the Nova Scotia stock, these total 870.

CONCLUSION

Two separate stocks of sei whales may exist, with centres of abundance on the Nova Scotia shelf and in the Labrador Sea. Tag-recapture data give estimates for the Nova Scotia stock from 1,393 to 2,248 whales, and census data give

Table 4

Estimates of sei whale population size from shipboard strip censuses in the northwest North Atlantic, spring and summer cruises, 1966–1969. As = area searched (in square nautical miles). Regions defined by Mitchell (in prep.)

Region	Total Area (sq. nautical mi.)	As	As/Total	No. sei seen	Sei/ 1000 sq. mi.	Est. Stock
(1) Gulf of St. Lawrence	69,174	6,685	.10	0	0.0	0
(2) Nova Scotia Area	228,045	22,543	.10	16	0.7	159
(3) Labrador Area	99,955	13,394	.13	0	0.0	0
(4) Baffin Area	119,494	6,095	.05	0	0.0	0
(5) West Greenland Area	124,243	7,013	.06	8	1.1	137
(6) East Greenland Area	132,659	3,669	.03	0	0.0	0
(7) Iceland	131,315	991	.01	0	0.0	0
(8) Labrador Sea	295,869	1,416	.005	4	2.8	828
(9) Mid Atlantic Ridge Area	412,450	1,623	.004	0	0.0	0
(10) Eastern Gyre	709,595	4,932	.01	1	0.2	142
(11) Gulf Stream Area	195,662	2,765	.01	7	2.5	489
(12) American Area	267,282	3,631	.01	1	0.3	80
(13) Northern Sargasso Sea	589,042	1,530	.003	0	0.0	0
(14) Bahama Sea	304,630	3,707	.01	0	0.0	0
(15) Southern Sargasso Sea	694,592	2,290	.003	0	0.0	0
(16) Caribbean Sea	607,476	5,328	.01	2	0.4	243
(17) Lesser Antillean Region	347,296	820	.002	0	0.0	0
(18) Amazonian Region	153,398					
(19) Northwest Africa Area	1,088,824	11,478	.01	0	0.0	0
(20) Guinean Region	473,066	5,549	.01	0	0.0	0
			Total estimated population			2,078

counts of a minimum of 870. The Labrador Sea stock, on the basis of census data, is a minimum of 965 whales.

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Distribution and Composition of Sei Whale Schools in the Southern Hemisphere

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INTRODUCTION

At present the structure of schools of smaller cetaceans has received the most study, namely white-sided dolphins (Sleptsov, 1941; Tarasevich, 1951, 1957; Kleinenberg, 1956) and white whales (Kleinenberg, Yablokov, Belkovich and Tarasevich, 1964; Belkovich and Yablokov, 1965; and others). There is still little information on the school structure of the larger baleen and toothed whales.

The subject of differentiated migration of baleen and toothed whales was covered by Andrews (1914), Mackintosh and Wheeler (1929), Zenkovich (1937, 1952), Mackintosh (1942), Fujino (1960), Nemoto (1962a, 1962b), Tomlin (1957, 1962), Ivashin (1969) and others. Isolated groups of young cetacea were recorded in the works of Scammon (1869), Gray (1882), Andrews (1914), Tomlin (1936, 1937), Zenkovich (1934, 1945, 1952), Nemoto (1964) and others.

The most comprehensive studies on the school structure of sperm whales and fin whales were made by Nemoto (1964), Tarasevich (1967a, 1967b) and Tormosov (1970).

Information on the school structure of sei whales and their distribution in the waters of the Antarctic is available only in works by Matthews (1938), Zemsky (1965), Ivashin (1966), Gambell (1968) and Yukhov (1969). The following conclusions were drawn from the material available to the author.

1. Small groups of sei whales, consisting of three to five individuals are probably families.
2. Schools differ in size (age) and physiological condition (i.e. immature, mature, pregnant, non-breeding).
3. In the course of migration the school structure observed on the breeding grounds is broken down on the feeding grounds. A certain order in migration is recorded.
4. Schools in latutides 40° to 50°S consist mainly of immature specimens of both sexes and lactating females with calves.

The paper is based on the observations of sei whale school structure in different regions of the Southern Ocean, these observations being carried out by the members of the *Yury Dolgoruky* whaling expedition from 1960 to 1974. If necessary, various published papers and articles as well as the data of the International Whaling Statistics are used.

SOUTH ATLANTIC OCEAN

The structure of sei whale schools in the South-West Atlantic was described by Paiva and Grangeiro (1965, 1970) who collected information at the land station in the state of Paraiba. Studying in detail the size and sex composition of the sei whales caught in winter (July to September), they pointed out the predominance of large males (up to 60 to 70%). The size composition of the whales caught (males up to 14.0 to 15.6 m. and females from 15.3 to 16.1 m.) allows one to make the assumption that in this area mature whales of both sexes were predominant. However, if the selectivity of whaling is taken into account, it is possible that immature females and males occur in this area. After finding that the stomachs of the whales of different species caught were empty, the author came to the conclusion that whales appeared in this area mainly for reproduction. Thus the most characteristic feature of sei whales in the area of reproduction was the predominance of males among the mature animals. In October the sei whales started migrating towards the south and the catches at the coastal station of Paraiba in Brazil were considerably reduced (Paiva *et al*, 1965; 1970).

At this time along the east coast of South America in latitudes 10° to 30°S it is possible to see small separate groups of sei whales, three to five in number. They are normally seen from the whalers sailing to the Antarctic. In November in latitudes of 42° to 45°S sei whales form considerable schools of up to 20 to 40 animals. Slightly farther south, at latitudes 45° to 55°S, sei whales appear singly and in groups from December to April. In the whales caught in this region, the sex ratio remains the same as was observed in the northern part of the breeding area. According to the results of biological analysis for several seasons, males comprise the major portion of the catch (56 to 63%) from December to February. Among the females the majority are pregnant (about 70%) followed by non-breeding (25%) and immature females (5%) – Budylenko (1970). In January in the same area one can find many cows accompanied by calves: they may shift to the south as far as the Falkland Islands (Ivashin, 1966).

Near the Falkland Islands the catch consists mainly of females (up to 75%), among which pregnant animals are predominant (from 58 to 70%), and the numbers of non-breeding animals and immature ones are insignificant (Ivashin, 1972).

According to Matthews (1938), near the island of South Georgia the catches consisted mainly of large males. However, according to the data from the International Whaling Statistics for 1937 to 1966, the catch consisted mainly of large females. The females caught in this area were pregnant (66 to 80%), non-breeding (6 to 13%) and immature (10 to 12%) – Budylenko (1970). Farther south near the South Sandwich Islands there were more females at different stages of pregnancy (70 to 80%); non-breeding females were recorded as 10 to 25% and immature females as from 4 to 5%.

The structure of sei whale schools and their distribution in the South West Atlantic can only be judged from catch data published by the Bureau of International Whaling Statistics. Near the coast of Gabon and the Congo the number of males was greater than females (52 to 64% male). Off the south-western coast of Africa (Donkergat) the catches for several seasons (from May to September) consisted mainly of females (54 to 72%). Rather substantial schools of sei whales consisting of separate groups of two to four animals also appear west of South West Africa as far as Tristan da Cunha. Observations made in November and December in this vast area allowed an estimate to be made that about 25% of the sei whales were cows accompanied by calves that were considered to be suckling. Many large animals were recorded with them, the ratios of sexes and physiological groups probably being similar to the ratios recorded in the South-West Atlantic.

In higher latitudes of the Atlantic, near Bouvet Island, the catches were composed of about 58% females in February and March, among which 75% were pregnant, about 20% non-breeding and 5% immature (Budylenko, 1970).

INDIAN OCEAN

Information of sei whale school structure at the latitude of 30°S in the Indian Ocean (South-East Africa, Durban) was given by Bannister and Gambell (1965) and Gambell (1968).

Analysing the information on the catches taken during the ten-year period 1954 to 1963 and also taking into account the sex and maturity of the whales in these catches, the authors arrived at the conclusion that the structure of sei whale schools fluctuated during a season. In the first part of the season (April to July) immature whales of both sexes predominated, the number of females being larger. In the second part of the season (July to October) the sei whale schools consisted basically of mature animals. The sex ratio changed as well. During this period mature males constituted the major portion of the catch. The sex ratio also changed among immature animals: as compared with the first part of the season, there were more males at this time.

The changes in the structure of the sei whale schools observed near Durban can be easily explained by the migrations of these animals, the mature specimens of which on their return from the Antarctic (April to May) move farther from the coast and to the north, while the immature animals stay in this area. In July mature males and females begin to move from the north to the region of Durban, where they constitute the major part of the catches. From October to December in 30° to 40°S latitude in the central part of the Indian Ocean, it is possible to record considerable numbers of sei whales, consisting of separate groups of three to five animals. Interpretation of the structure of sei whale groups during this period may be only tentative. Evidently males still predominate as in the structure found at Durban. About one-third of the school is females accompanied by suckling calves, and the remaining animals are probably pregnant females, non-breeding and immature animals.

Pregnant females and mature males move into the higher latitudes of the Indian Ocean (Crozet, Kerguelen, Heard Island, etc.) first, followed by non-breeding females and immature animals of both sexes. In these regions the number of females in the catch is higher by 10 to 12%. The largest proportion is of pregnant females (up to 60%), then non-breeding (about 20%) and immature females (10%). Within these latitudes during the feeding period (January to March), the ratios of physiological groups may change, especially at the end of this period (March to April) when pregnant females start to migrate northwards and among the females non-breeding and immature animals are predominant.

SOUTH PACIFIC OCEAN

Similar structure in the groups of sei whales is observed in the very southern part of the feeding ground (58° to 68°S). According to Yukhov (1969) near the Balleny Islands females comprise about 76% of the sei whales taken. These are mostly pregnant (up to 60%) together with non-breeding (35%) and immature animals (5%). Catches in this region mainly consist of mature animals of both sexes.

In high latitudes of the Pacific Ocean (59 to 67°S, 148° to 162°W) more females (up to 60%) were caught in February. All were mature, 78% being pregnant and 22% non-breading (Ivashin, 1972). Near the coast of Chile from 40° to 50°S male sei whales predominated in January and February (54 to 58%) and the relative number of pregnant females is much smaller than in other regions (14 to 40%). Non-breeding females were rather numerous (up to 65%). In January about 9 to 17% of immature females were recorded, as were many cows accompanied by calves. Farther south near the Antarctic Peninsula and Peter I Island males predominated slightly (55%), as they did near the coast of Chile, and among the females non-breeding animals (58%) were predominant, while pregnant animals comprised only 30 to 35%.

SUMMARY

The above description of sei whale school structure in various parts of the species' reproductive and feeding range (Timofeev-Resovsky, Yablokov and Glotov, 1974) indicates that in the course of distribution sei whales differentiate according to size (age), sex and physiological groups.

Depending on the season and position of the region, sei whales form the following types of school:

1. Mature animals of both sexes constitute the basis of the schools, while males predominate. Here females in early stages of pregnancy are also present (the coast of Brazil, Congo, Gabon).
2. Immature animals with females predominant constitute the basis of the schools (Durban).
3. The number of mature males exceeds that of females by 10 to 15%. In the same area many (about 25%) females accompanied by suckling calves can be seen (Durban, 30°–50°S latitudes of the Atlantic and Indian Oceans).
4. Mature animals comprise the basis of the schools. The number of females exceeds that of males by 20 to 25%. Among the females the percentage of pregnant or non-breeding animals is rather high (60 to 80%). The number of immature animals of both sexes is insignificant (high latitudes of the Southern Ocean).

This analysis of sei whale school structure and their distribution over areas of the Southern Ocean only allows us to trace the main and distinct types of school. The first type of sei whale school occurs in warm water zones on breeding grounds. The second and third types of school are recorded in intermediate zones, prior to further migrations to the south. The fourth type occurs in high latitudes of the Antarctic on whale feeding grounds.

The schools of sei whales recorded are formed for a certain period of time and they are much clearer after completion of migration.

The knowledge of the structure of sei whale schools, their distribution and period of their formation will allow us to conduct a selective whaling in such a way which will minimise the damage caused to the reproductive part of the population.

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SC/27/Doc 17

On the Biology of the Eastern North Atlantic Sei Whale, *Balaenoptera borealis* Lesson

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Abstract

A brief review of the history of whaling for eastern North Atlantic sei whales is given. On the basis of earlier studies and postwar examinations of 87 animals caught off western Norway, present knowledge of the general biology of the eastern North Atlantic sei whale has been summarized. The species occurs in both temperate and warmer waters, occasionally also colder waters as far north as Bear Island and Spitsbergen. The migration pattern is northward in the spring and southward in late summer. Sudden appearances and disappearances may take place during the feeding migration. 'Invasion years', where unusually large number of sei whales occur in an area, are typical for this species. The sei whale feeds on copepods and euphausiids, preferring copepods. Off western Norway the food consists of *Calanus finmarchicus, Meganyctiphanes norvegica* and *Thysanoessa sp.* Males and females attain sexual maturity at a length of 42 ft and 44 ft respectively. Mating takes place in late autumn and winter. Gestation lasts for about a year. The calf is probably about 4.8 m long when born. In general, the reproductive cycle seems to be two years in duration.

INTRODUCTION

This paper deals only with eastern North Atlantic sei whales. It is based upon the information from earlier studies on this species and the work performed at the Norwegian land stations in postwar (World War II) seasons. The references given in this paper are mainly based upon original data.

As for the other rorquals, pursuit of the sei whale was not profitable until after development of Sven Foyn's harpoon gun in 1868. As long as larger species were abundant, the sei whale was also ignored because of its smaller size. But already by the 1880s, blue whales were becoming more and more scarce off Finmark, and the number of sei whales in the yearly catches began to increase (Risting, 1922). The sei whale catch was particularly high in 1885 when they appeared in unusually large numbers off the coast of North Norway from Tromsø to the Murmansk coast. In that year, 771 sei whales were caught from the Finmark land stations out of a total catch of 1,287 whales (Collett, 1886). From that time onward, the sei whale was hunted from the Finmark coast until the end of land station whaling in that area in 1903 (Risting, 1922). However, their presence off North Norway was quite variable from year to year as can be seen from the extremes of the catch statistics. For example in 1889 only 22 were taken, but the following year the number was 547. Then in 1901, the level sank again to 22. To some extent, these numbers also reflect the relative abundance of the larger, more preferred species (Ruud, 1937). More recently, the sei whale has been almost absent from this area. Only three have been caught since the Skjelnan whaling station in North Norway started whaling in 1948 (Jonsgård, 1974).

The sei whale has also played a part in the Scottish whale fishery, which began in 1903 when land stations were established on the Outer Hebrides and Shetland Islands (Thompson, 1928). As off Finmark, the sei whale harvest in Scottish waters was quite erratic from year to year. The extremes varied from 260 animals caught in 1920 to 12 caught in 1923, representing 41.1% and 3.2% of the total annual catch respectively (Thompson, 1928). Thompson (1928) also gives the information that the percentages of sei whales in the total catch in the years 1908 to 1914 and 1920 to 1927 was 25.2%, so this species was a significant factor in the industry.

Whaling from Iceland began in 1883, but there were very few sei whales in the early catches (Jónsson, 1965). Both Risting (1922) and Collett (1912) state that sei whales were only rarely seen in Icelandic waters. In 1948 when whaling from Icelandic land stations was again resumed, sei whales were caught in small numbers. There was a sharp increase in sei whale catches in the years 1952 to 1954 which coincided with a decrease in the fin whale catches. Then, after 1955, the catches of sei whales decreased again, coincidental with an increase in the number of sperm whales caught. In this area, the sei whale has always been the third choice of the whalers, the fin and sperm whales being the preferred species (Jónsson, 1965).

EARLIER STUDIES

Distribution and migration

From whaling statistics and other observations, some knowledge has been gathered at least with regard to the distribution and migration of the sei whale.

On the eastern side in the spring, sei whales first appeared close to land off West Ireland and then passed northern Scotland and the Shetland Islands and from there moved northward (Lillie, 1910; Kellogg, 1929). In the late 19th century, sei whales frequently reached the waters off North Norway, sometimes in large numbers (Risting, 1922), and occasionally they were seen as far north as Spitsbergen and Bear Island (Ingebrigtsen, 1929). However, the extent of their northward movements in these waters has always been quite variable, and as has been stated earlier, in postwar years they have seldom reached Finmark at all (Jonsgård, 1974).

The timing of these movements along Western European shores showed great seasonal fluctuations. Kellogg (1929) states that sei whales first appeared off Iceland in late May and June and off Scotland in June and July. However, other figures show that sei whales arrived off the Shetlands as early as April (Thompson, 1928; Ingebrigtsen, 1929). According to Thompson (1928) the peak for sei whale numbers off the Shetlands was in June, but that there were some sei whales in these waters throughout the summer until late September.

The arrival times at the coast of Norway also varied greatly from year to year, but the most common time off Møre, where they first reach Norwegian waters, seemed to be in mid May (Risting, 1928; Hjort and Ruud, 1929; Ingebrigtsen, 1929). Hjort and Ruud (1929) give two peaks of sei whale abundance for this area, one in early May and the second (smaller) one in July. They also state that by late August sei whales have usually disappeared from these waters. When sei whales were common off North Norway, they generally reached the Finmark coast around mid June and disappeared by late August and early September (Ingebrigtsen, 1929). Whaling statistics from Iceland for the years 1961 to 1964 show that the sei whale arrived in Icelandic waters in June and disappeared in September (Jónsson, 1965).

Ingebrigtsen (1929) states that sei whales stay in the southern part of the North Atlantic during the winter, and that their northward migrations seem to take place in the open sea so far out that usually they cannot be caught from the shore stations in Spain and Portugal. Allen (1916) asserts that sei whales were rarely seen south of the straits of Gibraltar. Finally, sei whales were observed, sometimes in large numbers, in the area that stretches from the Madeira Islands, past the Canary Islands southward toward the Cape Verde Islands (Anon, 1914).

Sei whales seem to be subject to sudden appearances and disappearances (Hjort, 1902; Risting, 1922; Kellogg, 1929). There are many records of 'invasion years' where unusually large number of sei whales occur in an area. This may be followed by an equally sharp decrease in numbers the following year. Some examples of invasion years are 1885 and 1898 off Norway and 1906 off Scotland (Ruud, 1937; Thompson, 1928).

Feeding

With regard to the food of the sei whale, *Calanus finmarchicus* seems to predominate in the diet of this species in the eastern North Atlantic. Nearly all records of stomach contents mention this species of copepod. This includes examinations of whales caught off Norway and Scotland (Collett, 1886; Risting, 1922; Hjort and Ruud, 1929; Ingebrigtsen, 1929; Thompson, 1928). However, the sei whale does not feed exclusively on *Calanus finmarchicus* as has sometimes been supposed. Collett (1886) mentions that *Euphausia inermis* was sometimes found in the stomachs of sei whales caught off the west coast of Finmark, and Thompson (1928) states that sei whales in Scottish waters fed on both copepods and krill.

Ingebrigtsen (1929) describes the way in which the sei whale feeds. He writes that this species 'skims' the food from the water, especially in the evening and in the morning, when copepods are most often at the surface.

Reproduction

Little is known of the breeding of the sei whale in the eastern North Atlantic. Collett (1886) wrote that, according to information he had received from whaling station managers, the majority of sei whale females caught off Finmark were pregnant. The foetuses ranged from 3 ft to 4 ft in the beginning of July, 6 ft to 7 ft in mid July, and to 8 ft to 12 ft in August. In the same year, Guldberg (1886) published length measurements of 14 sei whale foetuses caught off the Norwegian coast. The foetuses showed a smooth progression of lengths corresponding to the dates of capture. The lengths ranged from 1 m to 1.3 m in the first half of June, 1.5 m to 2.5 m in the first half of July, and to 1.8 m to 3 m in the second half of July. There was one exception: a foetus found in August measured only 1.3 m. Comparing this information to that already known about minke (*B. acutorostrata*) and humpback whales, (*Megaptera novaeangliae*) Guldberg speculated that the sei whale's gestation period had a possible duration of one year. Risting (1922) stated that most sei whale females caught off Finmark were pregnant but that foetuses found simultaneously showed great variation in length. He therefore concluded that the sei whale did not have a very definite mating time, but that this activity must extend over a long period in the winter. However, Risting (1928) revised this theory based upon the study of length measurements of 95 sei whale foetuses from females caught in the northeastern Atlantic, the majority from off Møre and a minority from off the Shetlands and Finmark. The lengths of the foetuses showed an exceptionally regular increase, from those found in the beginning of the season to those found at the end. From these measurements, Risting estimated the length of a full-grown foetus to be 4.8 m, and the gestation period to be 360 days. He then calculated that, of the 95 foetuses, 63% had been conceived between 25 November and 10 March, and that 55% had been conceived between 26 November and 12 February. This meant that, in fact, the sei whale has a shorter, more definite mating period than both blue and fin whales.

Finally, Ingebrigtsen (1929) wrote that adult females arriving off Møre in April were accompanied by calves, presumably born in more southerly regions in February or March, He also stated that pregnant females with foetuses from 10 cm to 40 cm long were caught in April.

PRESENT STUDIES

Material

In several postwar whaling seasons, four shore stations were in operation on the coast of Norway. Three of them were situated in western Norway (at Blomvåg, Steinshamn and Hestnes) and the fourth one at Skjelnan in Tromsø, North Norway. In the 1951 season, a research programme was instituted with the aim of carrying out biological research on whalebone whales. Whaling inspectors on duty at the stations were responsible for the collection of the material. The inspectors previously had performed similar work on whales caught in Antarctic waters. To avoid mistakes when collecting material, one of the authors (Å. J.) also paid a visit to them in 1951 and 1952 to make sure that all data were collected in the same manner. For recording the data a special form had to be completed (Fig. 1).

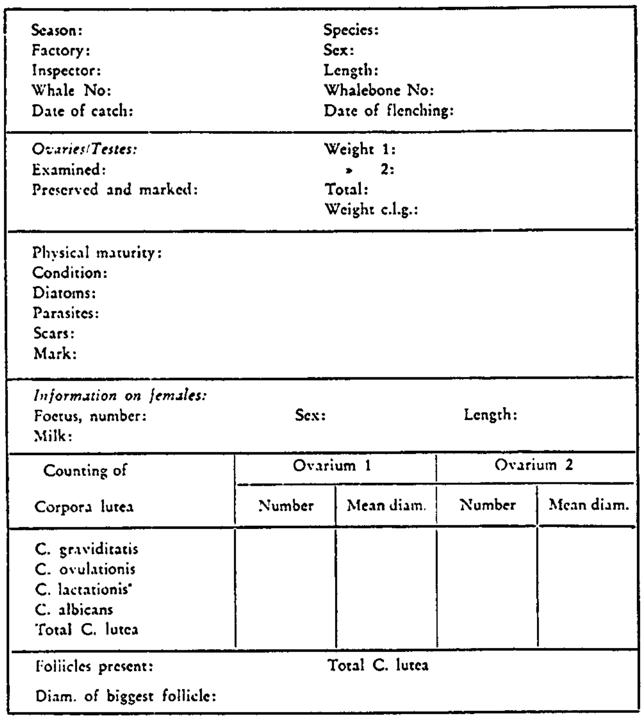
The number of sei whales examined at the different stations in different seasons is shown in Table 1. Altogether 46 males and 41 females have been examined during the seasons 1951 to 1957, the majority of which, 29 males and 35 females, were caught in June and July.

Records of the place of capture were made by the inspectors in cooperation with the gunners. The ovaries were first examined by the inspector at the station, thereafter preserved and sent to the Institute of Marine Biology, University of Oslo after the close of the whaling season. They were later re-examined, to make sure that no mistake had been made with regard to the counting of corpora lutea. A slice of about 2 cm thickness was cut from one of the testes, preserved in formalin and sent to the Institute for

Table 1

Total number of sei whales examined at Norwegian shore stations in 1951, 1952, 1953, 1954, 1956 and 1957. Eight animals only were examined in the three last-mentioned seasons.

Shore stations	April ♂	April ♀	May ♂	May ♀	June ♂	June ♀	July ♂	July ♀	August ♂	August ♀	September ♂	September ♀	Total ♂	Total ♀
Steinshamn	2	–	5	4	10	15	10	11	6	2	2	–	35	32
Blomvåg	–	–	–	–	5	3	2	2	–	–	1	–	8	5
Hestnes	–	–	1	–	2	3	–	1	–	–	–	–	3	4
Total	2	–	6	4	17	21	12	14	6	2	3	–	46	41



Season:
Factory:
Inspector:
Whale No:
Date of catch:

Species:
Sex:
Length:
Whalebone No:
Date of flenching:

Ovaries/Testes:
Examined:
Preserved and marked:

Weight 1:
» 2:
Total:
Weight c.l.g.:

Physical maturity:
Condition:
Diatoms:
Parasites:
Scars:
Mark:

Information on females:
Foetus, number: Sex: Length:
Milk:

Counting of Corpora lutea	Ovarium 1		Ovarium 2	
	Number	Mean diam.	Number	Mean diam.
C. graviditatis C. ovulationis C. lactationis* C. albicans Total C. lutea				

Follicles present: Total C. lutea
Diam. of biggest follicle:

Fig. 1. Form used for recording biological data. In addition stomach contents were examined.

further examination. Sexual maturity in males was determined in accordance with the method used by Mackintosh and Wheeler (1929). Females were considered sexually mature which had one or more corpora lutea in the ovaries.

Unfortunately it was impossible to make a complete examination of all the material desired. This was because when a whale had been killed, the belly was opened in order to let the water cool the carcass while the whale was towed to the station. During this operation most foetuses and in a few cases also reproductive organs were lost. In addition to a uterus or the remains of a uterus bearing signs of pregnancy, a female was considered to be pregnant if a large sized corpus luteum with well developed superficial veins was present in the ovaries. Examination of stomach contents was carried out in 1952 and 1953. Altogether 52 stomachs were examined, and samples were taken from 14 of these.

Distribution and migration

The capture positions for male and female sei whales examined at the three western stations in 1951, 1952 and 1953 are shown in Fig. 2. This material includes 79 out of 83 animals caught in these seasons combined. No capture positions are available for 8 other animals, one of which was examined at Blomvåg in 1954 and the others at Steinshamn in 1956 and 1957. No sei whales have been examined at Skjelnan station in North Norway (Table 1). This is due to the fact that this species is very seldom observed in this area of whaling (see Jonsgård, 1974). A comparison between the capture positions in each of the three seasons in question has been made, and no significant differences have been found. In Fig. 2, the three seasons therefore have not been separated.

The great majority of the catches have taken place in two different main areas; an area of concentrated catches relatively close to the coast between about 5°E and 7°E, and between 63°15'N and 63°55'N, and another area with more dispersed catches between about 1°E and 3°E, and 62°25'N and 63°50'N. Both areas have been inhabited by males and females of different sizes. However, in the first-mentioned area 29 animals out of 47 have been taken early in the season between 30 April and 2 June, while in the last-mentioned area only 11 out of 30 were caught during this period. Our material therefore seems to point to the fact that sei whales of both sexes inhabit the same waters off the coast of western Norway and that a concentration seems to take place in a special area off the Møre coast in the early part of the whaling season.

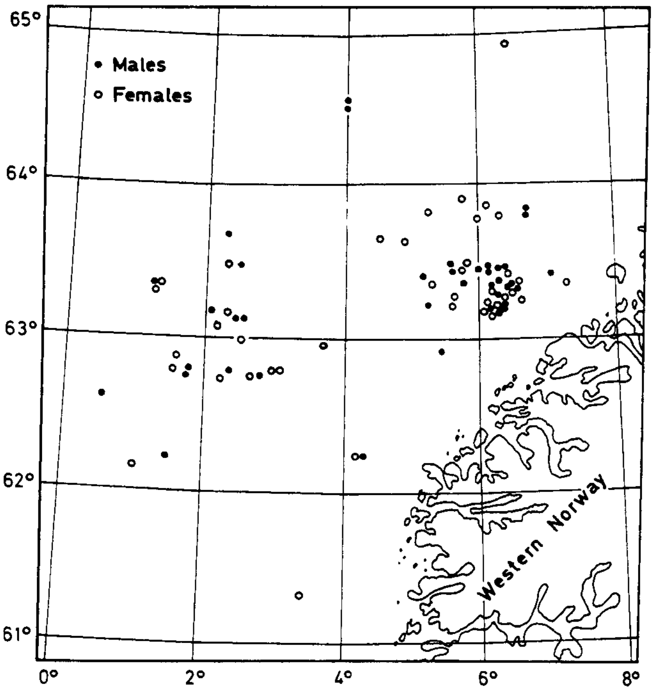


Fig. 2. Capture positions of sei whales caught off western Norway in 1951, 1952 and 1953.

Food

In Tables 2, 3 and 4 data are given on the stomach contents of sei whales caught off western Norway. Table 2 shows that 13 stomachs were examined in 1952 and 39 in 1953.

The stomach contents consisted of crustaceans only, represented by calanoids and euphausiids (Table 3). Calanoids had been eaten by 48.1% of the animals examined, while 9.6% had fed upon euphausiids and 7.7% had a mixture of these crustaceans in their stomachs. As many as 34.6% had empty stomachs.

Table 2

Number of sei whale stomachs examined and number sampled at each station.

Stations	Stomachs examined 1952	Stomachs examined 1953	Samples taken 1952	Samples taken 1953
Steinshamn	8	33	2	9
Blomvåg	4	1	1	0
Hestnes	1	5	0	2
Total	13	39	3	11

One of the animals, a 34 ft 7 in. long female caught by a Steinshamn catcher on 22 August 1952, was reported by the crew of the catcher to have vomited a large amount of herring while being killed. The stomach of this animal was empty when examined at the station.

Very little can be said about the stomach contents in the different months because of the scanty material. However, calanoids only were found in April and May, calanoids and euphausiids in June and July, and from July onwards the majority had empty stomachs (Table 4).

Examination of the samples taken showed that *Calanus finmarchicus, Meganyctiphanes norvegica* and *Thysanoessa sp.* were present.

Although *Calanus finmarchicus* predominated in the stomach contents, considerable quantities of euphausiids were recorded in a couple of stomachs, pointing to the fact that euphausiids are also searched for as food by sei whales inhabiting the waters off western Norway. There are indications that the food supply diminishes from July onwards.

Breeding

The available data for studying the breeding of the sei whale are scarce, especially because most foetuses were lost at sea.

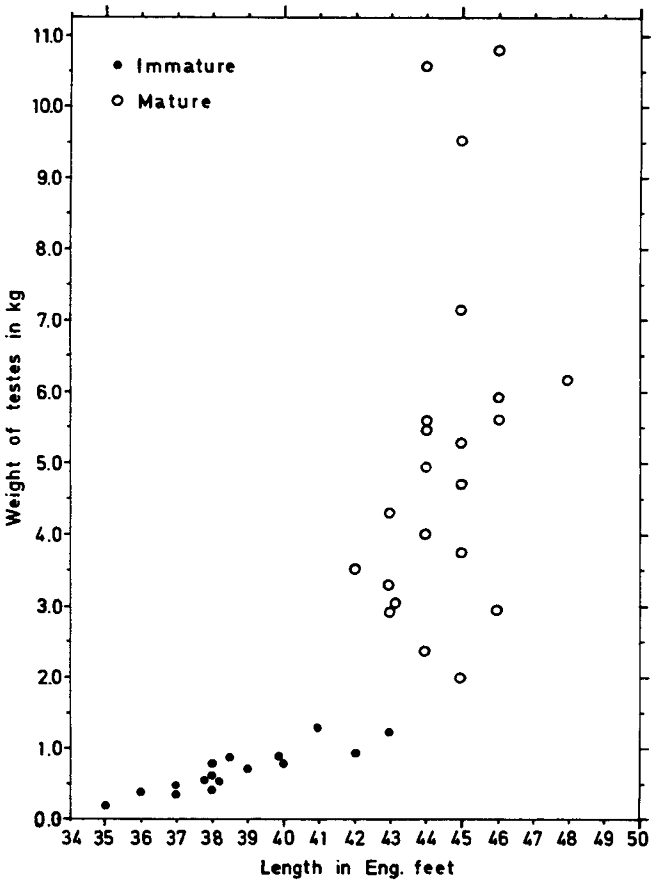


Fig. 3. Weight of testes combined in relation to body length of sei whales caught off western Norway.

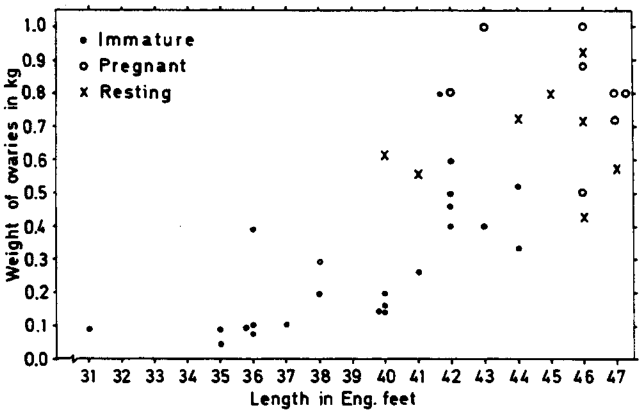


Fig. 4. Weight of ovaries combined in relation to body length of sei whales caught off western Norway.

The weights of testes and ovaries in relation to body length for 38 males and 39 females with both reproductive organs intact, are shown in Figs. 3 and 4 respectively. The combined weights of testes of immature males ranged between 0.2 kg and 1.3 kg, while the corresponding data for mature males were 2.0 kg and 10.8 kg. The largest immature male was 43 ft in length, while the smallest mature one was 42 ft. The combined ovary weights of immature females ranged between 0.04 kg and 0.8 kg while the corresponding data for mature females were 0.42 kg and 1.0 kg. The largest immature female was 44 ft in length while the smallest mature one was only 40 ft.

The percentages of mature males and mature females in relation to body length are shown in Fig. 5. The curves have been interpolated according to the formula $y' = \frac{1}{4}(X_1 + 2X_2 + X_3)$. The 50% mature figure in relation to length was just above 42 ft in the males and just below 44 ft in the females. Although the material is scarce, it may be concluded that male and female sei whales inhabiting the waters off western Norway attain sexual maturity at about 42 ft and 44 ft, respectively.

Among the mature females there were three animals with only a corpus luteum graviditatis in the ovaries. These animals, which had attained sexual maturity very shortly before being caught, were 42 ft, 43 ft and 44 ft in length.

Eight of the mature females were resting while nine were pregnant (one of which had the ovaries only partly intact), indicating a two-year reproductive cycle (see Discussion).

None of the females had milk in their mammary glands, which may indicate that females which have already weaned their calves appear off western Norway in the summer. However, the fact that females accompanied by a calf are not permitted to be caught must also be taken into consideration (see Discussion).

Table 3

Stomach contents of sei whales examined at each of the stations.

Stations		Stomach contents: Calanoids	Euphausiids	Calanoids and Euphausiids	Empty stomachs	Total
	1952	3	4	0	1	8
Steinshamn	1953	20	0	2	11	33
	Total	23	4	2	12	41
	1952	1	0	0	3	4
Blomvåg	1953	0	0	0	1	1
	Total	1	0	0	4	5
	1952	1	0	0	0	1
Hestnes	1953	0	1	2	2	5
	Total	1	1	2	2	6
	1952	5	4	0	4	13
Total	1953	20	1	4	14	39
	Total	25	5	4	18	52
Percent		48.1	9.6	7.7	34.6	100

Table 4

Stomach contents of sei whales examined in different months.

Month	Calanoids 1952	Calanoids 1953	Calanoids Total	Euphausiids 1952	Euphausiids 1953	Euphausiids Total	Calanoids and Euphausiids 1952	Calanoids and Euphausiids 1953	Calanoids and Euphausiids Total	Empty stomachs 1952	Empty stomachs 1953	Empty stomachs Total
April	–	2	2	–	–	–	–	–	–	–	–	–
May	2	–	2	–	–	–	–	–	–	–	–	–
June	3	16	19	4	1	5	–	2	2	4	3	7
July	–	2	2	–	–	–	–	2	2	–	8	8
August	–	–	–	–	–	–	–	–	–	–	2	2
September	–	–	–	–	–	–	–	–	–	–	1	1
Total	5	20	25	4	1	5	–	4	4	4	14	18

The mean diameter of the smallest and largest corpus albicans was 0.9 cm and 4.6 cm respectively, and the corresponding figures for the corpus luteum graviditatis were 4.0 cm and 9.0 cm, with an overall average of 7.1 cm.

The highest number of corpora lutea recorded was 10, though the majority of the animals had less than 4 corpora.

DISCUSSION

When comparing the results of the postwar investigations with previous information on the eastern North Atlantic sei whale, an important point with regard to the breeding of this species needs to be discussed. Collett (1886) was informed by the whaling station managers that the majority of female sei whales caught off Finmark were pregnant. In later literature this statement has been cited by other authors, some of whom have not even mentioned that the information originated from whaling station managers. The accuracy of the information may be doubted, but it cannot be denied that it may be correct. If so, it indicates that the reproductive cycle may be less than two years. However, very little is known about segregation in eastern North Atlantic sei whales, and the possibility cannot be excluded that Finmark waters were visited mainly by pregnant females.

However, Ingebrigtsen (1929), who was a highly respected whaling captain cooperating with Norwegian scientists, gives the information that adult females when arriving off Møre (western Norway) in April were accompanied by calves, and that in this month pregnant females with foetuses from 10 to 40 cm in length were caught. This information, which is in all probability correct, indicates that even some of the females accompanied by calves, which were allowed to be caught in those days, may have been pregnant. If so, and if the calves – as supposed by Ingebrigtsen (1929) – were only one or two months of age, some of the females would have mated just after giving birth, as almost all North Atlantic minke whales do. The

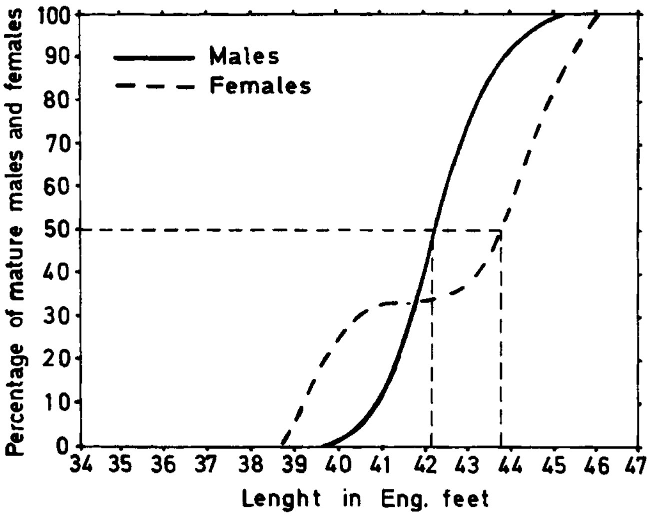


Fig. 5. Percentage mature male and female sei whales caught off western Norway, in relation to body length.

postwar material from western Norway, which mainly includes females caught in June and July, does not indicate any segregation in pregnant and resting animals. As females accompanied by calves are not permitted to be taken, some animals belonging to this category might have been present in the area in June and July. If so, and if such females were not pregnant, the two-year reproductive cycle indicated by the proportion of females in the catches will be somewhat longer. On the other hand, about half the mature females examined were pregnant and none was lactating, suggesting that the incidence of post-partum ovulations might not be high.

On balance, the available information on the breeding of the eastern North Atlantic sei whale indicates that the reproductive cycle in this species generally lasts two years. This statement is in excellent agreement with what is known for other larger species of baleen whales.

ACKNOWLEDGEMENTS

The investigation of the sei whale presented in this paper is only a part of the research programme carried out at the land stations in Norway in postwar whaling seasons. This fact may explain how important it was to have the most excellent cooperation with all persons engaged in the work. We are very much indebted to all of them, directors, gunners, whaling inspectors, and so many others, who contributed to make the programme successful.

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SC/27/Doc. 23

Application of White Scars to the Study of the Location and Migrations of Sei Whale Populations in Area III of the Antarctic

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Abstract

The incidence of white scars on the skin of sei whales is used as a method of distinguishing between different stocks of sei whales in Antarctic Area III. These scars are thought to be caused by bites from warm-water sharks while the whales are at the northern end of their migration range in winter. The number of fresh scars is much higher on whales in the South East Atlantic (average 242) than in the Indian Ocean sectors (average 25). Comparable differences in the degree of scarring are also observed using the frequency of scars on the side of the caudal peduncle only.

INTRODUCTION

A knowledge of the population structure of commercial whale species is the main basis for their efficient utilisation. At present nobody doubts the existence of local populations of sei whales, but the areas of their habitation and the demarcation lines between these areas, as well as peculiarities of the migration of sei whales, have not been investigated properly.

It is believed that within Area III of the Antarctic there is a feeding zone for sei whales from the East African and Crozet-Kerguelen populations. The warm water zone adjacent to this Area serves as the wintering region for the whales of three populations: East African, West African and part of the Crozet-Kerguelen population (Ivashin *et al.*, 1972). Winter and summer habitats of the above populations were determined as being mainly similar to local populations of fin whales in the area under consideration.

No morphological or physiological criteria have been established for distinguishing between sei whales from separate populations. This phenomenon is connected, no doubt, with the insignificant geographical variability of the species arising from the lack of geographical barriers between separate populations and the homogeneity of the environment and nutrition.

METHOD AND RESULTS

For the purpose of distinguishing sei whale populations in the south-east Atlantic and in the western part of the Indian Ocean, white scars, found as a natural marking on the body of every whale were used. It has long been known that pits and wounds, in the place of which white scars later appear, are found only in the warm zone of the oceans, so that their presence on the skin proves that the whale visited those areas (Lillie, 1915; Lows, 1961; Slijper, 1962).

It has also been noted that the number of white scars on the whale's body increases with age, as they accumulate on the skin, so it has been concluded that whales visit warm waters periodically, i.e. they regularly shift from the warm zone to the Antarctic (Mackintosh and Wheeler, 1929). The application of white scars to population assessment was started at the beginning of the 1950s by Japanese scientists (Omura, 1950; Ohno and Fujino, 1952).

Further investigation into the subject of whale migrations using the white-scar method was suspended due to the fact that the quantitative aspect of this phenomenon was not taken into account and the causes of these scars were not known. For example, the most popular assumption in recent years has been that these white scars appear as the result of bites of predatory lampreys (Pike, 1951). This assumption not only failed to explain the location in which scars appeared, but even complicated this problem, because the lamprey's distribution is much wider than that shown by the occurrence of white scars on the skin of whales, the habitat of the former covering moderate and even cold latitudes, where new oval and sickle-shaped wounds have never been noted on whale skin.

In 1970 the author ventured the hypothesis that the bites of small, warm-water sharks were the cause of white scar formation (Shevchenko, 1970). Jones (1971) independently concluded that the small shark (*Isistius brasiliensis*) might be responsible for fresh bite marks of a similar nature on small cetaceans and fishes. The habitat of such biting sharks is limited to warm water only. This region is here termed 'the vulnerable zone'. On the basis of holes and sickle-shaped wounds on the skin of sperm whales caught in warm waters, the limiting lines of the vulnerable zone in the regions under investigation have been established (Fig. 1). The examination of several minke whales (*Balaenoptera acutorostrata*), four sei whales and two pigmy right whales (*Carperea marginata*), caught in the warm zone of the south-east Atlantic proved that baleen whales also get bite-wounds in the same regions. The southern border of this vulnerable zone in November/December has been marked fairly clearly because many sperm whales caught north and south of it have been inspected.

The northern border has not been established because whaling in the tropical zone was limited in quantity and was not regular enough. However, it is reasonable to assume that such a border does exist, and does not extend to the equator; this is proved by the absence of new wounds and pits on sperm whales in the Gulf of Aden and in the Arabian Sea, and they have not been found on Bryde's whales caught for scientific purposes in 1965 in the Arabian Sea.

There were pits in different stages of healing on the bodies of sperm whales caught near the equator in the central part of the Indian Ocean, but no new wounds were found.

It has been determined that the latitudinal limits of the vulnerable zone in the eastern part of the Atlantic Ocean and in the western part of the Indian Ocean during the same month do not coincide. In the Atlantic Ocean new wounds were found down to 34° to 35°S, while in the

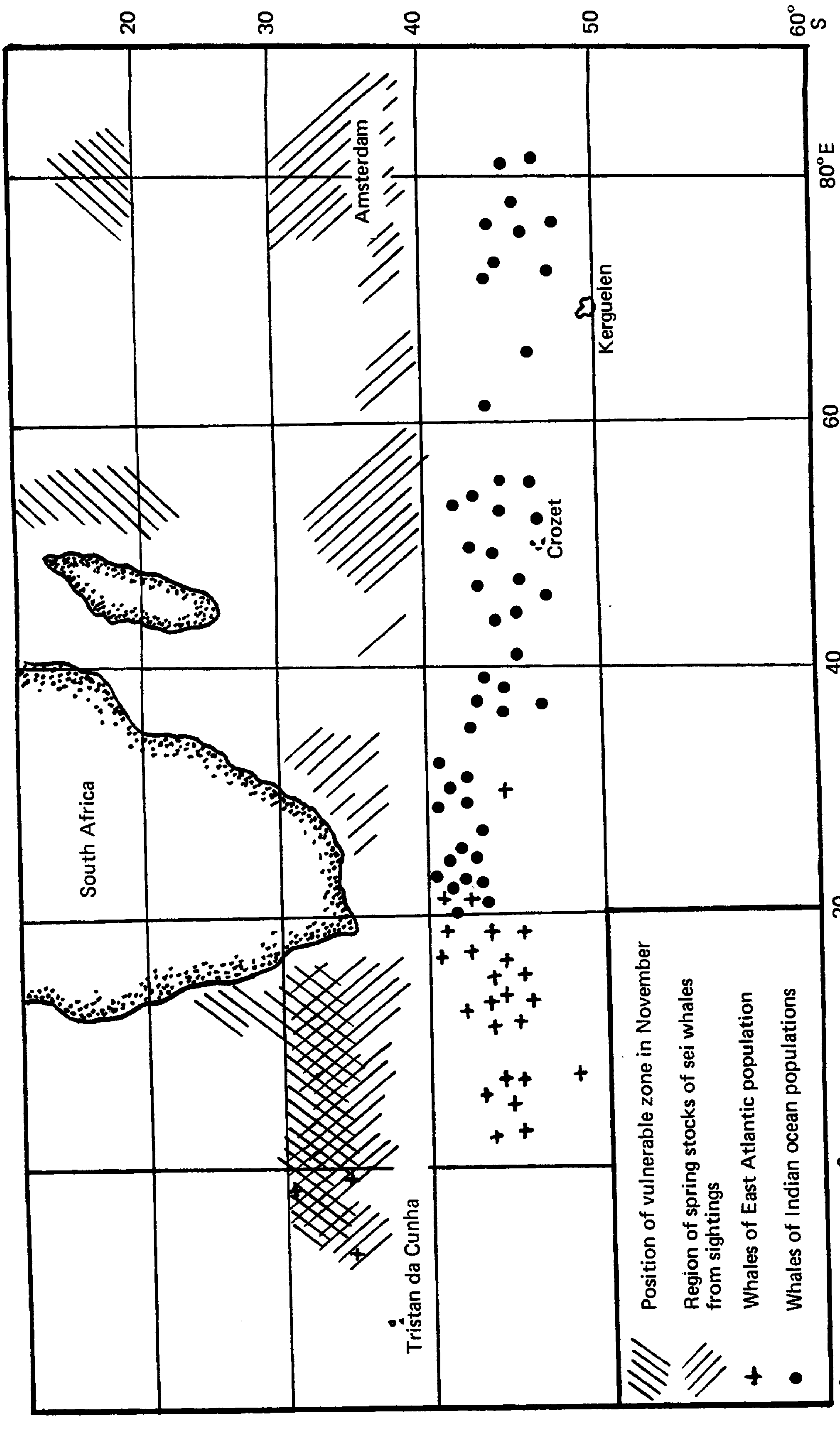

Fig. 1. Distribution of sei whales from different populations in Area III (according to data from a study of 'white scars'). Crosses and dots represent up to eight whales examined at one position.

Indian Ocean they were recorded north of 20° to 22°S. This phenomenon may be connected with different hydrological regimes (the shift of frontal zones in the Indian Ocean to the north) or it is possible that different species of small pelagic sharks have similar methods of feeding. Unfortunately, information on the biology and distribution of small sharks is insufficient at present, and many species are described on the basis of the examination of a few specimens only (Pinchuk, 1972).

It has therefore been found that new wounds on whales occur not over the whole area of the warm zone of the oceans, but only in certain areas (vulnerable zones), the borders of which have their own peculiarities in each ocean.

In order to establish the rate of white scar accumulation (the number of scars appearing during one winter period), a well-known fact was used: new scars (of the year of occurence) have a distinct white-coloured epidermis, ('bright white scars'). The calculation of the total number of bright white scars on the whole surface of sei whales, together with the number of pits not yet healed, was made at the beginning of the whaling season in latitudes between 40° and 50°S (Table 1).

The reasons for the different number of white scars accumulated annually on sei whales in the east Atlantic and in the regions of the Indian Ocean under investigation are, no doubt, connected with the differences in the latitudinal borders of the vulnerable zone mentioned above.

There is little information on the regions of winter habitation of sei whales. However, one may assume from the annual appearance of new scars on the skin that the whales reach the vulnerable zone (20°–22° S in the Indian Ocean and 34°S in eastern Atlantic). As a result of visual observations from whaling boats (Budylenko, 1970; Dolzhenkov, 1969; Golubovsky *et al.*, 1972; our information) it is possible to trace approximately the regions in which stocks of sei whales occur in spring (from the end of October to the beginning of December) in latitudes between 30° and 40°S (Fig. 1).

It was found that the limits of sei whale stocks in spring in the south-east Atlantic coincided mainly with the vulnerable zone, while in the Indian Ocean they were noticeable to the south of the border of the biting sharks' habitat. Sei whales of the west African population are therefore exposed to the sharks in spring two to three months longer (this being the approximate period of the spring stock's existence in these latitudes), and consequently they accumulate more white scars every year. This phenomenon accounts for the fact that in the latitudes from 40° to 50°S in the Atlantic Ocean, one may find small pits in place of old shark bites on the sei whales from December to February, while in the Indian Ocean such pits are found (in much smaller quantities) only in December: these wounds were probably healed during the time of the spring stock's existence beyond the vulnerable zone.

Table 1

Number of white scars on sei whales formed during the winter season

Region	No. of whales examined	Number of bright white scars Min.	Max.	Average	σ
South-east Atlantic (0°–15°E)	37	171	395	242.3	±2.6
Prince Edward Island (30°–42°E)	33	11	88	24.7	±0.2
Crozet–Kergeulen Island	42	8	64	25.6	±0.2

As a result of the different rate of accumulation of white scars on the whales of the south-east Atlantic and of the Indian Ocean, the total number of white scars present on their bodies is different, and this difference is so extreme that even on superficial inspection a whale from one ocean differs in appearance from a whale of the same size but from the other ocean (Fig. 2). Sei whales of the west African population seem parti-coloured as they are covered with white spots, while sei whales from the western part of the Indian Ocean seem a plain, light grey with infrequent white scars on the skin.

For the purposes of population analysis, and because of the difficulty of calculating the total number of bright white scars (BWS) on the bodies of whales, it is possible to confine oneself to the number on one side of the caudal peduncle (from the level of the posterior end of the dorsal fin to the beginning of the tail flukes), and to estimate the degree of spottedness according to a five-unit system, as follows:

'very little' – white scars (including BWS) within limits of 5–30 per animal;
'little' – white scars (including BWS) within limits of 30–60 per animal;
'moderate' – white scars (including BWS) within limits of 60–200 per animal;
'many' – white scars (including BWS) exceed 200 and are impossible to count because they are too numerous and overlapping;
'very many' – marble-like pattern on caudal peduncle.

From Table 2 it is possible to see that spotted colouration ('many' – 75.6%) is the most frequently observed condition for sei whales of the west African population, and that a considerable number of these animals (19.5%) had a marble-like pattern on the caudal peduncle. By contrast, in the Indian Ocean animals with a weak spottedness prevailed. On this basis (frequency of occurrence of different degrees of spottedness) only, it is possible to attribute a particular group of whales investigated to the west African or Indian Ocean population with some degree of confidence.

The number of bright white scars on one side of the caudal peduncle is an additional feature for attributing individual specimens to certain stocks (populations). In both oceans one can see whales in the narrower size range of 14.0 to 14.5 m with a degree of spottedness classified as 'moderate' or 'many'. However, in the south-east Atlantic from 30 to 74 bright white scars are found on such animals (average being 51.2), while in the Indian Ocean there are only 2 to 21 (average being from 5.7 to 6.1, depending on the region).

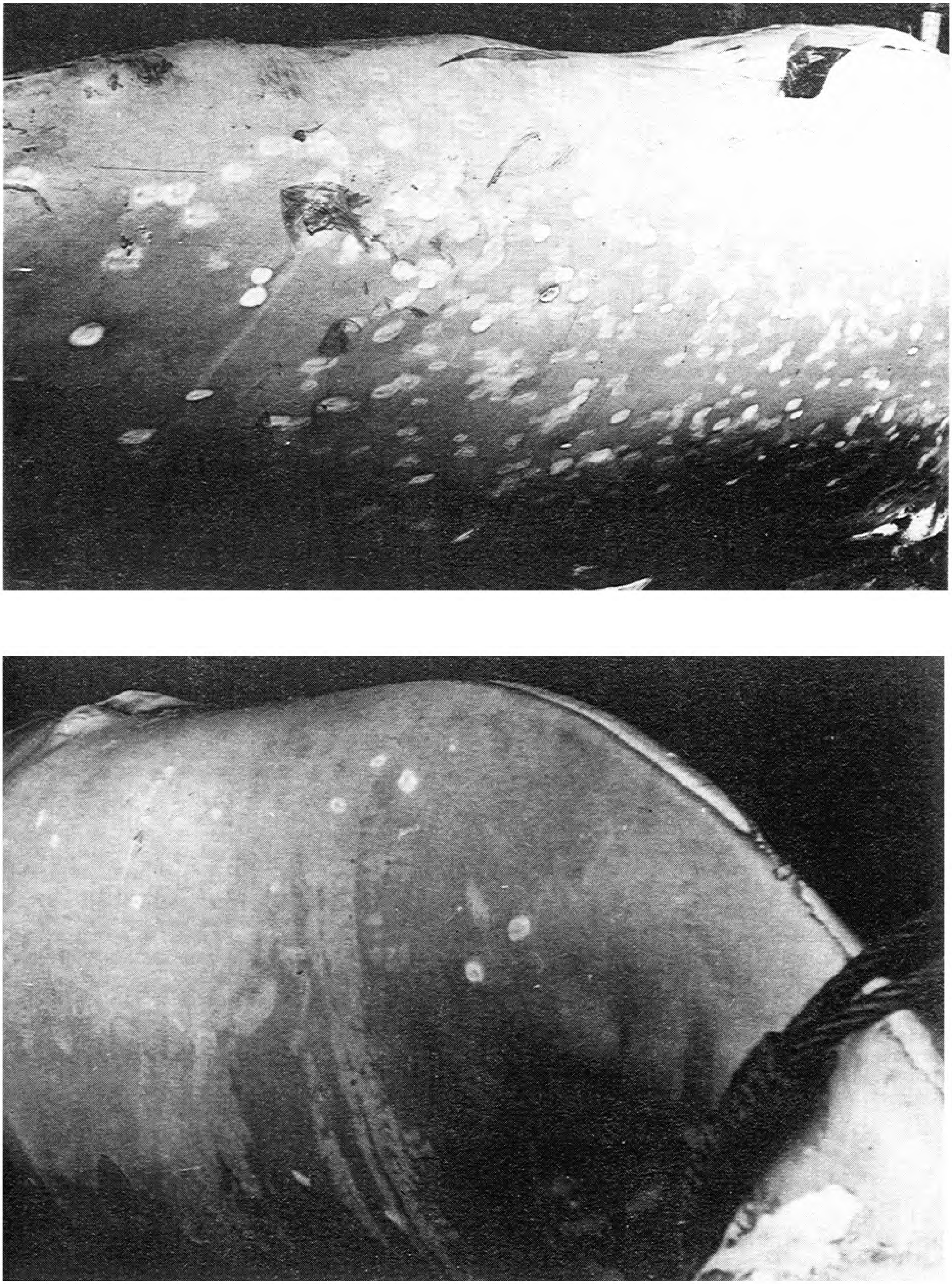

Fig. 2. Degree of spottedness of sei whales. Above: 13.8 m female from the west African population (46°S, 10°E). Pits at a late stage of healing may be seen. Below: 14.1 m female from the Crozet-Kerguelen population (region of Kerguelen Island).

Table 2

Results of caudal peduncle inspection of sei whales from different regions of Area III.[1]

Region	No. inspected	Mean BWS	% of whales with pits	Degree of spottedness (%) very little	little	moderate	many	very many
S.E. Atlantic (0°–15°E)	41	51.2	82.9	–	–	4.9	75.6	19.5
Prince Edward I. (30°–42°E)	31	5.7	9.7	32.3	41.8	22.6	3.2	–
Crozet–Kerguelen I.	47	6.1	–	36.2	36.2	27.6	–	–

[1] The above data were collected from the end of December to January in latitudes 40° to 50°S from male whales 13.5 to 14.5 m long.

DISCUSSION

The method of differentiating between sei whale populations in the south-east Atlantic and in the western part of the Indian Ocean from the number of white scars on their bodies is fairly simple, not labour-consuming, reliable, and allows collection of much information and facts.

According to the number of white scars on their body, sei whales of the west African population clearly differ from sei whales from the western part of the Indian Ocean. Animals from the east African and Crozet-Kergeulen populations are similar in this feature.

The study of sei whale stock structure at the merging of two oceans is especially interesting, because according to a recent diagram of migrations (Ivashin *et al*, 1972), sei whales from the east African population partly feed in the eastern part of the Atlantic Ocean up to the 0° meridian inclusive, and the west African population west of the 0° meridian. From the information collected by us between 40° and 50°S in Antarctic Area III, it is possible to conclude that the above diagram is not absolutely correct, in any case for this particular zone. Part of the sei whales from the west African population feed to the south of their places of winter habitation, i.e. from the zero meridian towards the east. Between neighbouring populations there is a rather clear demarcation line about 20°E, and only individual animals of the west African population extend as far east as the 30° meridian. Based on the data of the 1971/72 season, sei whales of different populations do not mix extensively on the feeding grounds in latitudes from 40° to 50°S. Individual animals, entering the adjacent region (Fig. 1) at the end of the season, probably return again to the main habitat of their population.

To our regret, we have no data on the population structure of sei whale stocks from 50° to 60°S on the South African transect because of the absence of whaling in this region in recent years.

The suggested method of sei whale stock-differentiation according to the number of white scars on their bodies may be effectively applied to distinguish between east and west Australian populations, because the borders of the vulnerable zone in the regions of their winter habitation are also different. In the Tasman Sea the southern border of the vulnerable zone coincides with 38° to 39°S, and in the eastern part of the Indian Ocean with 20° to 24°S.

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Calculation of Apparent Increases in the Antarctic Sei Whale Population Between 1930 and 1960

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Abstract

Recent evidence suggests that changes in reproductive rates of Southern Hemisphere sei whales occurred between 1930 and 1960, prior to direct harvesting (Gambell, 1975, 1977; Lockyer, 1974). Such changes imply an increasing population during this period. The possible magnitude of such changes are estimated here, using a computer simulation model based on work by Leslie (1945, 1948). For various sets of assumptions about the parameters involved, the population is estimated to have increased between 67% and 93% between 1930 and 1960. The annual rate of increase in 1960 is estimated to be between 4.9% and 6.2%. These estimates are shown to be quite sensitive to the description of the onset of sexual maturity.

INTRODUCTION

Because baleen whales have been heavily exploited in the Antarctic in this century their numbers have declined substantially. Considering the several species involved Gambell (1975, 1977) estimated that the total biomass declined between 1930 and 1960 from an initial 40 million tons to 11 million tons, a 72% decrease. Corresponding to this decline in numbers certain reproductive rates have apparently increased (Gambell, 1975, 1977). This increase in reproductive rates has occurred for both blue whales and fin whales as these populations have been harvested. It has generally been assumed that such changes are the individual population's direct response to exploitation, thus allowing a sustainable yield to be taken.

Recent information provided by Gambell (1975, 1977) and Lockyer (1974) suggests that similar changes in reproductive rates occurred for sei whales during the period from 1930 to 1960, when this species was not hunted to any significant degree, and hence these changes cannot be a direct response to exploitation. A reasonable hypothesis is that such changes are an indirect response by the sei whale population to the reduction in the numbers of blue and fin whales.

Whatever the cause of these changes, they must be accounted for in the management of the present hunting for sei whales in the Antarctic. In particular the concept of a pre-exploitation equilibrium population size, or 'carrying capacity', must be examined.

The purpose of this paper is to explore the consequences of the following deduction:

IF the Antarctic sei whale population was of 'equilibrium' size prior to the large-scale exploitation of baleen whales starting around 1925, and

IF the observed changes in reproductive rates are real and not compensated for by changes in mortality rates,

THEN the size of the Antarctic sei whale population increased between 1930 and 1960.

Although the assumptions in this deductive sequence are open for discussion, as are certain implied assumptions, such as a single 'stock' of sei whales in the Antarctic, it is of interest to determine the possible magnitude of such increases in population size.

The available data are given by Gambell (1975, 1977), Doi *et al.* (1967) and Lockyer (1974). Gambell reported the percentages of the mature females in the kill which were pregnant for each whaling season from 1946/47 to 1972/73, and the estimated age at sexual maturity for each year class from 1925 to 1946, and 1963. It is not clear if these ages of sexual maturity are for females or males and females combined. In the present analysis these values are applied to females. My reading of Gambell's graphs are given in Tables 1 and 2. Doi *et al.* gave estimates of the instantaneous natural mortality rate for mature sei whales ranging from 0.059 to 0.079. Lockyer reported the percentage of females sexually mature by age in her Fig. 4. My reading of her graph is given in Table 3.

Table 1

Percentage of mature female sei whales in the Antarctic catch from 1946/47 to 1972/73

(after Gambell, 1977)

Season	% Pregnant	Season	% Pregnant
1946/47	22	1959/60	45
1947/48	26	1960/61	50
1948/49	24	1961/62	48
1949/50	39	1962/63	54
1950/51	29	1963/64	50
1951/52	41	1964/65	51
1952/53	42	1965/66	48
1953/54	41	1966/67	48
1954/55	34	1967/68	51
1955/56	48	1968/69	56
1956/57	40	1969/70	60
1957/58	42	1970/71	57
1958/59	51	1971/72	55
		1972/73	53

METHODS

In this paper I use a mathematical model based on work by P. H. Leslie (1945, 1948). In this approach one considers each age class separately. The parameters of this model are the individual annual reproductive and survival rates. Leslie originally considered only the situation where

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Table 2

Estimated age at sexual maturity of sei whales for year classes 1925 through 1946, and 1965

(after Gambell, 1977)

Year class	Age at sexual maturity	Year class	Age at sexual maturity
1925	10.7	1937	9.9
1926	10.2	1938	10.0
1927	10.6	1939	10.1
1928	11.7	1940	8.7
1929	10.9	1941	9.8
1930	11.4	1942	9.7
1931	10.2	1943	9.1
1932	11.4	1944	10.0
1933	11.7	1945	10.7
1934	11.0	1946	9.0
1935	10.2	–	–
1936	10.7	1965	8.0

Table 3

Percentage of female sei whales by age class which were sexually mature (after Lockyer, 1974)

Age (years)	Percent mature	Sample size
1	0.0	2
2	0.0	3
3	0.0	7
4	25.0	4
5	0.0	3
6	33.3	9
7	20.0	5
8	31.7	6
9	75.0	4
10	66.7	6
11	0.0	1
12	100.0	6
13	100.0	6
14	100.0	3
15	100.0	5
16	75.0	4
17	100.0	1
18	100.0	3
19	100.0	1
20	100.0	3

these rates have fixed values. He derived the matrix equation:

$$\tilde{N} \cdot \vec{N}_t = \vec{N}_{t+1} \qquad (1)$$

where $\tilde{M}$ is a matrix containing these rates, and $\vec{N}$ is the vector of numbers in each age class. Thus the total population size at time t is the sum of the elements of the vector $\vec{N}_t$.

In reality, however, reproductive and survival rates may vary in time. Leslie's original formulation can be enlarged to allow for this situation (Leslie (1948), Pennycuick (1969), Smith (1973)). One obtains a corresponding matrix equation, in the present case,

$$\tilde{M}(t) \cdot \vec{N}_t = \vec{N}_{t+1} \qquad (2)$$

Here $\tilde{M}(t)$ denotes the matrix of reproductive and survival rates as functions of time, t. In general this equation is intractable to analysis, but does allow the simulation of $\vec{N}_t$ over time. With the proper definition of $\tilde{M}(t)$, this allows the determination of the population size and age structure after an arbitrary period of time.

The age specific fecundity parameters used in this model, denoted F_i, are the number of daughters which survive to their first birthday which are produced by a female of age i. The age specific survival parameters, denoted S_i, are the fraction of the individuals of age i which survive to age i+1. In the present case the fecundity parameters are functions of time, $F_i(t)$. The survival parameters are assumed constant.

The following equations relate these model parameters to the observed data.

$$E_i(t) = \delta \cdot Q(i, t) \qquad (3)$$

where

$$Q(i, t) = 1/(1 + EXP(-R \cdot (i - A(t-1))))$$

$$\delta = \begin{matrix} 1 \text{ if } Q(i,t) > C \\ 0 \text{ if } Q(i,t) \leq C \end{matrix}$$

$$A(\tau) = a_1 + a_2 \cdot \tau + a_3 \cdot \tau^2 \qquad (4)$$

$$P(t) = b_1 \cdot b_2 \cdot t + b_3 \cdot t^2 \qquad (5)$$

$$CI(t) = G/(P(t) \times 0.01) \qquad (6)$$

In these equations

$E_i(t)$ is the fraction of females age i which are mature in year t;
R is the rate parameter which determines the shape of the maturity function E;
C is a clipping value to avoid animals becoming sexually mature too early;
$A(\tau)$ is the age at which 50% of the females of year class τ are sexually mature, with constants a_1, a_2, a_3;
P(t) is the percent of the mature females which are pregnant in year t, with constants b_1, b_2, b_3;
CI(t) is the interval between successive births in year t;
G is the length of the gestation period in years.

The age specific fecundity parameters F_i are then defined as:

$$F_i(t) = E_i(t) \cdot SX \cdot S_0/CI(t), i = 1, K \qquad (7)$$

where SX denotes the sex ratio at birth, S_0 denotes the annual survival of immature females, and K denotes the maximum age attainable.

The age specific survival parameters are defined as:

$$S_i(t) = E_i(t) \cdot S_m + (1 - E_i(t)) \cdot S_0, i = 1, K-1 \qquad (8)$$

where S_m denotes the annual survival of mature females.

In this model two separate survival rates are considered, S_m and S_0. It is assumed that the survival rate is constant from birth to sexual maturity, after which it changes to a new rate which is constant until age sixty. The survival rate after age sixty is zero. It would probably be more realistic to consider a third rate, survival from birth to age one. However, sufficient information does not appear to be available to allow such a parameter to be estimated.

The values given to the various parameters in this model are derived from the references cited above. The parameter R in equation (3) was estimated by fitting a logistic equation to the data in Lockyer's (1974) Fig. 4, as shown in Table 3. The estimation was done by least square fitting of $\log_e ((1/X) - 1)$ to age, where X denotes the fraction sexually mature at each age. For those ages where X was zero, X was set to 0.01, and where 1.0, set to 0.99. Using the 18 mean values, R = 0.578. This fitted equation is shown in Fig. 1. Because of the relatively small sample sizes at each age class and because of the variability between successive ages, this parameter estimate is probably rather variable. Its formal statistical variance could be calculated approximately, but this calculation was not done. In the simulation runs a value of R = 0.50 was used. Alternate calculations were done with values of R of 0.4 and 0.6 to examine the sensitivity of the estimated 1960 population size to this parameter.

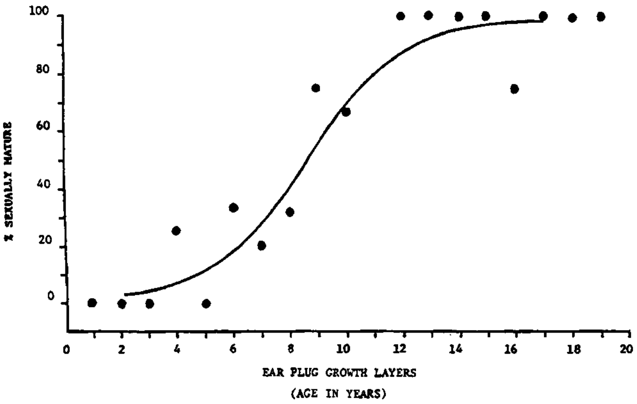

Fig. 1. Percent of each age class which is sexually mature in female sei whales at Durban (after Lockyer, 1974). Data points are represented by dots, fitted logistic equation by solid line.

The parameter C in equation (3) determines the truncation for the logistic maturity function Q(i,t) for younger animals. It prevents the model from allowing some animals to mature sexually at very young ages. Alternate calculations were done with values of C of 0.05 and 0.15 to examine the sensitivity of the estimated 1960 population size to this parameter.

Equation (4) describes the mean age at sexual maturity for the various year classes. A second order polynomial was used to describe the data in Table 2, as shown in Fig. 2. The data prior to 1930 were omitted from the estimation of the parameters a_i, i = 1, 2, 3, in order to obtain a better fit over the period 1930 to 1960.

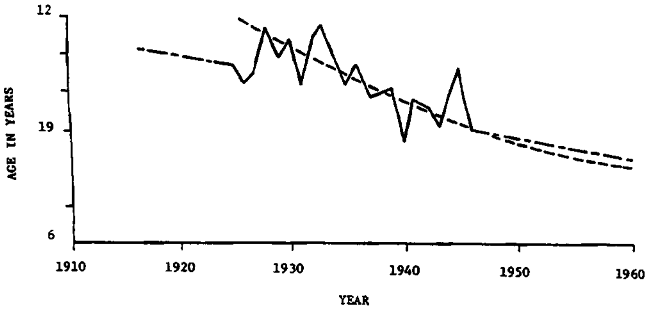

Fig. 2. Mean age of sexual maturity of sei whales for various year classes of southern sei whales (after Gambell, 1977). Solid and dot dash line represents data points; short dashed line represents fitted polynomial in equation (4).

Equation (5) describes the proportion of the mature females which were pregnant in each year's catch. Again a second order polynomial was used, as shown in Fig. 3.

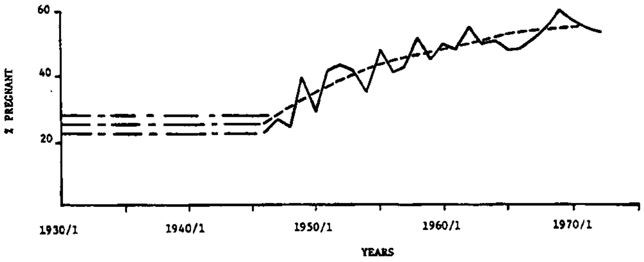

Fig. 3. Percentage of pregnant sei whales in the Antarctic pelagic catch of mature non-lactating females (after Gambell, 1975). Jointed line represents data points; dashed line represents fitted polynomial in equation (5); dot-dashed lines represent initial values of pregnancy rates.

All of the data were used in estimating the parameters b_i. The estimated values of these constants in equations (4) and (5) are shown in Table 4.

As the data on percentage pregnant only goes back to 1946/47, it is necessary to make assumptions about the rates between 1930 and 1946. The minimum pregnancy rates for both fin and blue whales appear to be around 25% (Gambell, 1975, 1977). The 1946/47 value for sei whales is around this value, and it is not unreasonable to suppose it did not change greatly between 1930 and 1946. Due to the variability in the observations of pregnancy rates it is not clear what value to use, however, if one does assume constancy over this time period. Three possibilities were examined here; namely, the values obtained from equation (5) for 1945, 1946 and 1947, of P(1945) = 0.223, P(1946) = 0.247 and P(1947) = 0.270, respectively. These are shown by the dash-dot lines in Fig. 3.

The length of the gestation period in equation (6) was assumed to be one year (Gambell, 1968). The sex ratio at birth was assumed to be 0.5 females as is frequently assumed for large whales. The maximum age attained was assumed to be 60 years, and this is checked below.

Table 4

Estimated values of parameters a_i and b_i in equations (4) and (5), respectively

	i		
Parameter	1	2	3
a	16.95	−0.236	0.00151
b	−181.805	6.625	−0.0464

The estimate of the survival rate S_m in equation (8) was taken directly from Doi *et al.* (1967). Those authors estimated the instantaneous coefficient of natural mortality from the age structures of the catches in the early 1960s. A range of 0.059 to 0.079 was given in that paper, corresponding to a range of annual survival rates of 0.9427 to 0.9240.

The parameter S_o, the survival of immature sei whales, in equations (7) and (8) was determined from the other parameter values and under the assumption that the population was in equilibrium prior to 1930. A value of S_o was obtained for each combination of other parameters at time 1930 such that

$$\tilde{M}(1930) \cdot \vec{N}_{1930} = \vec{N}_{1930}$$

This was done iteratively using techniques described by Smith (1973). With these survival rates the fraction of females still alive after 60 years is between 1.9% and 2.2%, while the fraction of the population at age 60 is less than 0.1%.

RESULTS

With these parameter values the elements of the matrix $\tilde{M}(t)$ were constructed. Starting in 1930, the value of $\tilde{N}_{1960}$ was computed. The total population size in 1960 is then the sum of the sixty elements of this vector, say N_{1960}. The percentage increase in population size from 1930 to 1960 is reported in Table 5. The growth rate of the population between 1959 and 1960 is also given, being $\log_e (N_{1960}/N_{1959})$.

The calculations summarised in Table 5 suggest that the changes in the reproductive rates of sei whales reported by Lockyer (1974) and Gambell (1975, 1977) were of sufficient magnitude for the population to have increased by a considerable amount between 1930 and 1960. For the various range of parameters considered here the percentage increase in the population varies between 47% and 66%, and the population growth rate in 1960 is seen to lie between 0.040 and 0.048. The sensitivity of the predicted change in the population between 1930 and 1960 to varying the rate at which sexual maturity occurs with age (R in eq. 3) and the minimal proportion sexually mature (C in eq. 3) depends on both C and R, especially for R small. The overall sensitivity is, however, of the order of only a few percent for the range of values considered.

DISCUSSION OF ASSUMPTIONS

Several of the assumptions inherent in these calculations need to be examined further. One obvious problem is that the pregnancy rates from the kill data may be biased because lactating females are protected. As this bias may be countered by underestimating the numbers actually pregnant, it is not clear what correction, is any, is necessary (Gambell, 1977).

A second point is the effect on the model if the survival rates were not constant during the period of increasing reproductive rates. The survival rate estimates given by Doi *et al.* (1967) are based on catch data since 1960, so to an extent these represent mortality rates in 1960 rather than in 1930. If the survival rates did change during this period the above calculations on the magnitude of the population change are in error. If the survival rates increased during this period, the calculated changes are overestimates, whereas if the survival rates decreased, the changes are underestimates.

The problem of estimating survival rates is further complicated if the population did in fact increase between 1930 and 1960. Doi *et al.* (1967) appear to have estimated mortality coefficients by sex for each year's catch. As the age of full recruitment to the fishery is about 20 years, and due to problems of determining age in older animals with an age-length key, only that part of the catch aged between 20 and 45 years was used in estimating the mortality coefficient. The regression of the logarithm of numbers on age appears to have been used.

As is well known, valid estimates of mortality rates can be obtained from the age structure at a point in time if the population is in equilibrium, with constant year class strength, constant mortality rates, and constant total size. If in fact the Antarctic sei whale population increased between 1930 and 1960, these assumptions do not hold. It may be possible, however, to derive valid estimates of mortality rates from portions of the age structure if the mortality rates have not changed during this period of population increase.

The period during which the population may have been increasing is 30 years. The age structure for animals beyond age 30 should, therefore, reflect the pre-exploitation equilibrium conditions, while age structure for animals less than 30 years should include the effects of the increasing recruitment rates.

The magnitude of these effects can be explored by estimating mortality rates from the simulated age distribution $\tilde{N}_{1960}$. For the model with an initial percentage pregnant of 0.247, P(46), and coefficient of mortality of 0.0590, the coefficient of mortality estimated (Chapman and Robson, 1960) from the age distribution of animals aged 30 to 45 is 0.0582. The corresponding rate estimated from ages 1 to 15 is 0.1580. This latter estimate is to be compared to the assumed immature mortality coefficient of 0.1092, and can be seen to be grossly biased.

To check the validity of the estimates provided by Doi *et al.* (1967) the simulated age structure from age 20 to 45 can be used in the above fashion. The resulting estimate of the coefficient of mortality is 0.0617, very close to the value used in the simulation.

These calculations suggest that the estimates of the coefficient of natural mortality calculated on a portion of

Table 5

Estimated changes in the size of the Antarctic sei whale population between 1930 and 1960

		Sm					
Initial percent pregnant		Survival rate = 0.9427 (Mortality coefficient = 0.059)			Survival rate = 0.9240 (Mortality coefficient = 0.079)		
P	R	S_o	Population increase %	Growth rate in 1960	S_o	Population increase %	Growth rate in 1960
(1945) 22.3	0.50	0.9488	66.1	0.048	0.9691	66.8	0.050
(1946) 24.7	0.50	0.9405	55.6	0.044	0.9606	55.5	0.046
(1947) 27.0	0.50	0.9332	47.2	0.040	0.9531	46.8	0.042

the age distribution of the catch in the early 1960s are not biased significantly by growth of the population between 1930 and 1960. Thus it can be concluded that if the mortality rates have not changed during this period of growth of the population, then the estimates given by Doi *et al.* (1967) are reasonable.

A third point which needs to be considered at much greater length is the rate at which sexual maturity is attained with age. This is incorporated in the parameter R in equation (3) in this model. It is important to consider in greater detail the possible shape of this relationship and possible changes in its shape over time. The nature of the relationship for very young animals is important due to the higher reproductive value of these animals. Additional information is needed here.

A fourth important point is that the pregnancy rates are given only in the aggregate for a year's catch. It would be of interest to segregate this rate by year class and/or by age. The latter may be very important if the pregnancy rate changes with age.

A final point is the biological basis for the changes in reproductive rates which have been observed. In this model it is assumed that the age of sexual maturity is fixed for a year class while the pregnancy rate is determined by prevailing environmental conditions in each year. This is assumed primarily because of the way the data are presented in Lockyer (1974). An understanding of how these changes are effected is important here.

IMPLICATIONS FOR MANAGEMENT

If as is suggested here the Antarctic sei whale population was increasing prior to initial exploitation in the early 1960s, then the concept of single-species maximum sustainable yield is not immediately applicable to determining optimum harvesting levels. In particular there is no meaningful equilibrium population size as a known reference point. The other species of baleen whales in the Antarctic must be considered before any sort of equilibrium can be defined. The population dynamics tools required for multispecies exploitation need to be developed.

One approach toward multispecies population dynamics has been explored briefly (Smith, 1974). It appears from that work that the crucial information needed is a measure of interspecies interaction. A possibility here would be to relate this interaction to changes in geographical and temporal distributions of the populations involved.

It would be anticipated that such a multispecies approach to management would allow many alternate management strategies. For instance, if one were to attempt to manage in order to allow depleted populations to regain their earlier abundance, it might be advisable to maintain competing populations at relatively lower levels so as to minimize competition. Such an approach hinges on the assumption that changes in the structure of ecosystems (of the magnitude of the reduction of baleen stocks in the Antarctic) are reversible.

A second approach to determining management goals is to consider only the sei whales in the Antarctic. It appears on biological grounds that this population may be reaching its maximum rate of increase. If so, in the absence of hunting it would have continued to increase at this rate for some time. Eventually, though, the population would have become large enough to cause the rate of increase to start to decline. It appears intuitively that, in the absence of competing baleen species, the population size giving maximum sustained yield is greater than or equal to the population size at which the rate of increase first starts to decrease. Thus if single-species population dynamics are still reasonable, the maximum sustained yield would be obtained with the management goal being to allow the sei whale population to increase at least until its rate of increase starts to decline.

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SC/SP 74/Doc. 23

Bryde's Whales in the Pelagic Whaling Ground of the North Pacific

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INTRODUCTION

Systematic studies of the Bryde's whale (*Balaenoptera edeni*) in the North Pacific were developed by the endeavour of Dr. Hideo Omura and his colleagues (Omura, 1950a; Omura, Nishimoto and Fujino, 1952; Omura and Fujino, 1954; Omura, 1959), and several papers were published on the ecology of this species in the North Pacific by Omura (1950b), Mizue (1950), Omura and Nemoto (1955), Nishiwaki, Hibiya and Kimura (1954), Nemoto (1959), Omura (1962) and Omura and Ohsumi (1964).

However, the population assessment of the Bryde's whale has remained in a primitive stage, though some preliminary analyses were tried by Doi, Nemoto and Ohsumi (1967) and Ohsumi, Shimadzu and Doi (1971) on the Bryde's whale from the western region of the North Pacific. Because this species is distributed widely in tropical and sub-tropical waters even in summer, and catches have been prosecuted in a small part at the north-west margin of its wider distribution in the North Pacific, catch results do not represent the whole population. In practice, it is impossible to assess the population without biological data from the open sea.

As pelagic whaling grounds shifted southward in the North Pacific in recent years, whaling fleets began to take Bryde's whales in 1970, and biological data from the open sea have gradually accumulated since then.

The present paper is mainly based on the biological data which were obtained from the Bryde's whales caught by Japanese whaling fleets in the years 1971 to 1974. USSR whaling fleets have also caught this species since 1970, and catch statistics which were sent from USSR have been used in some parts of this paper. The Whales Research Institute conducted biological research on the whales caught by Japanese coastal whaling during the years 1959 to 1965, and some of these data are also used in this paper.

CATCH

Brief history

Bryde's whales have a long catch history in waters adjacent to Japan, but they were formerly confused with sei whales (*Balaenoptera borealis*), and recorded as sei whales in the whaling statistics, though some whalers recognised them as a different type of sei whale.

Bryde's whales have been identified by whalers since 1955 due to the endeavour of Dr. Omura and his colleagues. Meanwhile, so-called sei whales which were caught in pelagic whaling around the Bonin Islands during the years 1946 to 1952 were recognised to be actually Bryde's whales (Omura and Fujino, 1954). Therefore 1946 was the first year when Bryde's whales were caught by pelagic whalers in the North Pacific.

Pelagic whaling did not include Bryde's whales from 1952 to 1969, because it operated in the northern part of the North Pacific during these years. As the pelagic whaling ground shifted gradually southward since the middle of the 1960s to take sei whales, chances of encountering Bryde's whales increased. USSR whaling fleets caught 66 Bryde's whales in 1970 for the first time, and Japanese fleets took 109 Bryde's whales in the next year.

Table 1 shows the number of Bryde's whales caught from 1970 to 1974.

Table 1

Catch of Bryde's whales in the North Pacific in recent years.

Year	Coastal Japan	Pelagic		Total
		Japan	USSR	
1970	73	–	66	139
1971	172	109	638	919
1972	125	5	71	201
1973	71	2	656	729
1974	187	522	654	709+

Fig. 1 shows the annual catch of Bryde's whales since 1946. As noted in the introduction, they were included as sei whales until 1954. Catch data are therefore not available until that year, but catches of sei whales in pelagic whaling in the waters around the Bonin Islands were regarded as Bryde's whales, so that these catch data are shown in this Figure. There are large yearly fluctuations in the coastal whaling catch. It is considered that the availability of this species to coastal whaling is related to the size of the warm water mass in the whaling ground (Nasu, unpublished). The smallest catch in Japanese coastal whaling was 8 in 1966, and the largest was 504 in 1963. However, 919 whales were caught in the North Pacific in 1971, due to the large pelagic catch. Catch quotas for the Bryde's whale were included in those for the sei whale.

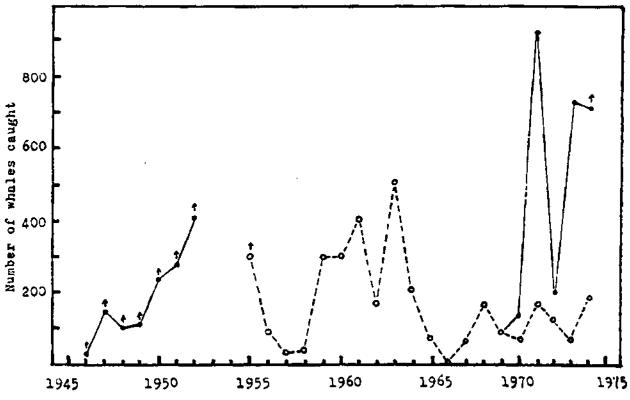

Fig. 1. Annual catch of Bryde's whales in the North Pacific. Open circle and broken line: coastal whaling, closed circle and solid line: total catch including pelagic whaling.

Whaling ground

Fig. 2 shows the number of Bryde's whales caught in each 10° square. Although Omura (1959) estimated that Bryde's whales are distributed between 40°N and 40°S, both USSR and Japanese whaling fleets took them in Zone–N (40°N to 50°N; squares N23, N24 and N25). Detailed data are not available from the USSR, but Japanese fleets took 109 Bryde's whales in the waters of 40° to 43°N, 171° to 177°E in 1971. However, the Japanese whaling ground for this species was mainly in the waters south of 35°N in 1974.

Pelagic catches show that the Bryde's whale is distributed densely in the central part of the North Pacific in summer, and it is not always a coastal species. Catch records have not been available from the waters east of 150°W, and this may be because the pelagic whaling ground in the North Pacific is legally restricted east of 150°W to the waters north of 35°N.

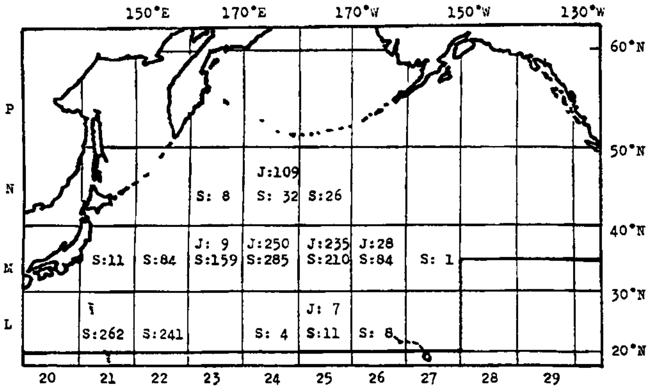

Fig. 2. Number of Bryde's whales caught by pelagic whaling in each 10° square during the years 1970 to 1974. J: Japanese whaling fleets, 1971 to 1974, S: USSR whaling fleets, 1970 to 1973.

Relation between catch and water temperature

It is clear from Fig. 3 that the Bryde's whale is distributed within warm water masses even in summer. The lowest sea surface temperature in the position where a Bryde's whale was caught was 16.3°C, and only 1.3% of whales were caught in waters below 18.0°C. Nemoto (1959) reports that Bryde's whales are migrating in water temperatures of more than 18°C and never visit water colder than 15°C in general. His conclusion is still applicable to the open sea, but isotherms of 20°C as the limit of distribution in summer, as Omura (1959) estimated, are higher than the actual figures.

The highest surface temperature from which Bryde's whales were caught was 26.9°C, but Nemoto (1959) reported that they were observed in waters of 28° to 29°C around the Bonin Islands in early summer.

Fig. 3 also shows the relation between water temperature and catches of fin and sei whales. Only 2.7% of sei whales were caught in waters warmer than 20.0°C. In the case of fin whales, 97.6% were caught in waters colder than 15.0°C.

Whaling season

Table 2 shows the number of Bryde's whales caught in each month from May to October. The reason why the catch in July is comparatively small is that whaling mainly operated in the northern part of the North Pacific in this month.

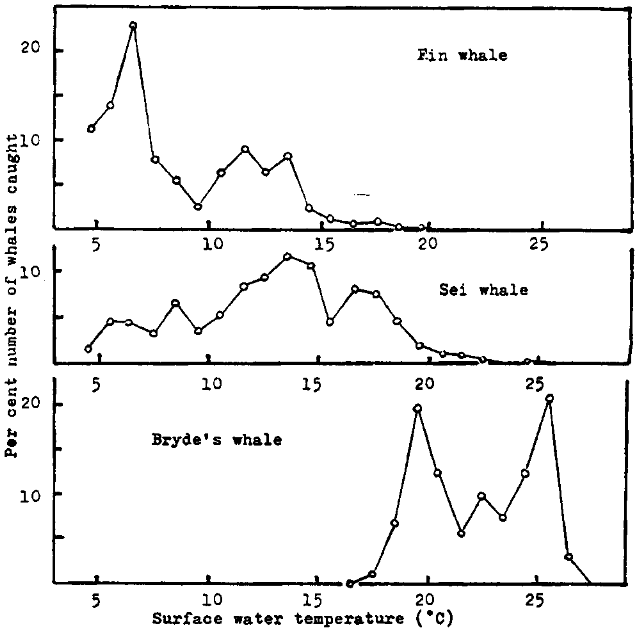

Fig. 3. Frequency distributions of water temperature in the positions where whales were caught by Japanese fleets from May to September, 1971 to 1974.

Table 2

Catch of Bryde's whales by pelagic whaling in the North Pacific.

Month	JAPAN (1971–74)	USSR (1970–73)	Total	%
May	86	16	102	4.9
June	177	547	724	35.1
July	18	134	152	7.4
August	305	162	467	22.6
September	52	359	411	19.9
October	–	208	208	10.1

Fishing effort and catch per unit effort (CPUE)

It is very difficult to estimate the actual fishing effort for Bryde's whales, as for other species. The catch of Bryde's whales is closely related to water temperature as noted above, and only 0.16% of the whales were caught in waters colder than 17.0°C. The quota for Bryde's whales was also included in the sei whale quota. I therefore consider in the present paper that fishing effort (Catcher's Day's Work = CDW) for this species is estimated to be CDW in waters warmer than 16.9°C during the sei whaling season.

Table 3

Fishing effort and catch of Bryde's whales by Japanese whaling fleets.

Year	CDW	Catch	CPUE
1971	139	109	0.78
1972	453	5	0.01
1973	343	2	0.01
1974	763	522	0.68

Table 3 shows the estimated fishing effort thus calculated and the catch of Bryde's whales since 1971, when Japanese whaling fleets entered warmer waters for the first time and caught 109 Bryde's whales. More time was spent in warm waters in the next two years, but the catch was very small. A similar figure was obtained in 1974 as in 1971. There may be yearly fluctuations in the distribution and migration of Bryde's whales in the open sea, as in Japanese coastal waters. However, USSR fleets took many Bryde's whales in 1973, though Japanese fleets took only two whales in the same year. Another factor may be the difficulty of separating the effort for each whale species, so that the present figures of CDW do not represent the true values.

STOCK UNITS

Nemoto (1959) and Omura and Ohsumi (1964) reported evidence of the close relationship between Bryde's whales in the Bonin Islands, Sanriku and Kinan areas from whale marking. Bryde's whales marked in the waters around the Bonin Islands were recaptured in Sanriku and Kinan areas. Similar evidence has been obtained in recent years (Ohsumi and Masaki, 1975). As Nemoto (1959) portrayed their migration course, Bryde's whales in these areas can be regarded as belonging to the same stock.

No mark recovery has been recorded from the Bryde's whales caught by pelagic whaling east of 150°W though many Bryde's whales were marked in the waters between the Bonin and Hawaii Islands in the winter of 1971 and 1972 (Ohsumi and Masaki, 1973).

The separation of stock units from the catch distribution of Bryde's whales is still difficult, as shown in Fig. 2.

CATCH COMPOSITION

Sex ratio

Among 638 Bryde's whales caught by Japanese whaling fleets from 1971 to 1974, 377 or 59.1% were female, and according to USSR catch statistics, the proportion of females was 63.7% among 1,426 whales caught from 1970 to 1973. This may be partially caused by the legal size limit (40 ft) for pelagic whaling, females being selectively caught as they are larger than males. However, females are also dominant in the Sanriku area in coastal whaling, in which the legal size limit is 35 ft (Omura, 1962). Omura estimated that a segregation between males and females was taking place during migration. The foetal sex ratio will be noted in a following section.

Size distribution

Table 4 shows the size distribution of Bryde's whales caught by Japanese fleets from 1971 to 1974. The largest were 45 and 49 ft in males and females, respectively. USSR catch statistics show the largest were 51 ft in both sexes. According to Omura (1962), the largest were 48 and 49 ft in males and females, respectively. That of males in the present result is very small compared with other data.

The average body lengths of males and females are 41.21 and 42.33 ft., respectively. Females are about one foot longer than males.

Maturity rates

Sexually mature males were determined by means of testis weight. According to Nishiwaki *et al.* (1954), who examined testis tissues histologically, 75% of testis were mature at 0.74 kg in testis weight in Bryde's whales from the Bonin Islands. Thus I regard a male which has its larger testis weighing 0.8 kg or more as sexually mature. Sexually mature females are determined as whales which have one or more corpora lutea or corpora albicantia in the ovaries.

Sexual maturity rates are calculated from Table 4 to be 90.0 and 82.8% in males and females, respectively. These figures are relatively high.

Pregnancy rate

The average pregnancy rate of Bryde's whales caught on the pelagic whaling grounds during the years 1971 to 1974 is calculated to be 41.7%. It seems that there is a seasonal change in pregnancy rate as shown in Table 5. Pregnancy rate decreases gradually with month.

Ovulating whales (which have a corpus luteum in the ovaries, but in which no foetus was found) were observed frequently from May to August. The rate of ovulating females in mature whales in 5.1%. These whales seem to have just ovulated or to be in very early stages of pregnancy, and indicate that the Bryde's whale has a long breeding season.

Table 4

Size distribution of Bryde's whales caught by Japanese fleets from 1971 to 1974

Body length (feet)	Males				Females			
	Immature	Mature	Unknown	Total	Immature	Mature	Pregnant	Total
37	1	–	–	1	–	–	–	–
38	1	–	–	1	3	–	–	3
39	–	4	–	4	2	–	–	2
40	17	46	–	63	38	31	10	69
41	6	89	1	96	19	50	27	69
42	1	65	–	66	2	60	21	62
43	–	24	–	24	1	71	25	72
44	–	5	–	5	–	54	25	54
45	–	1	–	1	–	24	14	24
46	–	–	–	–	–	16	6	16
47	–	–	–	–	–	3	1	3
48	–	–	–	–	–	2	1	2
49	–	–	–	–	–	1	–	1
Total	26	234	1	261	65	312	130	377
Av. Length	40.12	41.33		41.21	40.28	42.76	42.81	42.33

Table 5

Sexual condition of female Bryde's whales in the pelagic whaling ground

Month	Immature	Mature	Pregnant	Ovulating	Total
May	15	59	27	2	74
June	13	78	42	5	91
July	2	9	4	2	11
August	28	148	51	7	176
September	7	18	6	–	25
Total	65	312	130	16	377

Corpora composition

Fig. 4 shows the frequency distribution of the number of corpora lutea and albicantia in ovaries of Bryde's whales. The maximum corpora number was 21, and the mode was at 2 corpora.

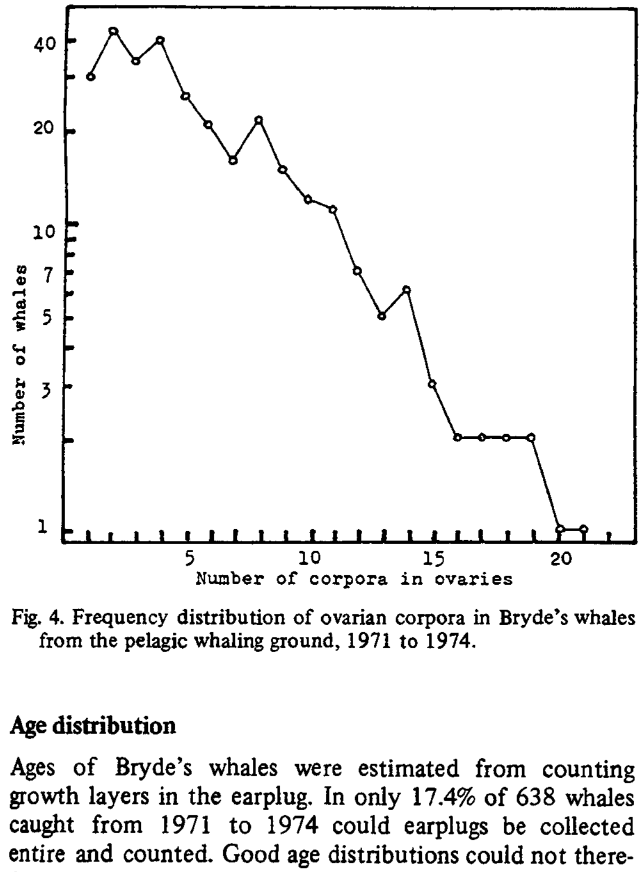

Fig. 4. Frequency distribution of ovarian corpora in Bryde's whales from the pelagic whaling ground, 1971 to 1974.

Age distribution

Ages of Bryde's whales were estimated from counting growth layers in the earplug. In only 17.4% of 638 whales caught from 1971 to 1974 could earplugs be collected entire and counted. Good age distributions could not therefore be drawn.

Fig. 5 shows an age distribution of Bryde's whales (males and females combined). The range of ages covered is between 3 and 38 years. According to the age determination of Bryde's whales caught in adjacent waters of Japan from 1959 to 1965 (see below), the oldest male was 55 years, and the oldest female was 52. The mode is situated at 18 years of age.

AGE-LENGTH KEY

Good age-length keys cannot be constructed using only the biological data of the whales caught by Japanese whaling fleets. Ages were determined for 103 males and 171 females of the Bryde's whales caught in Japanese coastal whaling from 1959 to 1965, and by adding these data to the present material, a set of age-length keys was made as shown in Appendix Tables 1A and 1B. However, the data are still too few in number to give good keys.

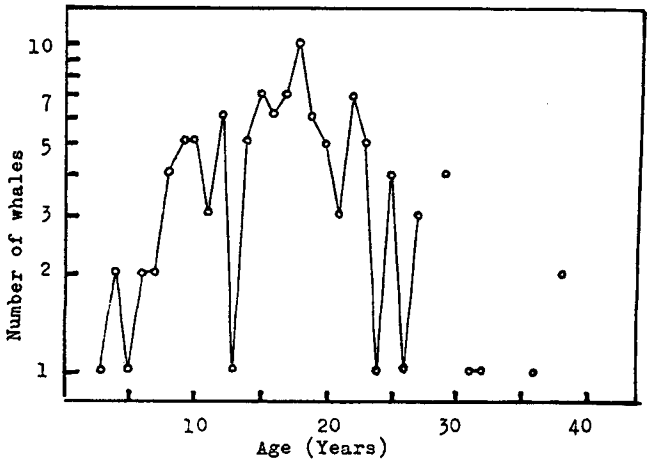

Fig. 5. Age distribution of male and female Bryde's whales caught by Japanese whaling fleets from 1971 to 1974.

Growth curves

Preliminary growth curves of males and females are drawn in Fig. 6. Due to the difficulty in collection, preparation and counting of earplugs in younger animals and to the legal size limit, the growth curves for younger ages are under-represented. Average maximum body lengths are 42.0 and 43.8 ft in males and females, respectively. Growth may stop by about 20 years of age.

BODY LENGTH AND AGE AT SEXUAL MATURITY

Body length at sexual maturity

It is difficult to estimate the body length at sexual maturity using catch results in pelagic whaling, for the legal size limit for pelagic whaling is set around the body length at sexual maturity as shown in Table 4, though it seems that males attain sexual maturity at less than 40 ft, and females do so around 40 ft in body length.

It is better to use biological data from the whales caught in coastal whaling in which the legal limit is set at 35 ft. Fig. 7 shows the relation between body length and sexual maturity of the Bryde's whales examined on the coast of Japan from 1959 to 1965. At the body lengths of 38.8 and 39.5 ft, 50% of males and females attain sexual maturity, respectively. Similar results are obtained from examination of the figures by Nishiwaki *et al.* (1954), and Omura (1962) reported that sexual maturity may be attained on average at a body length of around 39 ft.

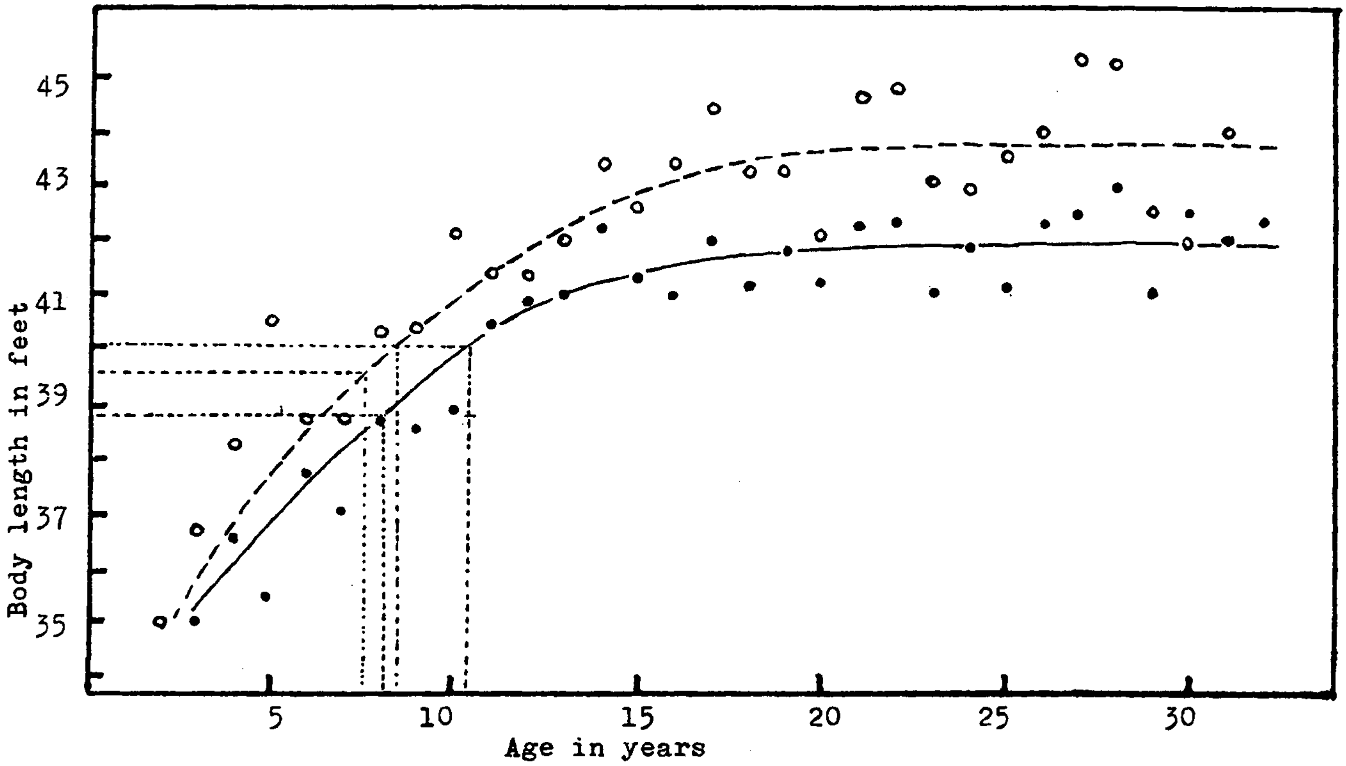

Fig. 6. Growth curves of the Bryde's whale in the North Pacific. Closed circle and solid line: males, open circle and broken line: females.

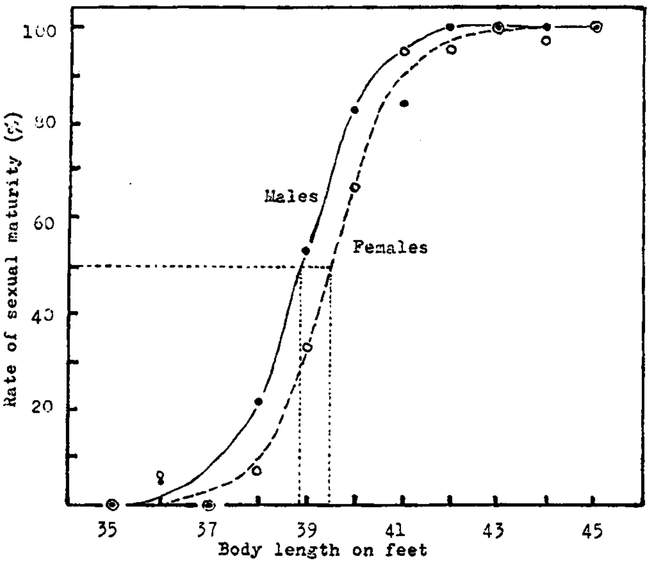

Fig. 7. Relation between body length and sexual maturity.

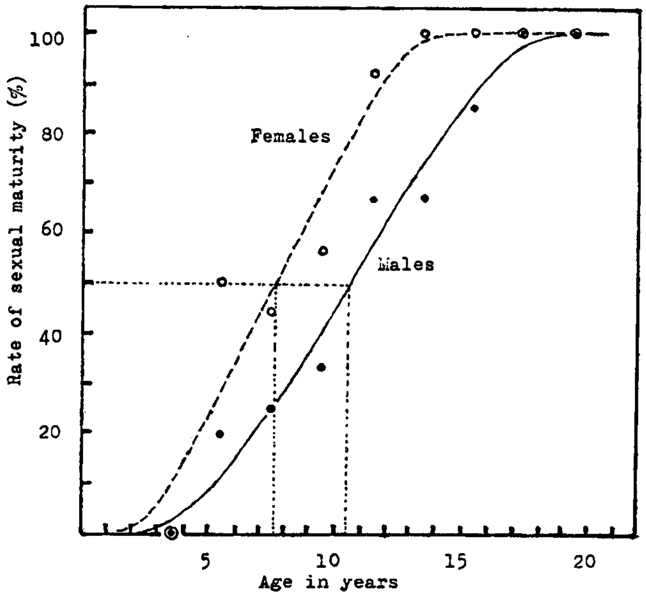

Fig. 8. Relation between age and sexual maturity.

Relation between age and rate of sexual maturity.

Fig. 8 shows the change in the rate of sexual maturity with age of Bryde's whales using materials obtained in both pelagic and coastal whaling. Due to the scarcity of material, good figures are not drawn, but 50% sexual maturity may be obtained at 10 and 8 years of age in males and females, respectively.

From growth curves

The body length at sexual maturity was estimated to 38.8 and 39.5 ft. in males and females respectively. The ages at which growth curves reach these two body lengths are 8 and 7 years in males and females, respectively, (Fig. 6).

Relation between age and corpora number

As shown in Fig. 10, the age at attainment of one corpus is 8 years from linear regression. This is regarded as the age at sexual maturity in females.

The three results above indicate that 8 to 10 and 7 to 8 years would be the recent ages at sexual maturity in male and female Bryde's whales, respectively.

FOETUSES

Foetal growth

Fig. 9 shows foetal records from Bryde's whales caught on the pelagic whaling ground. Foetal lengths are distributed

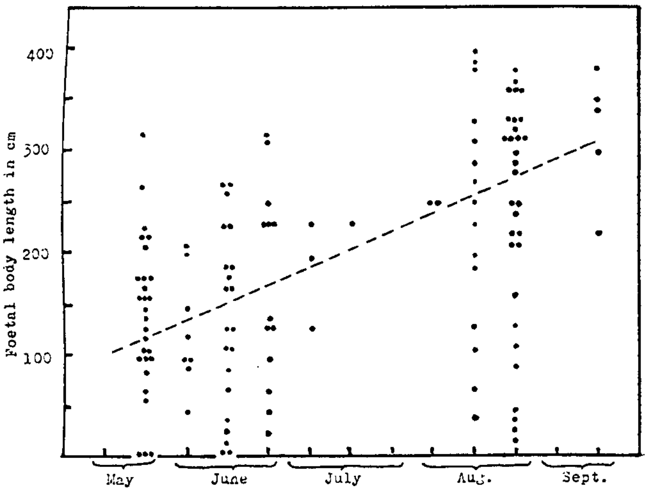

Fig. 9. Foetal records of Bryde's whales from the pelagic whaling ground.

widely in each decade of the month, and very small foetuses were found even in August. Furthermore, ovulating whales are also caught in August as noted in a previous section. This means that the breeding season lasts for a relatively long time. This phenomenon is also seen in Bryde's whales from Saldanha Bay, South Africa, and Best (1960) states that there does not seem to be a restricted breeding season. However, Fig. 9 also suggests that there is a peak breeding season.

The largest foetus was recorded as 395 cm. Best (1960) shows the largest foetus as 14 ft (4.3 m). Foetal records are too scarce to estimate the neonatal body length of the Bryde's whale.

Foetal sex ratio

There were 58 male and 68 female foetuses, excluding small foetuses less than 10 cm in body length. The proportion of females is calculated to be 54.0%, but data are insufficient to provide the real figure for foetal sex ratio in the population.

Multiplets and 'litter size'

Only one example of twin foetuses was found amongst 130 pregnant whales. This whale was 12.8 m long and 22 years old. She had 2 corpora lutea and 11 corpora albicantia in the ovaries, of which 4 were in one ovary and 7 in the other. The twin foetuses of this whale were a 327 cm male and a 325 cm male. The multiplet incidence is 0.8%. 'Litter size' is then 1.008.

OVULATION RATE

Fig. 10 shows the relation between age and corpora number for Bryde's whales caught in Japanese pelagic and coastal whaling. The number of whales used in this key is 124. A regression line is calculated for whales from 4 to 36 years of age. The correlation coefficient is 0.718, and the line is represented in the following equation:

$$Y = 0.455\,X - 2.51$$

Where, X is age and Y is number of corpora in ovaries. This means that the annual ovulation rate is 0.455.

True pregnancy rate

The true pregnancy rate must be less then the ovulation rate. As noted above, the apparent pregnancy rate was 0.417, so this figure may be not so far from the true pregnancy rate.

MORTALITY RATE

From age distribution

The number of whales for which age was determined are

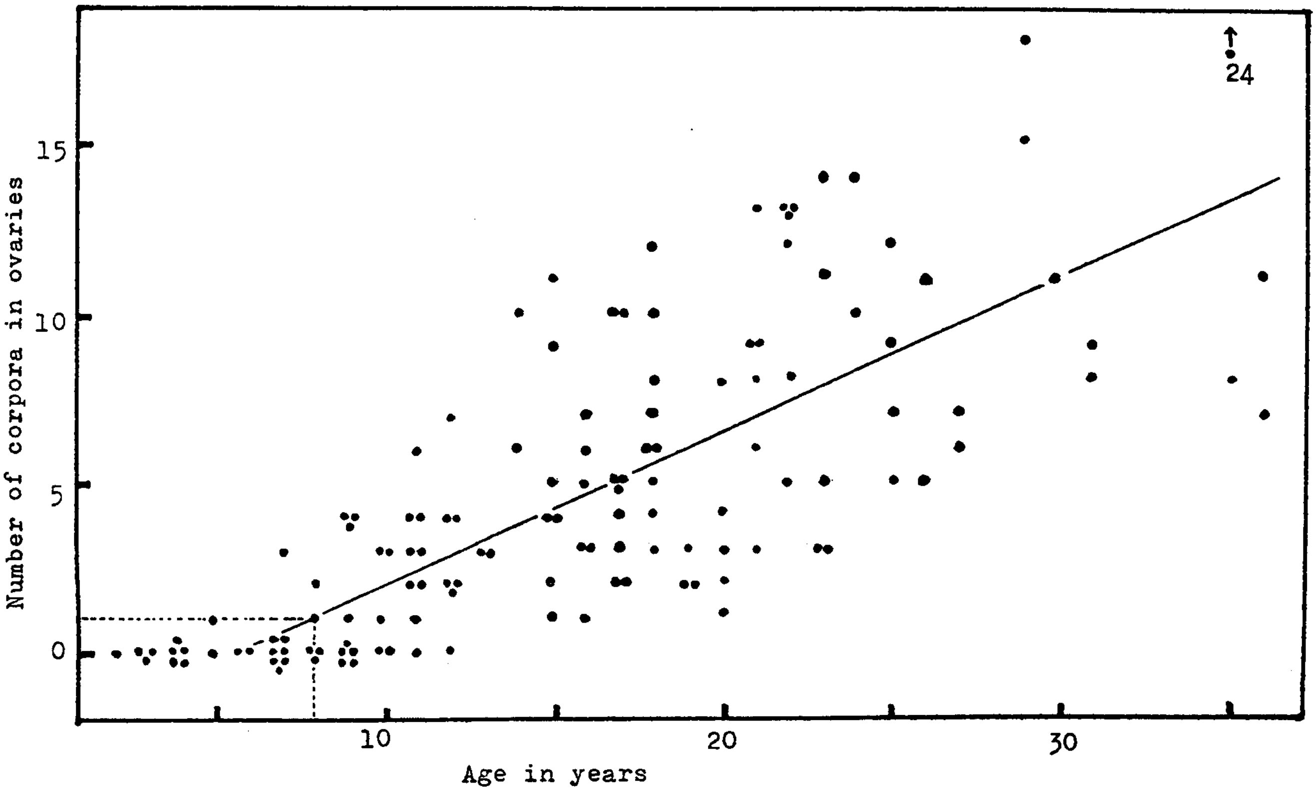

Fig. 10. Relation between age and number of corpora in the ovaries.

too few for their total mortality rate to be calculated from their age distribution, but total mortality coefficient (Z) of males and females combined is calculated by use of Fig. 5. It is 0.091 in the range of ages between 15 and 38 with a correlation coefficient of –0.747.

It is problematical whether this figure represents the natural mortality coefficient (M), or whether it includes some fishing mortality (F). The present data are based on whales caught in the waters east of 166°E. If this population is a different stock from the population which has been caught in the adjacent waters to Japan and around the Bonin Islands, this figure will represent the value of M, but if not, it may include M and F. Doi *et al.* (1967) estimated Z values for Bryde's whales from Sanriku, Kinan and the Bonin Islands using a preliminary age-length key and size distributions. These values range from 0.059 to 0.085.

From ovulation rate and corpora composition

A regression line is calculated from Fig. 4 in the range between 2 and 14 corpora, with a slope of –0.1765. This is equivalent to a Z value per corpus in the ovaries. As the annual ovulation rate was previously estimated to be 0.455, the value of Z is therefore changed to be 0.080.

Natural mortality rate in immature stage

The natural mortality rate can be estimated in an equilibrium situation, if several biological parameters are available, from the following equation:

$$1 - e^{-M} = p.l.h.e - x_m M'$$

Where, M = natural mortality coefficient in adult stage, p = pregnancy rate, l = litter size, h = proportion of females, x_m = age at sexual maturity and M′ = natural mortality coefficient in immature stage. When p (= 0.41), l (= 1.008) and h (= 0.54) are set, M′ is calculated for each of the given values of M and x_m (Table 6).

The values over 0.20 are considered to be too high, and the values less than 0.12 are also too low. The probable figure will be situated in the middle part of the Table.

Table 6

Calculated values of M′

	M′						
x_m	0.04	0.05	0.06	0.07	0.08	0.09	0.10
7	0.248	0.217	0.192	0.171	0.152	0.136	0.122
8	0.217	0.190	0.168	0.149	0.133	0.119	0.107
9	0.193	0.167	0.149	0.133	0.118	0.106	0.095

RECRUITMENT

Age at recruitment

Age at full recruitment is estimated to be 15 to 18 years from Fig. 5, though good age distributions are not yet available. The average age at recruitment is estimated by means of the following equations:

$$R_x = n_x - n_{x-1} \cdot e^{-Z}$$

$$x_r = \Sigma\, x\, R_x / \Sigma\, R_x$$

Where, n = number of whales at each age, R = number of recruits, and x is each age. The average age at recruitment (x_r) is calculated using the data shown in Fig. 5 and Z values of 0.08 and 0.09. It is 9.7 (Z = 0.08) or 9.9 (Z = 0.09). This age is for males and females combined.

A legal size limit of 40 ft is set for the pelagic whaling of sei and Bryde's whales. The ages at which a length of 40 ft is attained in Fig. 6 are 10.2 and 8.0 years in males and females, respectively. The age at recruitment is therefore older than that at sexual maturity, though the difference is only around one year.

Rate of recruitment

From the age distribution the recruitment rate (r) can be estimated by means of the following equation:

$$r = \Sigma\, R_x / \Sigma\, n_x$$

The results are 0.084 (Z = 0.08) and 0.097 (Z = 0.09).

FOOD

Food species

The stomach contents of all Bryde's whales caught by Japanese whaling fleets were examined. As shown in Table 7, euphausiids, fishes and *Calanus* sp. were recorded as food items. Euphausiids were the dominant food item, comprising 65.4% of the food items taken. The rates of occurrence of euphausiids increased with month. Fishes were dominant from May to July, but they became relatively few in August and September. *Calanus* sp. was found in only one whale in May.

Some of the stomach contents were sampled by whalers, and these were identified by Dr. A. Kawamura of the Whales Research Institute, as the following:

Fishes:	*Vinciguerria nimbaria* *Maurolicus muelleri* *Sardinops japonica*
Euphausiids:	*Nematoscelis difficilis* *Thysanoessa gregaria* *Euphausia gibboides* (Needs further study)

Additionally whalers noted some sprats in their catch records, but samples were not collected. The *Sardinops* collected were 6 to 11 cm long.

Interaction between baleen whale species is an interesting problem concerned with population dynamics. Mitchell (1975) illustrates a food web, and the same feeding habits as shown by him are observed in Bryde's whales from the open sea. However, Bryde's whales are distributed only in warm waters even in summer, whereas fin whales are distributed in colder waters as shown in Fig. 3. There may not therefore be close interaction between Bryde's and fin whales, at least in summer. Sei whales are distributed in warmer waters than fin whales, and they feed relatively often on fishes in the open sea of the North Pacific in lower latitudes. Some interaction may be considered between sei and Bryde's whales.

Relative quantity of stomach contents

There is a tendency for the frequency of empty stomachs to decrease with month, and the whales in which stomachs were full of food were relatively frequent in August and September. It is very interesting that the Bryde's whale can take much food, even though it is distributed in warm waters.

Thickness of blubber

The thickness of blubber was measured at a definite place on every whale caught. It ranged between 3.0 and 6.5 cm in the case of males. The average thickness increased with month, as follows:

May	June	July	August	September
4.71	4.74	4.56	5.03	5.22 cm

POPULATION ASSESSMENT

It is still very difficult to assess the populations of Bryde's whales in the North Pacific. Although the Bryde's whale has a long catch history in Japanese coastal whaling, catch statistics have only been obtained since 1955, and regular catches in pelagic whaling have just begun. Our biological investigation has not covered all areas of the North Pacific.

Trend of CPUE in Sanriku area

Sanriku area is the main whaling ground of Japanese coastal whaling, and Bryde's whales are taken every year in this area. The whaling season lasts from May to October. Fig. 11 shows the yearly change in CPUE of Bryde's whales in this area. Catching effort was corrected for the average horse power of the catcher boats. There are large yearly fluctuations in the CPUE figures. This is caused by the change in availability of this whale in the waters adjacent to Japan as explained above. It is thus very difficult to estimate a population trend from these data, but it seems that the population has not changed during the years 1955 to 1974. The development of pelagic whaling may influence the catch in coastal whaling in future.

Mark recovery

In the waters around the Bonin Islands, 92 'sei' whales were marked by Japan during the years 1949 to 1952. Recovery of these marked whales since 1955 were all of Bryde's whales, so the 92 whales can be regarded as Bryde's whales. Fourteen whales had been recaptured by 1974 from the waters adjacent to Japan and the Bonin Islands (*Table 8*).

Table 8

Number of marked and recaptured Bryde's whales in western North Pacific

	1949	1950	1951	1952	**Total**
Whales marked	6	39	7	40	92
Year recaptured					
1950	–	3	–	–	3
1951	–	–	1	–	1
1952	–	1	–	–	1
1958	–	1	–	–	1
1959	–	–	–	2	2
1962	–	1	–	–	1
1963	–	–	–	2	2
1971	–	–	–	1	1
1973	–	1	–	–	1
1974	–	1	–	–	1
Total	–	8	1	5	14

Although only 92 Bryde's whales were marked, they are still being caught in recent years. This phenomenon means that the natural mortality and fishing mortality rates have been low in the western stock of Bryde's whales. The number of marked whales surviving in each year can be estimated from the following equation:

$$n_{i+1} = (n_i - R_i)\, e^{-M}$$

Survivors were calculated where M is 0.04, 0.06, 0.08 or 0.10. In the last case the number of survivors became less than 10 after 20 years had elapsed since marking. These are too few to provide mark recoveries in 23 and 24 years, so 0.10 must be larger than the real value of M.

Fishing rates are calculated from the numbers of survivors and recaptured whales. They are shown in Table 9 for values of M of 0.06 and 0.08. Table 9 also gives the average number of Bryde's whales caught from the waters west of 150°E in certain years, and the population sizes estimated using fishing rate and catch amount are shown in the same Table. In both cases the estimated population size decreases remarkably during the years 1955 to 1974. This is inconsistent with the yearly change in CPUE in the Sanriku area as shown in Fig. 11. Averages will therefore be more reasonable as population estimates: These are 12,700 in the case of M = 0.06 and 9,700 in the case of M = 0.08.

Estimation of recruitment rate of the western stock

If the population size has been almost constant from 1955

Table 7

Stomach contents of Bryde's whales caught in pelagic whaling ground, 1971 to 1974

	Species			Relative quantity					
Month	Fishes	Euphausiids	*Calanus*	0	r	rr	rrr	R	Total
May	25	4	1	56	14	11	3	2	86
June	76	19	–	82	54	27	8	6	177
July	3	–	–	15	2	–	1	–	18
August	12	190	–	103	53	57	40	52	305
September	13	33	–	6	26	7	6	7	52
Total	129	246	1	262	149	102	58	67	638

Table 9

Estimated fishing rates and population size of Bryde's whales west of 150°E by use of whale marking and catch data.

Elapsed Years	Seasons	Fishing rate (E) M = 0.06	Fishing rate (E) M = 0.08	Average catch	Population size M = 0.06	Population size M = 0.08
0–5	1949/1957	0.011	0.011	–	–	–
6–10	1955/1962	0.011	0.013	205.8	18,700	15,800
11–15	1960/1967	0.017	0.022	217.8	12,800	9,900
16–20	1965/1972	0.008	0.011	96.9	12,100	8,800
21–24	1970/1974	0.025	0.044	180.2	7,200	4,100

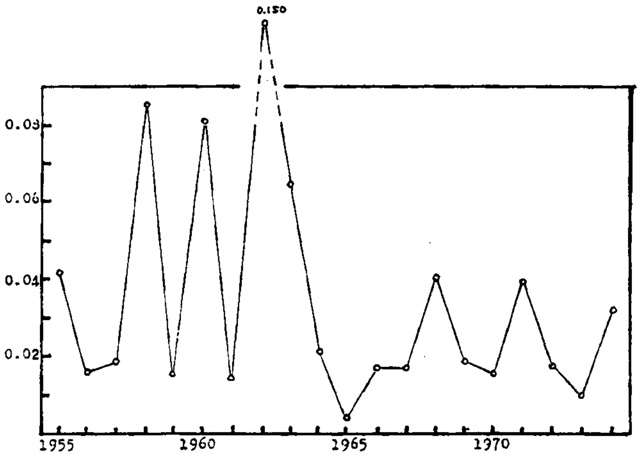

Fig. 11. Yearly change in CPUE of the Bryde's whales caught in Sanriku area by Japanese coastal whaling.

to 1974, the annual number of recruits (R) is estimated from the following equation:

$$N = (N - \bar{C})\,e^{-M} + R$$

Recruitment rate (r) is calculated as R/N, when R is estimated. The results are shown in Table 10.

Table 10

Estimates of recruitment rate.

M	N	$\bar{C}$	R	r
0.06	12,700	183.3	772	0.061
0.08	9,650	183.3	918	0.095

These results show that the estimated population size and number of recruits are reasonable, but if there is a long catch history for this stock, r must be larger than M. If this is true, the estimate of M = 0.08 will be more applicable than M = 0.06.

Estimation of population size from whale sighting

Bryde's whales had been included with sei whales in whale sighting records from Japanese scouting boats until 1973. They began to be recorded independently by most scouting boats in 1974, but these sighting data are still being analysed.

The indices of abundances of 'sei' whales by means of whale sightings in the summer of 1972 and 1973 are shown in Fig. 12 by 5° latitude x 10° longitude areas. Whale sighting has not covered the whole North Pacific, and data are lacking for lower latitudinal waters where Bryde's whales are considered to be abundant. It is very difficult to separate Bryde's whales from sei whales in this figure, but it is tentatively assumed in the present paper that all the whales which are distributed south of 35°N and half of the whales from 35° to 40°N are Bryde's whales. The ratio of Bryde's whales to sei whales in indices of abundance is 5400:12,700. Ohsumi and Fukuda (1975) estimated the population size of sei- whales in the North Pacific in 1972/1973 to be 19,000 to 20,000. The population size of Bryde's whales in the waters investigated will therefore be 8,000 to 9,000. The population size of Bryde's whales from the waters of 150°E was estimated above to be about 10,000, so compared with this size, the population size estimated for the open sea must be too low.

Estimation of maximum sustainable yield (MSY)

It is reasonable to assume that the present population of Bryde's whales in the North Pacific is not far from its initial population level, for the catch has been continuous only in the waters west of 150°E, and the fishing rate has continued to be low. Total population at its initial level of 20,000 to 30,000 would be a conservative estimate considering the above calculations Although the estimation of MSY is an important problem in population assessment, we have not enough data to assess it. In pelagic whaling, the age at recruitment is estimated to be a little older than the age at sexual maturity. The MSY population level should therefore be situated at a little less than half of the initial population level. The rate of exploitation for MSY is considered in general to be near the value of M at the MSY population level. The value of M at the MSY population level will be a little lower than the present value of M (0.08 to 0.06). Table 11 shows the estimated MSY using possible values for initial population size and other parameters of the Bryde's whale in the North Pacific.

Table 11

Preliminary estimates of MSY for the Bryde's whale in the North Pacific

Initial size of population	Rate of exploitation for MSY 0.05	0.06	0.07
20,000	500	600	700
25,000	625	750	875
30,000	750	900	1,050

The present (1974) regulation of sei and Bryde's whales is based on only the sei whale population assessment, and the catch of Bryde's whales is contained within the quota of the sei whale. Catch limits by species should be set for the rational management of the sei and Bryde's whales stocks, especially so since the catch of Bryde's whales in pelagic whaling has rapidly increased in recent years.

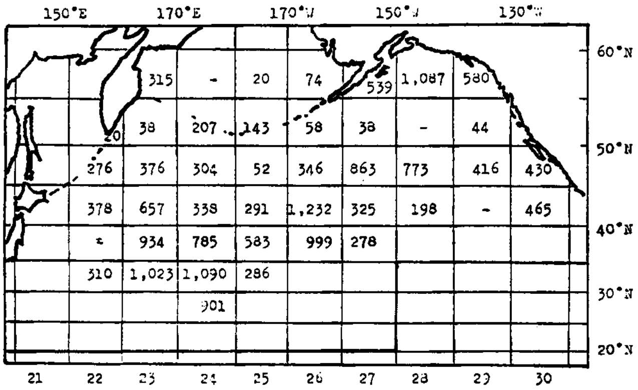

Fig. 12. Indices of abundance of the sei and Bryde's whales by means of whale sightings from scouting boats of Japanese whaling fleets, 1972 to 1973.

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APPENDIX TABLE 1

Age-length keys of the Bryde's whale in the North Pacific

A. Males

Age B.L.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	··	37	38	··	41	42	··	47	··	55	Total
35	1	2	1	2		1																																					7
36		1	1		1	1	1	3			1																																9
37				2		1	1																																				4
38				1	1			1	1	1			1																														6
39				1		1	1			1			1	1		1	1					1																					9
40		1		1				1	3		1	1	2	1		2	1	1	1		1		3				1								1			1					23
41				1							1		1	2		3	3		1	1	1	1		1	1		1		1	1					1					1			22
42						1	1	1		2	2	3	2	1	1		4	2	5	1	1	2	1				1	1	1	1												1	35
43						1				1	2			1		1	3		1					2		1		1	1		1			1									17
44								1	1							1				1			1		1					1		1		1			1						10
45												1	2				1					1																					5
46																																		1									1
47																			1																								1
Total	1	4	2	8	2	6	4	7	5	5	7	5	9	6	1	8	13	3	9	3	3	5	5	3	2	1	3	2	3	3	1	1		3	2		1	1		1		1	149

B. Females

Age B.L.	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	··	49	··	52	Total
35	1	2		1		2		1		1																																		8
36			1		1			1	1	1																																		5
37						2	1																																					3
38			1	1	1	1	2	1			2																																	9
39			1					2															1																					4
40		1	1	1	1		1	1	2	3				2	1		1	1	2	1																								19
41					1		1	1	1	4	5	3	1	1			2	1	1			1		1			1																	25
42				3		1	1	2	2		3		1	1	1	1	5	1	2	2	1	4		3	1			2	1					1										39
43						2	2	2	1	3	2	1	1	4	4	1	3	2	1	1	2	1		1		1		2		1											1			39
44				1					3	2		1		2		2	2	1	1	1	1	5		2		1				2				3				1	1				1	33
45									2	1			1		1	1	2	2	1	4	1	1		1		1	1			1			1	1										23
46								1		1	1		1	1	1	1	1			1				1	1		2								1									14
47															1		2	1			1		1	1								1				1								9
48																1											1																	2
49																				1						1																		2
50																				1	1																							2
Total	1	3	4	7	4	8	8	12	12	16	13	5	5	11	9	7	18	9	8	12	7	12	2	10	2	4	5	4	1	4		1	1	2	4	1		1	1		1		1	236