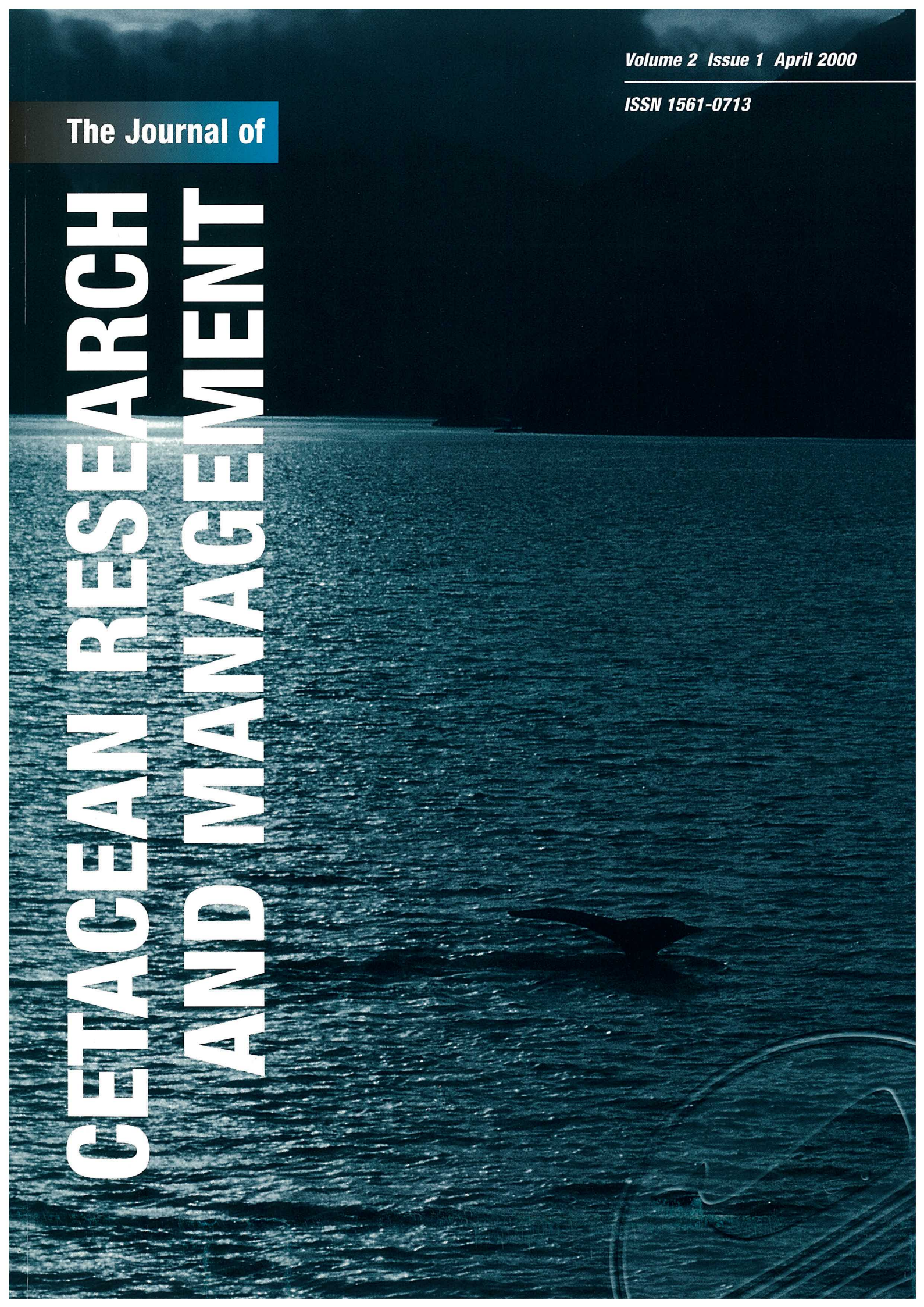


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Editorial

Welcome to the first issue of Volume 2 of the *Journal of Cetacean Research and Management*.

The Journal was established to publish papers on those matters of most importance to the conservation and management of whales, dolphins and porpoises, and in particular papers that are relevant to the tasks of the Scientific Committee of the International Whaling Commission (IWC). These include papers on:

- population assessment and trends
- population dynamics
- population biology
- taxonomy and stock identity
- risk averse management strategies
- direct and indirect exploitation
- environmental changes and threats in the context of cetaceans
- scientific aspects of whale watching and sanctuaries.

It is perhaps a good time to briefly review the first year of the Journal. At the end of the present issue (Volume 2, issue 1), an author and subject index to Volume 1 has been provided. A total of 30 papers were published in the first year and papers on all of the topics mentioned above have been included. Some 81 authors from 20 countries were involved with these papers. I am particularly pleased to note that several of the papers were submitted by authors for whom English is not their first language and/or from those countries where cetacean research is at its early stages.

Reviewers play a major role in the development of any Journal, and it is appropriate here to thank those scientists

who have freely given their time to review manuscripts in a comprehensive and constructive manner. These include: L.W. Andersen, J. Barlow, S.D. Berrow, P.B. Best, A. Bjørge, M.V. Bravington, J. Carretta, P.J. Clapham, C.W. Clark, A. Collet, J.G. Cooke, E. Crespo, K.J. Finley, J. Forcada, J.C.D. Gordon, F. Hester, J.E. Heyning, R. Hoelzel, J. Ianelli, T. Kasuya, G.P. Kirkwood, F. Larsen, C. Lockyer, S.C. Long, K.G. Magnússon, J. Mead, N. Øien, D. Palka, P. Palsbøll, W.F. Perrin, A.E. Punt, T.J. Quinn II, R.R. Reeves, E. Rogan, G.J.B. Ross, J.E. Scarff, E.R. Secchi, T.D. Smith, G. Stefánsson, T. Schweder, B.L. Taylor, P. Thompson, C. Tynan, W.A. Walker, H. Whitehead and the Editorial Board of J.L. Bannister, P.S. Hammond, E. Hofmann, H. Kato, A.J. Read, D. DeMaster, A. Aguilar, L. Walløe and J.E. Zeh.

For Volume 1, the mean time to publication from submission of the original manuscript by the authors is just under six months. In circumstances where all stages of the process go well, it is possible for a manuscript to go from submission to publication in one month.

In addition to the three regular issues of the Journal, the first year of the Journal also saw publication of a Supplement, containing the full report of the 1999 meeting of the Scientific Committee of the International Whaling Commission (*J. Cetacean Res. Manage.* 1 (Suppl.): 1-284) and publication of the first Special Issue (P.J.H. Reijnders, A. Aguilar and G.P. Donovan, eds. 1999. *Chemical Pollutants and Cetaceans*. ix + 273pp.).

G.P. Donovan
Editor

Early descriptions of whales

Many of the early descriptions of whales and their behaviour and ecology were published in languages other than English. These were often sections in books or articles that were more broad in scope, for example general works on zoology or geography. If translations into English exist at all, they are often not very precise with respect to the cetacean component. The Journal invites submissions of such descriptions. Submissions should include: full bibliographic information; a brief introduction to the author and the work in which the description is included; the full text in the original language; and a careful translation.

ABOUT 1250: THE KING'S MIRROR [KONUNGS SKUGGSJÁ]. PRINTED IN CHRISTIANIA (NOW OSLO) 1848 BY CARL C. WERNER. PART 2.

Introduction

'The King's Mirror' is a didactic document of a kind that was common in European countries in medieval times. The work was probably written by a high ranking member of the Norwegian priesthood for the sons of king Håkon Håkonarson (1217-1263). For more details about the document, see the 'Introduction' to Part 1 in *J. Cetacean Res. Manage.* 1999, 1(2): iii-iv.

The document contains detailed descriptions of some 18 different 'species' of cetaceans said to be found in the North Atlantic and around Iceland and Greenland. Of these, 13 can safely be identified from the descriptions and names given. The pilot whale, harbour porpoise, dolphin (in the Norwegian Sea, whitebeaked and whitesided dolphin), killer whale, minke whale, and fin and blue whales (not distinguished between) were presented in Part 1. In Part 2, the descriptions of the sperm whale, right whale, greenland whale (bowhead), humpback whale and narwhal are presented, as well as one paragraph which mentions the names of seven whale species, of which only the white whale can be safely identified. Four of the others may be the sei whale, bottlenose whale, Cuvier's beaked whale and Sowerby's beaked whale, but the remaining two can definitely not be identified. Indeed they may not be whales at all, but sharks (e.g. basking shark). It is interesting to note that this account contains none of the fanciful descriptions of mermaids, sea serpents or marine monsters, which were so abundant in texts from between 1500 and Linneus (1750).

The translation below is based on the translation from old Norse to English by Laurence Marcellus Larson (Twayne Publishers Inc, New York, 1917), but I have corrected obvious errors and translated the important sentences more literally.

English translation

Sperm whale

Another kind is called *burhvalir*. These are toothed whales, although the teeth are barely large enough to be carved into fair-sized knife handles or chess men. They are neither fierce nor savage, but rather of a gentle nature, and so far as possible they avoid fishermen. In size, they are similar to those that I mentioned last. Their teeth are so numerous that more than seventy can be found in the head of a single whale of this sort.

COMMENT: The word *bur* means small house and probably refers to the rectangular head of the sperm whale. The number of teeth is strikingly accurate.

Right whale

Still another kind is called *slettibaka*; this has no fins on the back and is about as large as the sort that we mentioned last. Seafaring men fear it very much, for it is by nature disposed to sport with ships.

COMMENT: *Slettibaka* means 'smooth back'.

Greenland whale (bowhead)

Then there is that kind which is called *nordhvalir*. This fish grows to a length of eighty or even ninety ells and is as large around as it is long; for a rope that is stretched the length of one will just reach around where it is bulkiest. Its head is so large that it comprises fully a third of the entire bulk. This fish is very clean in its choice of food; for people say that it subsists wholly on mist and rain and whatever falls into the sea from the air above. When one is caught and its entrails are examined, nothing is found in its abdomen like that which is found in other fishes that take food, for the stomach is empty and clean. It cannot readily open and close its mouth, for the whalebone which grows in it will stand across in the mouth when it is opened wide; and consequently whales of this type often perish because of their inability to close their mouth. This whale rarely gives trouble to ships. It has no teeth and is fat and good to eat.

COMMENT: The Greenland whale was called *nordhval* in Norway until about hundred years ago. The meaning of the word is 'the whale that lives north [of Norway]'.

Humpback whale

Some whales are dangerous for men to meet, while others are gentle and peaceable. One of the dangerous is called *skeljung*; this fish is large and very dangerous to ships. It has the habit of striking at the vessel with its fins and of lying and floating just in front of the prow where sailors travel. Although the ship may turn aside, the whale will continue to keep in front, so there is no choice but to sail upon it; but if a ship does sail upon it, the whale will throw the vessel and destroy all on board. The largest of these fishes grow to a length of seventy or eighty ells; they are good to eat.

COMMENT: The meaning of the word *skeljung*, is '[an animal] that carries or is covered by shells'.

Narwhal

There is still another sort called the *nahvalir*, which may not be eaten for fear of disease, for men fall ill and die if they eat of it. This whale is not large in size; it never grows longer

than twenty ells. It is not at all savage, but rather tries to avoid fishermen. It has teeth in its head, all small but one which projects from the front of the upper jaw. This tooth is handsome, well formed, and straight as an onion stem. It may grow to a length of seven ells and is as even and smooth as if shaped with a tool. It projects straight forward from the head when the whale is travelling; but sharp and straight though it is, it is of no service as a defensive weapon; for the whale is so fond and careful of its tusk that it allows nothing to come near it.

COMMENT: Tusk length of seven ells fits with 0.23 m/ell, but not with 0.47 m/ell as stated in an historical encyclopaedia – see 'Introduction' to Part 1.

White whale and six other possible whale species

There are two other kinds of whale, *andhvalir* and *svinhvalir*, the largest of which is not more than twenty-five ells in length. These are not fit to be eaten, for the fat that is drawn from them cannot be digested either by man or by any beast that may take parts of it. For it runs through them and even through wood; and after it has stood a while, scarcely any vessel can contain it, even if made of horn.

There are certain other types of whale which are worth a passing mention only, namely *hrafnhvalir* and *hvitingar*. *Hvitingar* are so named because of their snow white colour, while most other kinds are black, except that some of them have spots, such as *skjaldhvalir*, *geirhvalir* and *bardhvalir*.

COMMENT: *Hvitingar* must be the white whale. *Andhvalir* means 'duck whale', which possibly is a reference to the shape of the head of a beaked whale (Cuvier's beaked whale?). *Svinhvalir* means 'hog whale' and could perhaps be the name for the northern bottlenose whale whose meat even today has the reputation of a laxative. *Hrafnhvalir* means 'the black whale', and most likely refers to the sei whale, since a similar term was used for the sei whale later both in Norway and Iceland. *Geirhvalir* means whale with a pointed head, and could be Sowerby's beaked whale, since a term with the same meaning, *spisshval*, has been used for this species in Norwegian. *Skjaldhvalir* and *bardhvalir* cannot be identified, if indeed they are whales at all.

Original old Norse text

Enn er þat ok eitt hvalakyn, er burhvalir heita, ok hafa þeir hvalir tennr eigi stærri en gera má mjök stór knífsheptí af eða tafl. Ekki eru þeir ólmir né grimmir, heldr eru þeir hógværir, ok firrask sem þeir megu fund veiðimanna, ok því nær at vexti sem þeir, er nú rœdda ek næsta um; en einn hvalr hefir svá margar tenn í höfði, at hann hefir nökkura sjautigu, af þessu kyni enu sama.

Þá heitir enn hvalakyn eitt sléttibaka, ok er ekki horn á baki, ok svá miklir nökkut at vexti sem hinir, er nú gátum vér. En þeir menn hræðask hana mjök, er um sjó fara, þvíat hennar náttúra er sú, at leika mjök við skip.

Þá er þat enn eitt hvalakyn, er norðhvalir heita, ok er sá fiskr 80 álna langr eða 90, þeir er stærstir verða, ok jafndigr sem hann er langr; þvíat reip þat er dregit er jafnlangt hánum, þá tekr þat um hann þar sem hann er digrastr; hann hefir ok svá mikit höfuð, at þat er enn mesti þriðjungr af hánum. En þessi fiskr lifir hreinliga, þvíat þat segia menn, at hann hafi öngva fœzlu aðra en myrkva ok regn, ok þat eitt er fellr or lopti ofan á haf, ok þó at hann sé veiddr, ok innýfli hans opnuð, þá finnsk ekki slikt í hans maga sem annarra fiska þeirra, er fœzlu hafa, þvíat hans magi er hreinn ok tóm. Ekki má hann vel munn sinn opna, þvíat tálkn þau, er vaxin eru í munni hánum rísa um þveran munn hans, þegar hann lýkr hánum mjök upp, ok hefir hann iðuliga af því bana, at hann má eigi munni sínum aptr koma. Ekki er hann mjök ólmr við skip; öngvar hefir hann ok tennr, ok er feitr fiskr ok vel ætr.

Sumir ok af þessum eru hættir við lif manna, en sumir eru spakir ok hógværir. Skjelfjung kalla menn eitt kyn af þeim, ok er sá fiskr mikill vexti ok ólmr við skip. Þat er hans náttúra at ljósta skip med sundfjöðrum sínum, elligar at hann lætr fjótask ok leggsk fyrir skip, þar sem menn sigla; en þó at menn beiti frá hánum, þá ferr hann þó jafnan fyrir, ok er engi annar kostr en sigla á hann; en ef skip sigla á hann, þá kastar hann skipum, ok týnir öllu því í á er. Sá fiskr verðr 70 álna langr eða 80, þeir er stærstir verða, ok eru þeir fiskar vel ætir.

Þá er enn þat hvalakyn, er náhvalr er kallaðr, ok megu menn eigi eta fyrir sótta sakir, þvíat menn fá sótt af ok deysja, ef þeir eta hann. En sá hvalr er eigi mikill at vexti, eigi verðr hann lengri en 20 álna; at engu er hann ólmr, heldr forðask hann veiðimanna fund. En hann hefir tenn í höfði, allar smár fyrir utan eina, ok stendr sú í efra gómi í öndverðu höfði hans; hon er fögr ok vel vaxin, ok svá rétt sem laukur; hon er 7 álna löng, sú er lengst kann at verða, ok snúin öll, svá sem hon sé með tólum ger; hon stendr rétt fram or höfði hánum, þá er hann ferr leiðar sinnar; en svá hvöss sem hon er ok rétt, þá verðr hánum engi vörn at henni, heldr er hann svá virkr at henni ok kær, at hann lætr þar ekki vætta við koma.

Þat eru enn tvenn hvalakyn, þau er annat heitir andhvalir, en annat svinhvalir, ok verða þeir ekki stærri en 5 álna ok 20, þeir sem stærstir verða; ok eru þeir fiskar eigi ætir, þvíat þat smjör er rennr af þeim hvölum, þá megu menn eigi melta með sér, ok ekki annat kvikendi er þess neytir, þvíat þat rennr í gegnum hann ok jafnvel í gegnum tréit, ok þó mun illa halda, ef nökkura hrið stendr, at horn sé. Þá eru þau enn sum hvalakyn, er lítillar umræðu er vert, er bæði eru hrafnhvalir ok hvítar; ok eru þeir fyrir því hvítar kallaðir, at þeir eru snjóhvítir at lit, en flestöll önnur hvalakyn eru svört, fyrir utan þat, er flekkar eru á sumum, svá sem annathvart er á skjaldhvölum, eða á geirhvölum, eða á bardhvölum.

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Experimental testing of acoustic alarms (pingers) to reduce bycatch of harbour porpoise, *Phocoena phocoena*, in the state of Washington

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ABSTRACT

Field tests were conducted on the effectiveness of acoustic alarms (pingers) in reducing the incidental catch of harbour porpoise (*Phocoena phocoena*) in a salmon gillnet fishery in northern Washington in July and August of 1995-1997. The alarms produced a broadband signal with peaks at 3 and 20kHz, with mean source levels between 121.7-124.7dB re 1μPa @ 1m. For 1995 and 1996 combined, 47 harbour porpoise were taken in control nets and only two were taken in alarmed nets. The alarms significantly reduced the bycatch of harbour porpoise for both seasons (1995: $\chi^2 = 5.28$, $df = 1$, $p = 0.02$; 1996: $\chi^2 = 11.2$, $df = 1$, $p = 0.001$). In 1997, all nets were alarmed and 12 porpoise were taken; however, the expected catch without alarms would have been 79. There were no significant differences in catch rates of chinook salmon (*Oncorhynchus tshawytscha*) ($\chi^2 = 0.31$, $df = 1$, $p = 0.58$), or sturgeon (*Acipenser* sp.) ($\chi^2 = 1.44$, $df = 1$, $p = 0.23$) in control or alarmed nets. There were also no significant differences in the bycatch of harbour seals (*Phoca vitulina*) ($\chi^2 = 0.09$, $df = 1$, $p = 0.76$) or depredation of salmon by seals in nets with and without alarms ($\chi^2 = 0.07$, $df = 1$, $p = 0.79$). The results of these studies indicate that acoustic alarms significantly reduce the probability of harbour porpoise entanglement in bottom-set gillnets in the fishery without reducing the catch of target fish species.

KEYWORDS: HARBOUR PORPOISE; BYCATCH; PACIFIC OCEAN; EXPERIMENTAL; ACOUSTICS

INTRODUCTION

Harbour porpoise (*Phocoena phocoena*) are susceptible to incidental mortality in gillnet fisheries throughout their range (e.g. Gaskin, 1984; Read and Gaskin, 1988; Gearin *et al.*, 1994; Kastelein *et al.*, 1995). In the Gulf of Maine, Bay of Fundy, and the North, Celtic and Baltic Seas, incidental catches of harbour porpoise may exceed sustainable levels and potentially threaten local stocks (e.g. see Donovan and Bjørge, 1995).

Numerous workshops, symposia and meetings have been conducted to address harbour porpoise bycatch and the broader issue of cetacean mortality in gillnets (Fradley *et al.*, 1994; IWC, 1994; 2000; Reeves *et al.*, 1996). One of the primary objectives of these efforts has been to identify methods to reduce or mitigate gillnet mortality. Mitigation efforts using acoustic deterrents were developed primarily by Jon Lien and colleagues, from Memorial University in Newfoundland, who used sound making devices to reduce entanglements of humpback whales (*Megaptera novaeanglia*) in fish traps in Newfoundland (Lien *et al.*, 1992). Lien later developed a device he called a 'pinger', a simple homemade alarm using a piezo buzzer or truck back-up alarm as the sound source. Two preliminary trials of the devices were conducted in the New England sinknet fishery during the autumn of 1992 and 1993 (Lien and Hood, 1994). The results of the trials were statistically inconclusive, but the method showed some promise for reducing the bycatch of harbour porpoises. A review of the data and methodology by a NMFS (US National Marine Fisheries Service) scientific review panel in June 1994 concluded that further work was warranted, but that future experiments would require a more rigid design and a significant increase in sampling effort.

A large-scale experiment was conducted during the autumn of 1994 in the Gulf of Maine using a study design which conformed with the recommendations of the NMFS review panel. The results demonstrated conclusively for the first time that acoustic alarms reduced the bycatch of harbour porpoise in sink gillnet fisheries (Kraus *et al.*, 1995; 1997). However, Kraus *et al.* (1995) indicated that they did not know why the alarms were effective and, in particular, whether they functioned by alerting harbour porpoises to the nets or by scaring them away from a specific area. It is also not known whether habituation to the devices will occur over time, or whether the devices will function in another type of fishery for other species. Catches of Atlantic herring (*Clupea harengus*), a primary prey of the harbour porpoise, were lower in alarmed nets suggesting that alarms may function in part by scaring harbour porpoise prey away from nets (Kraus *et al.*, 1997).

Experiments using acoustic alarms were conducted in the Northern Washington Marine Set-net Fishery from 1995 to 1997. Observer programmes in the fishery since 1988 indicated that most harbour porpoises were taken during July and August (Gearin *et al.*, 1993; 1994). Most (99%) of the harbour porpoise observed or reported taken in the fishery from 1988 to 1997 ($n = 205$) were caught in the Spike Rock area, a small bay on the Pacific coast (Fig. 1). Catch rates at Spike Rock are among the highest reported in the world ranging from 0.10-0.70 porpoises taken per net day (Gearin *et al.*, 1994). Our goal was to determine if alarms would reduce the harbour porpoise bycatch in this fishery, and to learn more about how the alarms function. In addition, studies on observations of harbour porpoises in relation to alarmed nets were conducted and field measurements of alarms at the fishing grounds where the studies were conducted were obtained.

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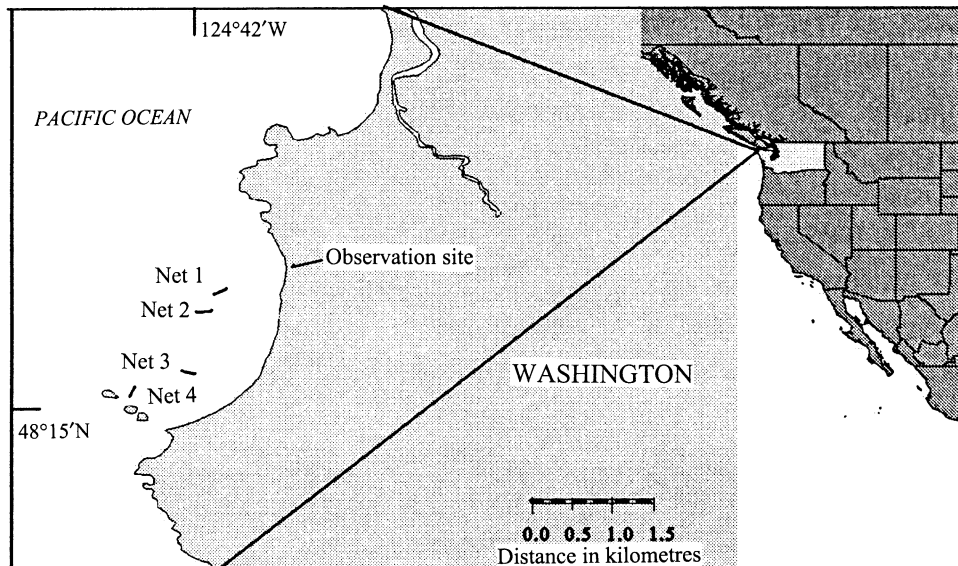


Fig. 1. Map of the Spike Rock fishing grounds on the outer Washington coast and location of set-nets, 1995-1997.

MATERIALS AND METHODS

Description of the fishery

The Northern Washington Marine Set-net Fishery is conducted by the Makah Indian Tribe and operates along the coast of Washington state in the Pacific Ocean and in the western Strait of Juan de Fuca (Fig. 1). The fishery is open from 1 May to 15 September each year and targets chinook salmon (*Oncorhynchus tshawytscha*) and sturgeon (*Acipenser* sp.) with peak landings during July and August. The fishing experiments were conducted in the Spike Rock fishing grounds, a small area relative to the overall fishing grounds utilised by the Makah Tribe. The Spike Rock area is 1km wide by 2km long and is a shallow sloping bay with a flat, sandy bottom. The area fished ranges from 11-30m in depth. Vessels used in the fishery are small: 5-8m in length and use gillnets with a maximum length of 100 fathoms (183m). The nets are composed of mono- or polyfilament nylon ranging from 19-22cm stretched mesh from 35-90 meshes deep. The nets are set on the bottom, anchored in position, and are checked on average every 24 hours. Fishing effort was defined in net days (ND), where 1ND equals a 100 fathom net set for 24 hours (Polacheck, 1989). A more detailed description of the fishery is provided in Gearin *et al.* (1994).

Design of alarms

The alarms used were slightly modified designs of Jon Lien's as described by Fullilove (1994). The alarm unit consisted of a piezo buzzer which operated on four 9 volt batteries, ABS pipe, screw caps, end caps and adapters. The central housing tube was cut from 5cm diameter ABS to lengths of 15-18cm. Rubber sealant and silicon was used instead of O-rings to seal the screw caps. The devices did not have a salt water switch and remained constantly active. Because the nets stayed in one location for long periods of time and remained in the water except for the brief period when they were checked, it was not necessary to save battery life by installing a salt water switch. Due to the short duration of the experiments, the four batteries installed were adequate to power the alarms for 6-8 weeks. Our alarms were simpler and probably less expensive than the Lien model, costing about US \$20.00 to produce.

Field testing alarms

The attenuation and sound source levels of three alarms were tested before the 1995 experiment began to determine optimal spacing patterns and required distances between nets (Bain, unpubl. data). A spherical spreading formula was used to calculate optimum spacing given varying sea states and background ambient noise. The formula used was:

$$SPL_R = SPL_1 - 20 \log(R)$$

where SPL_R is sound level measured at range (R) and SPL_1 is sound level measured at 1m (Urlick, 1983). The alarms produced a broadband signal at intervals of 4s centred at 3kHz with a second peak near 20kHz (Fig. 2). Minimum source levels were 90dB at 30cm (in air) according to manufacturers specifications.

Acousticians from Hubbs Sea World Research Institute were contracted to conduct field measurements of the ambient noise parameters and alarm attenuation at the Spike Rock study site in 1996 (Bowles *et al.*, 1997). Transmission loss and ambient noise levels in the area were measured using a broadband calibrated recording system including an ITC 6050C hydrophone and a Nagra IV-SJ recorder. The transmission loss was estimated using a shallow water loss model (spherical $[20 \log R]$ spreading out to bottom depth and approximately cylindrical spreading $[10 \log R]$ thereafter). The shallow water model was used to estimate the detection range of alarms at the two frequency peaks.

During the course of the field measurements, it became clear that the peak frequency of the alarms varied by unit depending on battery condition. Given that, calibration measurements were not made on all individual units in the field. Instead, the net was treated as a whole as the sound source for pinger attenuation measurements. As background noise appeared to have a large effect on the empirical data, the transmission loss was also modelled using decline in signal-to-noise ratio (SNR) of the alarms, or the difference between tonal level and ambient noise level in the appropriate bands ($SNR > 0dB$). SNR was obtained by subtracting ambient levels at 3kHz and 20kHz from the spectrum levels of the pings at each measuring station. SNR close to the net was 11-23dB at 3kHz and 12-24dB at 20kHz. Successive measurements of SNR were less variable than successive measurements of peak level. Therefore, SNR was also used to estimate attenuation rate using the equation

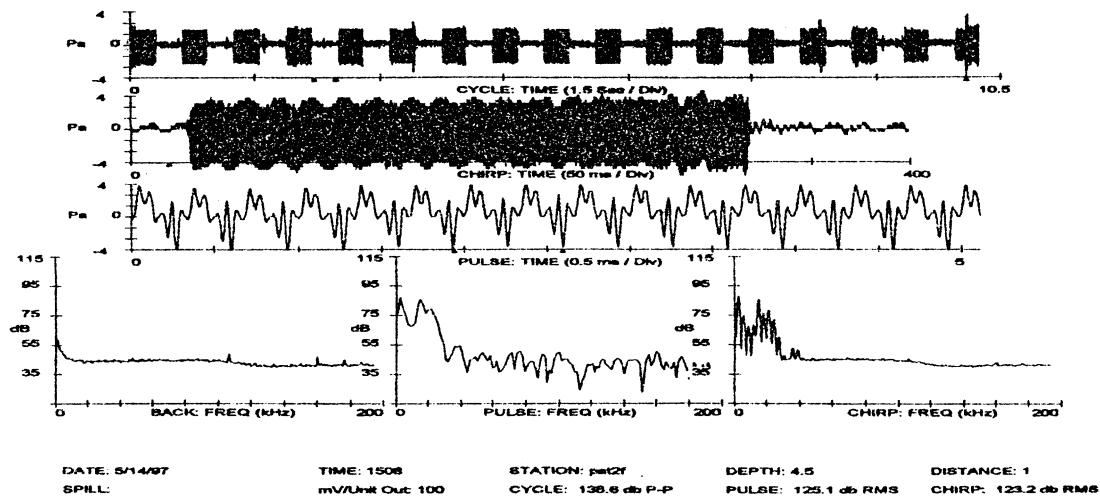


Fig. 2. Sound and pulse characteristics of an acoustic alarm (pinger) used in the experimental set-net studies during 1995-1997.

$SNRR = SNRO - X \log_{10}(R)$. A simple logarithmic decay model was used to fit the data; $dB R = dBO - X \log_{10}(R)$, where $dB R$ = level at R , dBO = estimated source level, and X = best-fit slope. Further detail is provided in Bowles *et al.* (1997).

Field testing alarms on salmonids

Field tests were also conducted on the alarm's effect on salmonids before the experiment began. In June 1994, three alarms were tested in the fish viewing window at the Hiram M. Chittenden Locks in Seattle, Washington, USA. The chamber held between 80-100 adult sockeye salmon (*O. nerka*) during the trials. The fish were clearly visible through the viewing window, allowing a general description of any reactions by the fish to the alarms. Each alarm was lowered into the chamber in inactive mode for a 5min trial and then the trial was repeated in active mode. Two complete trials (on/off) were conducted for each of the three alarms for a total of six trials. Two parameters were measured; closest approach to alarm and time of closest approach to alarm. The measurements were made in bins of increments of 10cm for distance and increments of 10s for time. The results of the trials provide a qualitative assessment of the reactions of the fish to the alarms. The tests however should be repeatable by other researchers to determine if similar results are obtained.

Alarm function and failure rate

Alarms were checked each day during net retrieval and faulty alarms were replaced. Alarms which were either of apparent low amplitude or which were completely inaudible were replaced by functioning alarms during that day's net retrieval. Some alarms fell off the net and were lost when the nylon tie wraps broke or loosened. The lost alarms were replaced each day.

Experimental design and net configuration

The experiments were conducted in the Spike Rock fishing grounds in depths ranging from 8-18m. One tribal gillnet vessel was used during the fishing experiments which were conducted from 27 July to 28 August 1995, 7 July to 9 August 1996 and from 30 June to 16 August 1997. Four tribal nets were constructed to be used in the experiments, in order to control for net size, mesh size and condition (Table 1). The nets were 19.5cm stretched mesh and 183m long. In 1995-96, two nets were composed of three-strand green nylon and were 50 meshes deep and two were three-strand

white nylon and 80 meshes deep. The 50 mesh nets fished approximately 7.5m deep and the 80 mesh nets fished 12m deep. In 1997 the nets were re-hung with new 19.5cm stretched mesh green colour web and each was 183m long and 50 mesh deep. The nets were checked once each day, weather permitting, and typically soaked for 24 hours. Each net was set and aligned so as not to overlap the other (Fig. 1). Minimum distance between nets was 300m in order to reduce the chance of sound overlap between nets. Alarms were rotated between different nets in an attempt to balance alarmed and control fishing effort through the season. The rotation schedule however could not be strictly adhered to as a result of inclement weather which prevented checking the nets on several occasions or large swell conditions which prevented changing alarms. Two nets were set on the south side of the bay and two in the centre of the bay acting as identical paired sets (Fig. 1). Nets were set in only four positions during each season and were not moved until pulled out of the water at the end of the season. Nets were set in approximately the same locations during each of the three fishing seasons. Each net acted as a control (without alarms) and as an experimental net when alarms were in place, except during 1997 when all nets were alarmed. The alarms were placed on the cork line of the nets using nylon tie wraps. When in position, the alarms were horizontal, parallel to the cork line. When fishing, the alarms were 4-7m below the surface. Each net was fitted with 11 alarms, spaced at intervals of 16.6m. When the nets were checked, observers recorded data on harbour porpoise bycatch, salmon and sturgeon catch and bycatch of other fish and marine mammals.

Table 1
Data for nets used in the experimental fishery 1995-1997.

Net #	Colour	Length (m)	Net depth (mesh)	Water depth (m)	Latitude/Longitude
1995 & 1996					
1	white	183	80	17	48°16.20' N; 124°41.40' W
2	white	183	80	16	48°16.03' N; 124°41.57' W
3	green	183	50	12	48°15.42' N; 124°41.72' W
4	green	183	50	11	48°15.23' N; 124°42.30' W
1997					
1A	green	183	50	17	48°16.19' N; 124°41.50' W
2A	green	183	50	16	48°15.91' N; 124°41.60' W
3A	green	183	50	12	48°15.40' N; 124°41.86' W
4A	green	183	50	11	48°15.17' N; 124°42.36' W

Statistical analysis

Fishing effort

Before the field trials began, a power analysis was conducted to determine the fishing effort required to detect a significant reduction in harbour porpoise entanglement rates given rates similar to previous years. Using entanglement rates of either 0.15 or 0.30 porpoise per ND, and a type I error rate of $\alpha=0.10$, to detect a 50% reduction in entanglement rate, would require between 100 to 140ND of fishing effort.

Harbour porpoise bycatch

A statistical approach similar to Kraus *et al.* (1995) with some minor differences was used to analyse the porpoise catch data. Entanglements of multiple harbour porpoises in the same net within the same ND were likely to be dependent (e.g. mother and calf pairs), so the assumption of a Poisson distribution was not warranted. There were too few sets with entanglements to test the distribution of the number of porpoises entangled. Therefore, the probability that one or more porpoises were entangled in a single ND was determined. Thus, the outcome for each ND was either a 0 or 1 (an entanglement). The probability of an entanglement in an alarmed net is P_{active} and in a control net is P_{control} . All nets were checked at approximately 24 hour intervals, so it was not necessary to adjust for soak time following Kraus *et al.* (1995). A 2×2 contingency table with the χ^2 corrected for continuity (Snedecor and Cochran, 1973, p.215) was used to test whether $P_{\text{active}} = P_{\text{control}}$. The odds ratio $O = [P_{\text{control}}/(1-P_{\text{control}})]/[P_{\text{active}}/(1-P_{\text{active}})]$ and its confidence interval (Fleiss, 1973) was also calculated for comparison with the results of Kraus *et al.* (1995). The relative age and reproductive maturity of porpoises taken during the fisheries was estimated using data from Gearin *et al.* (1994). Females greater than 155cm total length and males greater than 140cm were considered to be reproductively mature.

Harbour seal bycatch

Catches of harbour seals (*Phoca vitulina*) were compared between alarmed and control fishing effort. The CPUE values were determined and compared using a chi-square analysis similar to that used for harbour porpoise.

Fish catches

Catches of chinook salmon and sturgeon were compared using the same techniques as for harbour seals and harbour porpoises except that an odds ratio was not calculated. A chi-square analysis was also used to evaluate whether significant differences existed in numbers of salmon damaged by pinnipeds in alarmed versus control nets.

Observational studies

Shore-based observations were made from a 47m high cliff above the Spike Rock fishing grounds to observe the behaviour and distribution of porpoises around the experimental nets in 1996. A three member observer team recorded porpoise sightings in relation to Net 1 and calculated the positions of sightings and distances from the net. The observer team was unaware of whether Net 1 was a control or alarmed net. Theodolite bearings to the buoys marking each end of Net 1 were recorded at low and high tides each day, providing a record of net locations relative to porpoise sightings. Searching for porpoises was conducted through 7×50 reticle binoculars, which have a 5.44° optical field of view with 14 reticle marks which measure vertical

angle from the horizon. An internal magnetic compass provided 360° horizontal bearings. More detail on the methodology is provided in Laake *et al.* (1998).

RESULTS

Field testing alarms

Field measurements in the salt water environment of Puget Sound demonstrated that the three alarms tested each emitted sound source levels of between 121.7-124.7dB re 1 μ Pa @ 1m (Fig. 2). The optimal spacing of alarms on the nets was determined to be 20m, which would allow porpoises to hear the alarms in sea states up to Beaufort 4. The alarms were spaced, however, at closer intervals (16.6m) to allow for attenuation of diagonal distances between the cork and lead lines.

The field measurements conducted on site at the Spike Rock fishing grounds (Bowles *et al.*, 1997) were similar to but slightly different than the Puget Sound measurements (Bain, unpubl. data). The alarms tested had broadband source levels of 123dB re 1 μ Pa and peak tonals at 2.95 and 20.5kHz. They were nearly omnidirectional at low frequencies (< 2 dB of directivity at 2.95kHz), but had some directivity at high frequencies (6dB at 20.5kHz) in the horizontal plane. Broadband ambient noise levels in the area ranged from 90-102dB re 1 μ Pa. Most of the ambient noise energy was at the low frequency end of the spectrum, below 8kHz. In the band centred on the 2.95kHz tonal, levels ranged from 56 to 80dB. The inshore environment near Spike Rock was characterised by high energy wave action and the dominant sound sources at low frequencies were rocks rolling in the surge, surface noise and surf. At 20.5kHz, band-limited levels were more constant, varying from 50-60dB, with snapping shrimp (*Pandalus* sp.) being the dominant noise source. The sound source levels of an alarmed net as a whole at these frequencies were 113dB at 2.95kHz and 88.8dB at 20kHz. The estimated detection range of an alarmed net at 3kHz, given the typical range of ambient noise levels, would have been from 113m (80dB background level) to 2,196m (62dB background level). At 20kHz, the net would have been just detectable from 161m (62dB background level) to 1,615m (47dB background level). The SNR of the alarms reached 13-19dB close to the net (within 8-10m) at both frequencies and declined to 0dB at ranges of 400-600m. Based on the logarithmic decay model used to fit the data, the SNR declined to 0dB at a maximum range of 1,733m at 2.95kHz (67dB background level) and 1,033m at 20.5kHz (55dB background level). These estimates were consistent with reports of field observers who reported that alarms were difficult to detect at band-limited SNR < 4 dB. Assuming that harbour porpoise required 4dB or more of SNR to detect the signals, the effective range of the alarmed nets would have been 293m at 2.95kHz and 113m at 20.5kHz under typical conditions of ambient noise levels between 57 to 70dB.

Field testing alarms on salmonids

During the three trials using inactive alarms, the fish exhibited an initial startle response to the devices and moved quickly (within 1s) away from the alarms to a distance of 1-2m. In all three trials, the fish appeared to resume their normal swimming activity within 10-15s and in each instance, several fish had approached the alarms less than 10cm away within 30s. The alarms were then activated and separately lowered into the chamber. Again, an initial startle response was noted, but the fish resumed normal swimming activity within 10-15s and showed no response to the alarms.

During each of the three trials with active alarms, multiple fish were swimming within 10cm of the alarms less than 30s after the introduction of the alarms to the chamber. During the full 5m trials for each alarm, the fish did not appear to demonstrate any reaction or change in behaviour to the device except for the initial startle response. The approach distances and time of approach between the inactive and active trials were essentially identical. Based on these observations, we concluded that the sound from the alarms was either inaudible to the fish, or that the fish were not disturbed by the sound.

Alarm function and failure rate

In 1995, during the first 24 hours of the fishing experiment, about half of the 44 alarms failed when checked the following day. The failure was determined to be caused by water leaking into the central housing through the upper end (screw) cap. Silicon sealant had been used to seal the upper end caps rather than the O-ring in Jon Lien's initial design. The problem was corrected by using a rubberised sealant on the threads of the upper end caps and also silicon sealant around the outer margins of both the upper and lower end caps. In 1996 and 1997, electrical tape was used to tape over the silicon sealant and a tight wrap of plumbers' tape was applied over the electrical tape. These modifications reduced the failure rate considerably for the remainder of the study. Daily failure rates were still higher than one would expect from a commercially produced alarm. In 1995, overall failure rates were about two alarms per day or 4.5%. In 1996-97 with the added feature of taping alarms, the rate dropped to about a quarter of the 1995 rate (1.12%). During the 1995-97 studies, about 10 alarms fell off the nets and were lost but were replaced during the next net retrieval. Alarm failures and alarm loss did not appear to affect porpoise entanglement since alarms were replaced each day and since overall loss and failure rates were relatively low. No instances of porpoises being entangled near a malfunctioning alarm or in an area where an alarm was lost were recorded.

Statistical analysis

Fishing effort

The fishing effort for each of the seasons from 1995-97 is presented in Table 2. Each net was considered as an alarmed net when alarms were attached and as a control net when the alarms were removed. The 1995 experiment was conducted

from 27 July to 28 August. A total of 103ND was fished including 52ND with control nets and 51ND with alarmed nets (Table 2). The 1996 experiment was conducted from 7 July to 9 August. A total of 121ND was fished which included 60ND with control nets and 61ND with alarmed nets. In 1997, alarms were placed on all the nets (except during the first two days). For 1997, 188ND were fished, which included 180ND with alarmed nets and 8ND with control nets, from 30 June-16 August. Observer coverage at Spike Rock was 100% for the three field seasons.

Table 2
Fishing effort in net days (ND) fished and harbour porpoise bycatch for 1995-97 (bycatch in brackets).

Year	Alarmed effort	Control effort	Total
1995	51 (1)	52 (19)	103 (20)
1996	61 (1)	60 (28)	121 (29)
1997	180 (12)	8 (0)	188 (12)
TOTAL	292 (14)	120 (47)	412 (61)

Harbour porpoise bycatch

The number of harbour porpoises incidentally caught during each year for alarmed and control effort is shown in Table 2. The distribution of fishing effort for each net when alarmed or not and porpoise catches for 1995 and 1996 are shown in Figs 3 and 4, respectively. In 1995, only one harbour porpoise was caught in an alarmed net and 19 were caught in control nets, over nine different ND (Fig. 3). Alarmed and control net CPUE were 0.019 and 0.365 per ND, respectively. The CPUE was 19 times greater in control nets than alarmed nets. This represents a 95% reduction in harbour porpoise bycatch. However, the porpoise catch was not uniformly distributed over time during the duration of the 1995 experiment; the majority of animals were taken in the first half of August and only one was taken in the second half of August (Fig. 3). All harbour porpoises were caught on seven days between 30 July and 18 August. Twelve harbour porpoises were taken on one day during the fishery, in three different nets, including seven in one net. The probability of an entanglement in an alarmed net ($P_{\text{active}} = 0.019$) was significantly lower than the probability of an entanglement in a control net ($P_{\text{control}} = 0.173$) ($\chi^2 = 5.28$, $df = 1$, $p = 0.02$). The odds ratio was 10.5 (95% CI 1.78-61.4) which implies that the odds are 10.5 times greater that a porpoise entanglement occurred in a control net than an alarmed net.

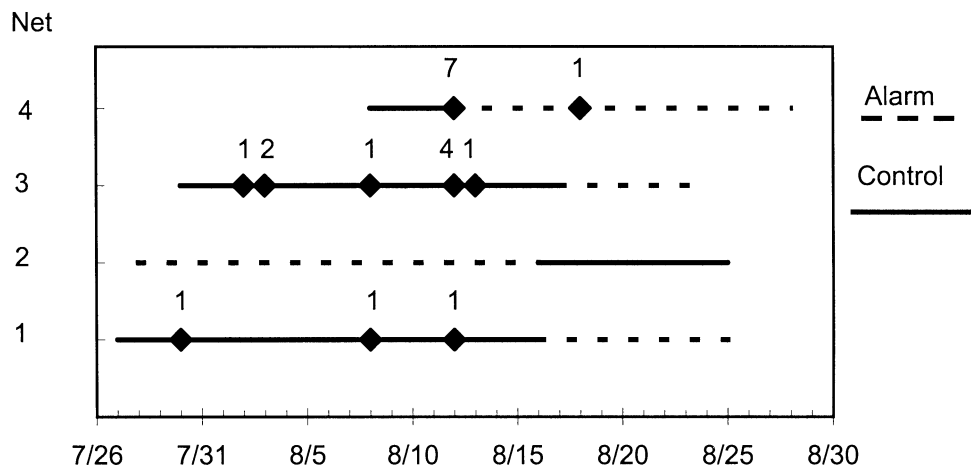


Fig. 3. Fishing effort by net and harbour porpoise bycatch indicated relative to treatment (control versus alarm), 1995.

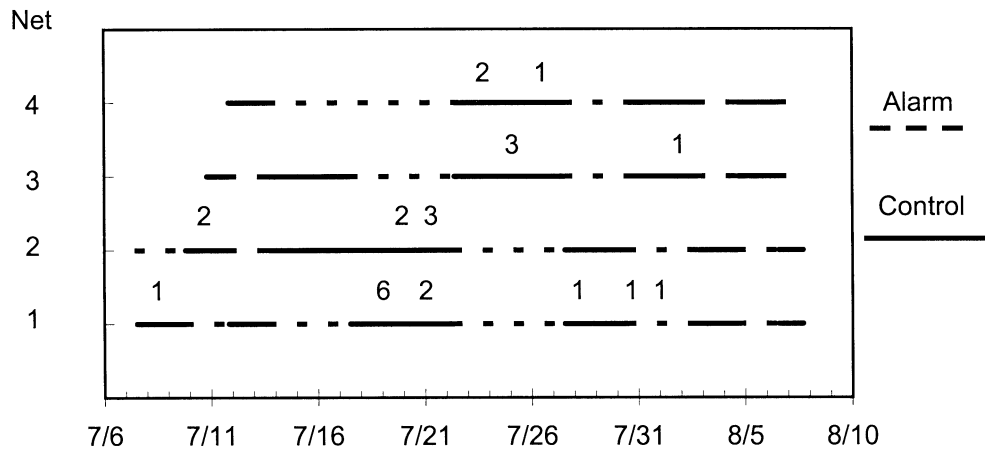


Fig. 4. Fishing effort by net and harbour porpoise bycatch indicated relative to treatment (control versus alarm), 1996.

The expected number of porpoises that would have been caught if alarms were not used was 38 ($0.365 \times 103\text{ND}$), as compared to the 20 which were observed taken.

The distribution of porpoise catches and fishing effort for 1996 is shown in Fig. 4. During 1996, only one harbour porpoise was taken in an alarmed net and 28 were taken in control nets in 13 different ND (Fig. 4). In 1996, the CPUE of harbour porpoises for alarmed and control nets was 0.016 and 0.467 per ND, respectively. The CPUE was 29 times greater in control nets than alarmed nets. This represents a 97% reduction in harbour porpoise bycatch. The alarmed and control effort and harbour porpoise catches were more evenly distributed in 1996 (Fig. 4) than in 1995. The chi-square analysis revealed that the probability of a porpoise entanglement in an alarmed net ($P_{\text{active}} = 0.016$) was significantly lower than the probability of an entanglement in a control net ($P_{\text{control}} = 0.217$) ($\chi^2 = 11.2$, $\text{df} = 1$, $p = 0.001$). The odds ratio was 16.6 (95% CI 2.9-93.5) implying that the odds of a porpoise take in a control net was 16.6 times greater than in an alarmed net. Thus, 56 harbour porpoises would have been expected to be taken in the fishery had no alarms been used in 1996.

In 1997, 12 harbour porpoises were taken during 180ND of fishing effort using alarmed nets compared to an expected 79 harbour porpoises if there had been no alarms, based on extrapolating from control catch rates from 1995 and 1996 (CPUE = 0.42 per ND). The observed bycatch reduction was 85% for 1997. A total of 59 harbour porpoises were collected during the fisheries; two porpoises dropped out of the nets before they could be retrieved. All sex and relative age categories were represented in the animals collected (Table 3). Ten of the 14 porpoises caught in alarmed nets were single entanglements of only one individual. The porpoises entangled in the control nets appeared to be uniformly distributed along the length of the nets but most were located near the lead line or bottom third of the net.

Table 3

Sex and relative age data for harbour porpoise collected from 1995-97.

Category	1995	1996	1997	Total	Alarmed bycatch
Adult female	4	3	2	9	2
Subadult female	2	10	3	15	4
Adult male	5	4	1	10	1
Subadult male	6	10	5	21	6
Calf	2	1	1	4	1
TOTAL	19	28	12	59	14

Harbour seal bycatch

The bycatch of harbour seals in alarmed and control nets from 1995-97 is presented in Table 4. Three harbour seals were caught during the 1995 fishery, all in alarmed nets. In 1996, nine harbour seals were caught, including four in alarmed nets and five in control nets. In 1997, 13 harbour seals were taken, all in alarmed nets. The CPUE value for harbour seal catch for all three seasons combined was 0.068 per ND for alarmed nets and 0.042 per ND for control nets. No significant differences in catches of harbour seals in alarmed versus control nets were obtained when pooling the 1995/96 data ($\chi^2 = 0.09$, $\text{df} = 1$, $p = 0.76$). The fact that 20 harbour seals were caught in alarmed nets indicates that they were not deterred by the sound.

Table 4

Harbour seal bycatch during the Spike Rock acoustic alarm studies from 1995-97 (entanglements in brackets).

Year	Alarmed	Control	Total
1995	3 (2)	0 (0)	3 (2)
1996	4 (4)	5 (5)	9 (9)
1997	13 (13)	0 no effort	13 (13)
TOTAL	20 (19)	5 (5)	25 (24)

Fish catches

Catches of chinook salmon were extremely low during the course of the 1995 experiment; only 21 fish were caught. Alarmed nets (51ND fished) caught 10 chinook salmon on eight different days and control nets (52ND fished) caught 11 on five different days (CPUE 0.20 and 0.21, respectively). There was no significant difference in catch of chinook salmon between alarmed and control nets in 1995 ($\chi^2 = 0.31$, $\text{df} = 1$, $p = 0.58$). However, the power of the test was low. Under the alternative hypothesis of a 50% difference ($P_{\text{active}} = 0.1$ and $P_{\text{control}} = 0.15$) the power was 0.15. In 1996, 45 chinook salmon were caught in the fishery. Alarmed (61ND fished) nets caught 21 chinook salmon in 18 ND and control (60ND fished) nets caught 24 in 15ND. There was also no significant difference in chinook salmon catch between alarmed versus control nets in 1996 ($\chi^2 = 0.12$, $\text{df} = 1$, $p = 0.72$). In 1997, 28 chinook salmon were caught including 26 in alarmed nets (180ND) and 2 in control nets (8ND). Forty-four sturgeon were caught in 1995, including 29 in alarmed nets and 15 in control nets. In 1996, 109 sturgeon were caught including 67 in alarmed nets and 42 in

control nets. In 1997, 152 sturgeon were caught, all in alarmed nets. Although catches and CPUE for sturgeon were higher in alarmed nets for both 1995 and 1996, the catches between alarmed versus control were not significantly different ($\chi^2 = 1.44$, $df = 1$, $p = 0.23$).

Seals or sea lions damaged four chinook salmon or 19% of the total catch in 1995. All of the damaged fish came from alarmed nets. In 1996, seals or sea lions damaged 11 of 45 (24%) chinook salmon caught in the fishery which included 6 of 24 (25%) from control nets and 5 of 21 (24%) from alarmed nets. In 1997, seals or sea lions damaged 7 of 26 (27%) chinook salmon caught in alarmed nets. There was no significant difference in numbers of salmon damaged by pinnipeds in alarmed versus control nets ($\chi^2 = 0.07$, $df = 1$, $p = 0.79$).

Observational studies

Only the primary findings of the 1996 field observations are given here. The complete details of the study are presented in Laake *et al.* (1998). Over the 27-day period of observations in 1996, 503 positions of harbour porpoise groups were recorded at Spike Rock during 136 hours of observation. Although group size varied from 1-10, groups of 1 or 2 individuals comprised 72% of the sightings. Harbour porpoise sightings were primarily clustered to the north of Net 1, but when Net 1 was unalarmed porpoises were seen closer to the net (Fig. 5). The distribution of distances between porpoises and Net 1 suggested that porpoises were displaced 100-150m from the net when it was alarmed. Laake *et al.* (1998) chose 125m as the radius of the displacement region for testing the significance of an alarm effect. Harbour porpoises were seen within the displacement region on 5 of the 13 days when the net was not alarmed but on only 1 of the 14 days when the net was alarmed (Fig. 5). This demonstrated that porpoises were less likely to surface within 125m of the displacement region when the net was alarmed ($p < 0.01$) (Laake *et al.*, 1998).

DISCUSSION

This study indicates that acoustic alarms reduce the probability of harbour porpoise entanglement in set-nets in the Spike Rock fishing grounds. The results of our 1995-96 studies are similar to those reported by Kraus *et al.* (1995; 1997) in the New England sinknet fishery. The results of the

1995 study were significant but the fishing effort with alarmed and control nets and porpoise catch was not evenly distributed through time. If a significant difference in harbour porpoise abundance occurred in the area during the latter two weeks of the experiment, it could possibly explain the reduced catch rates during that time period. The 1996 experiments were more balanced in the distribution of experimental and control fishing effort through time. The results were similar to 1995 and in fact a more dramatic reduction in porpoise bycatch was observed in 1996. The 1997 study was conducted for a longer period of time than the 1995-96 studies and all nets were alarmed, in part to evaluate whether habituation to the alarms might occur. The results are not, however, clear on this question. It is noteworthy that no harbour porpoises were taken for the first 18 days of the fishery and that 11 of 12 were taken in the last two weeks. Even given higher than expected catches during the 1997 study, the observed catch reduction was still 85%. The question of habituation remains to be answered (see discussion in IWC, 2000). Habituation, even if it does occur, may not necessarily result in significantly higher bycatch rates. It may also not be a problem in fisheries where nets are moved frequently or where fishing seasons are short. Problems with habituation might be expected in those fisheries where nets remain set in the same locations for long periods of time.

The use of acoustic alarms did not appear to affect target catch in the Spike Rock fishery. Catches of both chinook salmon and sturgeon were not significantly different in alarmed or control treatments. There were also no significant differences in harbour seal bycatch between alarmed or control nets. No significant differences in depredation of caught fish by seals or sea lions were noted during the studies although sample sizes were small. Few sea lions occur in the area during the time the studies were conducted and incidentally caught seals were primarily young-of-the-year which are more susceptible to incidental mortality than adults. The 'dinner bell effect' of acoustic alarms is a question that still needs to be explored.

The observations of harbour porpoise around the nets during 1996 (Laake *et al.*, 1998) indicated that harbour porpoises were displaced a minimum distance of 125m from alarmed nets. Many porpoises were sighted in the general area to the north within 200-300m indicating that the alarms did not displace them from a large area away from the alarm

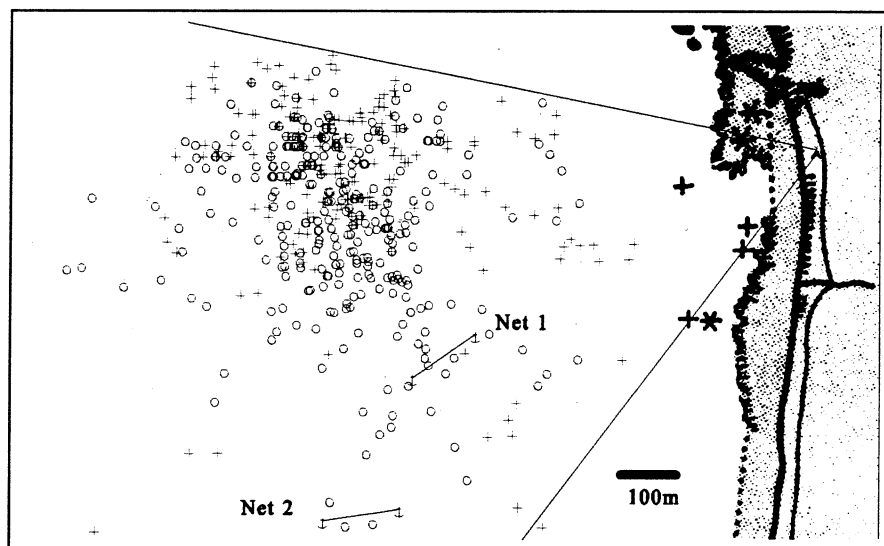


Fig. 5. Positions of harbour porpoise sightings when net No. 1 was not alarmed (circle) and alarmed (+).

source. We propose that the alarms function in an aversive manner by scaring or displacing porpoises away from the sound. If the alarms functioned by alerting animals to the presence of the net, porpoises would be expected to approach closer to the nets than the 125m minimum. Kastelein *et al.* (1995) have shown that harbour porpoises can detect and avoid gillnets under certain conditions. They demonstrated that, when focussed, harbour porpoises are capable of sensing and avoiding gillnets, although not with 100% precision. The fact that the porpoises do not approach closer suggests that they are deterred by the sound rather than by being alerted to the presence of the net.

The field measurements of the alarms at the Spike Rock fishing grounds (Bowles *et al.*, 1997) provide information on the effective range of an alarm and alarmed net. The effective range under typical conditions of ambient background noise would be between 113-293m. This effective range falls within the bounds of the 125m exclusion zone demonstrated by Laake *et al.* (1998). This finding provides further evidence that alarms function by excluding harbour porpoises from a certain area in an aversive manner, and not necessarily by alerting porpoises to an object.

The fishing effort on the northern Washington coast has declined considerably since 1988-89 when large numbers of harbour porpoises were incidentally caught. The observed plus reported catch of porpoises at Spike Rock from 1990-95 has averaged about nine per year (Gearin, unpubl. data). These levels of take are considerably less than previous years and pose no immediate threat to local harbour porpoise stocks based on recent stock assessments (Barlow *et al.*, 1995). The minimum population for the Oregon/Washington coastal Pacific stock is estimated at 22,049 animals, and the Potential Biological Removal (PBR) is 220 (Barlow *et al.*, 1995). If fishing effort returns to 1980s levels, however, due to increased salmon abundance, acoustic alarms may provide a tool to reduce the expected increased porpoise bycatch resulting from increased fishing effort.

We do not suggest that acoustic alarms will function in all types of net fisheries or be effective for other cetacean species. We recommend caution in applying acoustic alarm technology to management situations until they are adequately tested to determine if they will be effective in that particular situation. Furthermore, we do not recommend large-scale usage of acoustic alarms until more is known about the possible effects of large-scale sound transmission and habituation.

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REFERENCES

- Barlow, J., Brownell, R.L., DeMaster, D.P., Forney, K.A., Lowry, M.S., Osmek, S., Ragen, T.J., Reeves, R.R. and Small, R.J. 1995. US Pacific marine mammal stock assessments. *NOAA NMFS SWFC Tech. Mem.* 219. 162pp.
- Bowles, A.E., Anderson, R. and Stinson, H. 1997. Harbor porpoise net entanglement study: Ambient noise and propagation of pinger sounds. Final Report to the National Marine Mammal Laboratory, Seattle, WA. P.O. No.40ABNF601357. [Copies available at NMML, 7600 Sand Point Way NE, Seattle, WA 98115].
- Donovan, G.P. and Bjørge, A. 1995. Harbour porpoises in the North Atlantic: edited extract from the Report of the IWC Scientific Committee, Dublin 1995. *Rep. int. Whal. Commn* (special issue) 16:3-25.
- Fleiss, J.L. 1973. *Statistical Methods for Rates and Proportions*. John Wiley and Sons, New York. 223pp.
- Frady, T., Northridge, S. and Smith, T.D. 1994. Identifying potential modifications to sink gillnet gear to reduce harbor porpoise bycatch. Report of a workshop held 20-23 September 1994, Falmouth, MA. NEFSC Lab. Ref. Doc. 93-25 NOAA-NMFS, 166 Water Street, Woods Hole, MA 02543. 48pp.
- Fullilove, J. 1994. How to make a gillnet 'pinger'. *Natl. Fisherman* May 1994:29.
- Gaskin, D.E. 1984. The harbour porpoise, *Phocoena phocoena* (L.): regional populations, status and information on direct and indirect catches. *Rep. int. Whal. Commn* 34:569-86.
- Gearin, P.J., Gosh, M., Cooke, L. and Joner, S. 1993. Summary report on marine mammal observations in the northern Washington Chinook salmon set-net fishery in 1992. Final report for NOAA, National Marine Fisheries Service, Northwest Regional Office, Seattle, WA 98115. 16pp. [Copies available at NMML, 7600 Sand Point Way NE, Seattle, WA 98115].
- Gearin, P.J., Melin, S.R., DeLong, R.L., Kajimura, H. and Johnson, M.A. 1994. Harbor porpoise interactions with a Chinook salmon set-net fishery in Washington State. *Rep. int. Whal. Commn* (special issue) 15:427-38.
- International Whaling Commission. 1994. Report of the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps. *Rep. int. Whal. Commn* (special issue) 15:1-71.
- International Whaling Commission. 2000. Report of the Scientific Committee. Annex I. Report of the sub-committee on Small Cetaceans. *J. Cetacean Res. Manage. (Suppl.)* 2:235-64.
- Kastelein, R.A., de Haan, D., Staal, C., Nieuwstraten, S.H. and Verboom, W.C. 1995. Entanglement of harbour porpoises (*Phocoena phocoena*) in fishing nets. pp. 91-156. In: P.E. Nachtigall, J. Lien, W.W.L. Au and A.J. Read (eds.) *Harbour Porpoises - Laboratory Studies to Reduce Bycatch*. De Spil Publishers, Woerden, The Netherlands. 168pp.
- Kraus, S., Read, A., Anderson, E., Baldwin, K., Solow, A., Spradlin, T. and Williamson, J. 1995. A field test of the use of acoustic alarms to reduce incidental mortality of harbor porpoises in gillnets. Paper SC/47/SM17 presented to the IWC Scientific Committee, May 1995 (unpublished). 28pp. [Available from the Office of this Journal].
- Kraus, S.D., Read, A.J., Solow, A., Baldwin, K., Spradlin, T., Anderson, E. and Williamson, J. 1997. Acoustic alarms reduce porpoise mortality. *Nature, Lond.* 388:525.
- Laake, J., Rugh, D. and Baraff, L. 1998. Observations of harbor porpoise in the vicinity of acoustic alarms on a set gill net. *NOAA Tech. Mem. NMFS-AFSC* 84:40.
- Lien, J. and Hood, C. 1994. An investigation of acoustic devices to prevent harbour porpoise by-catch in groundfish gillnets, and recommendations from fishermen in the Bay of Fundy for future by-catch mitigation. Report to the Department of Fisheries and Aquaculture, Fredrickton, New Brunswick and the Department of Fisheries and Oceans, Halifax, Nova Scotia. 22pp.

- Lien, J., Barney, W., Todd, S., Seton, R. and Guzzwell, J. 1992. Effects of adding sounds to cod traps on the probability of collisions by humpback whales. pp. 701-8. In: J.A. Thomas, R.A. Kastelein and A.Y. Supin (eds.) *Marine Mammal Sensory Systems*. Plenum, New York. 773pp.
- Polacheck, T. 1989. Harbor porpoises and the gillnet fishery. *Oceanus* 32(1):63-70.
- Read, A.J. and Gaskin, D.E. 1988. Incidental catch of harbor porpoises by gill nets. *J. Wildl. Manage.* 52(3):517-23.
- Reeves, R.R., Hofman, R.J., Silber, G.K. and Wilkinson, D. 1996. Acoustic deterrence of harmful marine mammal-fishery interactions: proceedings of a workshop held in Seattle, Washington, 20-22 March 1996. US Department of Commerce, NOAA Tech. Memo.; NMFS-OPR-10; Y; 68.
- Snedecor, G.W. and Cochran, W.G. 1973. *Statistical Methods*. Iowa State University Press, Iowa. 539pp.
- Urick, R.J. 1983. *Principles of Underwater Sound*. 3rd Edn. McGraw Hill, Baskerville, New York. xiv+423pp.

Incidental catches of dolphins in mid-water trawls for Argentine anchovy (*Engraulis anchoita*) off the Argentine shelf

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ABSTRACT

Information on the incidental mortality of dusky and common dolphins in mid-water trawl fisheries along the Argentine shelf was obtained for the 1990s. The Argentine anchovy is believed to be an under-exploited resource and is usually taken in purse seine fisheries. However, on the few occasions when it was the target species of large mid-water trawlers, anchovy-eating dolphins were incidentally caught. A few incidents accounted for relatively high numbers of dolphins but in most of the cases the information obtained was insufficient for detailed analysis. For three cases, however, sufficient information was obtained to estimate mortality rates. Nevertheless, interpretation of these rates is difficult for a number of reasons. FV *Mar Salvaje* caught around 60 common dolphins (*Delphinus delphis*) in only a few days and in one tow 20 dolphins were caught. Biological information on 18 common dolphins (12 males and 6 females) was obtained and ages ranged from 5–10 for females and 2–18 for males.

KEYWORDS: ATLANTIC OCEAN; SOUTH AMERICA; COMMON DOLPHIN; DUSKY DOLPHIN; INCIDENTAL CATCHES; FISHERIES; TRAWLS

INTRODUCTION

Interactions between marine mammals and fisheries have been monitored along the coasts of Argentina since the mid-1980s. Previous detailed studies include Pérez-Macri and Crespo (1989) who surveyed the mortality of franciscana (*Pontoporia blainvillei*) in coastal fisheries of Buenos Aires Province; Corcuera *et al.* (1994), Crespo *et al.* (1994a) and Goodall *et al.* (1994) who reviewed all types of interactions between marine mammals and fisheries along the Argentine coasts; and Crespo *et al.* (1997) and Dans *et al.* (1997a) who concentrated mainly on the interactions of marine mammals with the trawl fishery off Patagonia.

During the 1990s, the Argentine fleet of high-sea trawlers comprised some 250 vessels, of which 150 were based in Patagonia. Interactions with several species of marine mammals have been shown for that region, including the dusky dolphin (*Lagenorhynchus obscurus*), Commerson's dolphin (*Cephalorhynchus commersonii*) and the South American sea lion (*Otaria flavescens*). The target species of the trawls were mainly the Argentine hake (*Merluccius hubbsi*) and the Argentine red shrimp (*Pleoticus muelleri*); bycatch species other than marine mammals were also caught.

Argentine hake is caught by bottom trawling; Argentine red shrimp by bottom trawling during daylight and mid-water trawling at night. This latter approach was only used by a few factory vessels (Crespo *et al.*, 1997).

While South American sea lions can become entangled in any kind of trawl, dolphins are usually caught in the mid-water trawls at night with estimated rates of around 70–200 per year for dusky dolphins (Crespo *et al.*, 1997; Dans *et al.*, 1997a). Of this, Crespo *et al.* (1997) had estimated an annual catch of around 54 dusky dolphins by four factory vessels using mid water trawls (estimated rate 0.148 dolphins per fishing day). Thus, even only a small number of vessels using this technique could result in

relatively large catches of dolphins (Dans *et al.*, 1997a; Schiavini *et al.*, 1999). In 1994, mid-water trawls were forbidden in the Argentine red shrimp fishery and dolphin mortality was thought to have decreased. Since then, twin-beam trawlers have been exclusively used for fishing Argentine red shrimp in order to decrease bycatches of Argentine hake. Nevertheless, mid-water trawling is not forbidden for other species such as the Argentine anchovy (*Engraulis anchoita*) or the Argentine shortfin squid (*Illex argentinus*).

During the 1990s, Argentine hake catches were greater than the recommended Total Allowable Catch level, and evidence of overfishing was apparent. In the late 1990s, fishing effort began to be reduced by increasing both temporal and spatial restrictions on fishing. As a consequence, the hake-based industry is looking for alternative targets. In this context, the Argentine anchovy represents an abundant pelagic resource, whose present annual catches (12,000 tonnes) are well below the estimated sustainable maximum annual removal of 155,000 tonnes (Anon., 1999). The fishery has been concentrated traditionally off Buenos Aires Province, using purse seines. Some dolphin mortality in purse seines was recorded in the early 1990s (Corcuera *et al.*, 1994; Crespo *et al.*, 1994a); at least dusky and common dolphins (*Delphinus delphis*) were included.

In recent years, several experimental and commercial mid-water trawling operations for Argentine anchovies were carried out off the Argentine shelf. Although it is not expected that the market for Argentine anchovy will replace that for hake, the species does represent a potential alternative target species, with the consequent possibility of an increase in fishing effort in the near future.

The objective of this paper is to summarise unpublished information regarding the bycatch of dolphins in mid-water trawls conducted for Argentine anchovy with special reference to common and dusky dolphins.

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MATERIALS AND METHODS

Study area and information gathering

This paper reviews the 1989-99 records of incidental mortality of small cetaceans in mid-water trawls for Argentine anchovies off the Argentine shelf between 38°S and 48°S and between the coast and the 200 n.miles EEZ in which the vessels of the national fleet operate (Fig. 1).

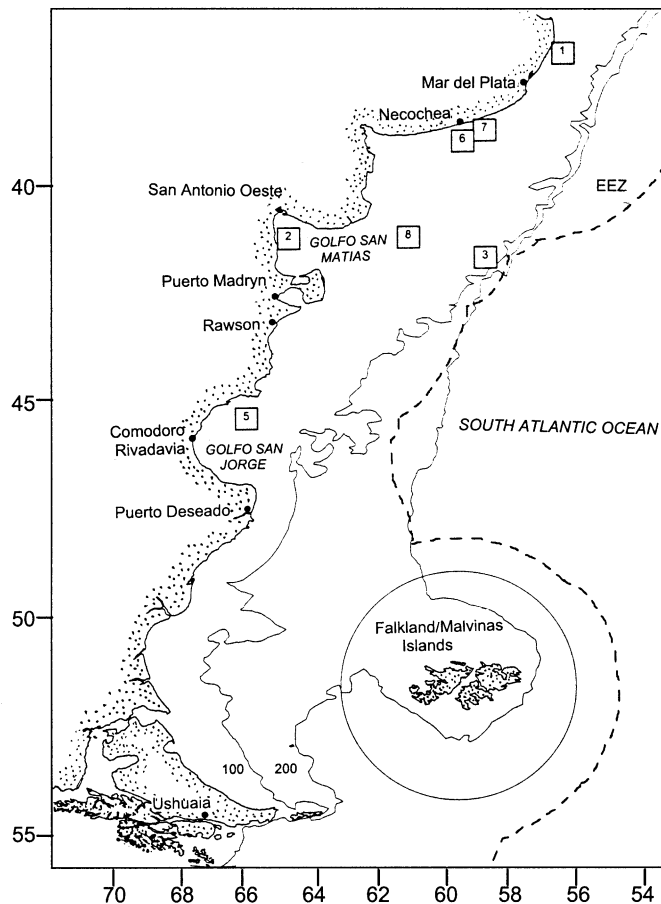


Fig. 1. Location of incidental catch events along the coast of Argentina. The location of event number 4 is unknown.

We have collected information on the incidental mortality of marine mammals in the Patagonian trawl fishery since 1989. This has been obtained from a number of sources including: long-term contacts in fishing companies; interviews with fishermen (captains and officers); and information related to marine resources supplied by the national authorities (Fisheries Secretary and Natural Resources Secretary).

Although most information was related to Argentine hake and red shrimp trawl fisheries, some related to mid-water trawls for Argentine anchovy. These were sporadic and opportunistic and largely dependent on market conditions. A special effort was made to obtain information from these given the previous reports of frequent dolphin bycatches (Crespo *et al.*, 1994a; 1997; Dans *et al.*, 1997a). The quality of information varied by event, but in all cases data were obtained as to whether or not dolphin bycatches occurred. Other information occasionally obtained included relatively detailed data on geographic position, time, depth, weather conditions, species affected, size, and other features of the fishing gear and operations.

In some cases where information was limited, inferences could be drawn from good information for other events. For example, even when the direct causes of entanglements could not be determined, information from one vessel, the FV *Mar Salvaje*, allowed an evaluation of the incidence of certain variables that might have been related to entanglements. This particular vessel operated in two different geographical areas. The northern area (north of 42°S) is mostly influenced by sub-tropical waters, while the southern area (south of 42°S) is mostly influenced by sub-Antarctic waters. Additionally, this vessel used mid-water trawling both during daylight and at night.

For those cases where sufficient information was available, capture rates were calculated. Rates were calculated as number of dolphins per tow or per fishing day. The latter was chosen because it allowed comparisons with previous studies by Crespo *et al.* (1997).

Biological data

Out of 60 common dolphins caught by the FV *Mar Salvaje*, a total of 18 specimens were collected and frozen on board at -20°C. Necropsies were carried out at the Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata. Standard length was recorded following Norris (1961) and several teeth were collected from each individual for age determination. After decalcifying them in 5% formic or nitric acid, haematoxylin-stained sections 16-18µm thick were obtained (Hohn, 1980; IWC, 1980; Crespo *et al.*, 1994b). Growth layer groups (GLGs) in dentine and cementum were counted, assuming annual deposition. Mammary glands were examined for presence of milk and uterine horns were examined for foetuses.

RESULTS AND DISCUSSION

Eight occasions of dolphin mortality were recorded for the mid-water trawl anchovy fishery during the 1990s (Table 1 and Fig. 1). The first five records merely reflect that entanglement occurred and have no associated fishing effort data. Of them, the number entangled by FV *Esturión* was particularly high.

However, for three records (Table 1: cases 6, 7 and 8), reliable and detailed information was collected. For these, which occurred in April 1998 and January 1999, a more thorough analysis could be carried out.

April 1998

Two fishing vessels, the FV *Humback* and FV *Harengus*, had been fishing for Argentine hake with bottom trawling nets but the low catches caused both vessels to change the target species to Argentine anchovy for a short period. From 2-13 April 1998, mid-water trawls were used and dusky dolphins were caught during both diurnal and nocturnal trawls (Table 1). The fishing area was between 39°S and 40°S, and depth ranged between 50 and 70m. The mouth of the trawl is usually around 40m high and 40m wide. The FV *Humback* completed 41 trawls during the period, while the FV *Harengus* completed between 38 and 44 trawls.

January 1999

The FV *Mar Salvaje* conducted fishing operations with the Argentine anchovy as the main target species. The vessel employed mid-water nets (mouth ca 40mx40m). From 22-31 December 1998, the vessel operated to the south of 42°S and from 1-7 January 1999 it operated to the north. A total catch of 60 common dolphins was recorded, all to the north of 42°S.

Table 1

Records of dolphin bycatch in mid-water fishing operations for southern anchovy off the Argentine shelf. Exact locations are shown in Fig. 1.

Case no.	Date	Vessel	Type of vessel	Species	No. of indiv.	Fishing area	Comments	Source of information
1	1989-1992		Coastal	Delphinids	4	Near Mar del Plata	Presumably <i>Stenella</i> sp.	Bastida <i>et al.</i> 1992
2	October 1995	<i>1 de Mayo</i>	Coastal	Dusky dolphin	1	Golfo San Matías	-	Scientist
3	1995	<i>Esturión</i>	Factory	Common dolphin	40	Slope near Golfo San Matías	-	Sailor
4	1995-1998	<i>Poseidón</i>	Factory	Delphinids	?	Unknown	Incidental catch is a common event	Sailor
5	December 1995	<i>Oca Balda</i>	Research	Dusky dolphin	5	Golfo San Jorge	Trials with MWT	Scientist
6	2-13 Apr. 1998	<i>Humbuck</i>	Factory	Dusky dolphin	5	Near Necochea	-	Captain
7	2-13 Apr. 1998	<i>Harengus</i>	Factory	Dusky dolphin	10	Near Necochea	-	1st Officer
8	1-17 Jan. 1999	<i>Mar Salvaje</i>	Factory	Common dolphin	60	Near Golfo San Matías	-	Fishing inspector

MWT: mid-water trawls.

However, even when detailed information was obtained about the haul characteristics and CPUE values for Argentine anchovy (Table 2), the information on common dolphins catches was not sufficient to estimate a reliable CPUE value for this species.

Table 2

Characteristics of the operations of the FV *Mar Salvaje*, regarding fishing area and time of the operation. Standard deviation given in brackets.

	Time of the tow		
Variable	Diurnal	Nocturnal	Total
South of 42° S			
CPUE(kg/h)	316.43 (478.74)	538.53 (1,199.39)	418.94 (874.58)
Depth (m)	58.43 (16.31)	48.67 (15.25)	53.92 (16.28)
Tow duration (hours)	1.29 (0.68)	1.74 (0.69)	1.5 (0.71)
Speed (knots)	4.51 (0.19)	4.44 (0.12)	4.48 (0.16)
No. of tows	14	12	26
North of 42° S			
CPUE(kg/h)	2,121.72 (2,957.55)	1,286.79 (1,187.49)	1,760.33 (2,382.36)
Depth (m)	40.55(4.14)	39.93 (2.78)	40.28 (3.6)
Tow duration (hours)	1.73 (1.29)	1.89 (0.55)	1.8 (1.03)
Speed (knots)	4.94 (0.59)	4.77 (0.37)	4.86 (0.51)
No. of tows	38	29	67
Total			
CPUE(kg/h)	1,635.68 (2,656.72)	1,067.79 (1,225.36)	1,385.32 (2,155.43)
Speed (m)	45.37 (12.01)	42.49 (9.25)	44.1 (10.92)
Tow duration (hours)	1.61 (1.17)	1.84 (0.59)	1.71 (0.96)
Speed (knots)	4.82 (0.55)	4.67 (0.35)	4.76 (0.48)
No. of tows	52	41	93

Most of the catch of dolphins (80%) occurred during night trawls with the rest during daylight. The proportion of nocturnal hauls was not significantly different from 0.5 (Binomial test $p = 0.3284$), while the proportion of dolphins caught at night was significantly higher (Binomial test $p < 0.001$). Thus, although not conclusive, these results suggest that the bycatch of common dolphins was mostly a night-related phenomenon. In addition, the dolphin bycatches appeared to show a contagious distribution: from 1-3 January 1999, 25 dolphins were caught, most of them (around 20) in the first tow; from 4-5 January another 18 individuals were caught; the remaining 17 dolphins were caught between 6 and 17 January 1999. Although the usual number of individuals caught per tow was reported between 1 and 2, in a few cases this increased to between 8 and 20 individuals. Unfortunately, more detailed information on the number of dolphins caught in each tow was not available.

One probable explanation for the bycatch is that dolphins became entangled whilst feeding inside the net. Although the stomach contents of only three animals have been analysed to date, anchovy comprised between 76-88% of prey items by number. Other prey items included a few pelagic fish and the Patagonian squid (*Loligo sanpaulensis*). If this hypothesis is true, the higher nocturnal dolphin catches could be associated with higher Argentine anchovy abundance during the night. Table 2 summarises CPUE values for Argentine anchovy catches as kg/hour trawling, depth, tow duration and trawling speed. In order to test the former hypothesis, the differences in Argentine anchovy CPUE (transformed as $\sqrt{\text{CPUE}+1}$) were tested by means of a two-way analysis of variance considering diurnal and nocturnal tows, and fishing areas to the north and south of 42°S. Statistical differences were found by area but not time of day (Table 3). Thus, although the abundance of Argentine anchovy was higher to the north of 42°S, where the dolphins were caught, the nocturnal trend in entanglement could not be related to differences in the abundance of Argentine anchovy in the simple manner tested for here, based on the available data.

Table 3

Analysis of variance of CPUE values for anchovy catches of FV *Mar Salvaje*. df: degrees of freedom; MS: mean squares; F: Fisher statistic; p : probability associated with F .

Source of variation	df	MS	F	p
Daytime	1	269.590	0.580	0.448
Area	1	10,047.122	21.620	<0.001
Daytime x Area	1	367.805	0.791	0.376
Error	89	464.722		

Comparison between capture rates of cases 6, 7 and 8

Although the available information for cases 6, 7 and 8 are of varying quality, it was sufficient for capture rates to be calculated. FV *Mar Salvaje* capture rates were calculated both for the whole fishing period and for the area to the north of 42°S. High rates of almost nine individuals per day and per vessel were calculated (Table 4). The capture rates for common dolphins were higher than those for dusky dolphins for cases 6 and 7 in April 1998 (Table 5).

In addition, these capture rates are also higher than those estimated for the Argentine red shrimp fishery (0.148 dolphins per day; Crespo *et al.*, 1997). Nevertheless, any comparisons should be treated with caution. Capture rates for Argentine red shrimp nets were calculated on the basis of one fishing vessel monitored for a period of two years. Those

for the FV *Mar Salvaje* were calculated on a single and short period of time. It should also be recognised that the fishing gear for both hake and red shrimp (and indeed Argentine anchovy and Argentine shortfin squid, *Illex argentinus*) is almost identical. With respect to the target species (and when the mid-water trawls are used close to the surface), the same assemblage of species is usually caught. Thus, Argentine squid, anchovies, small hake and red shrimps comprise an assemblage of species in which the proportions of individual species may vary but all are always present (Crespo *et al.*, 1997; Koen Alonso *et al.*, 1998).

Table 4

Capture rates of common dolphins in FV *Mar Salvaje*, from 22 December 1998 to 17 January 1999.

Date	Area	Depth	No. of dolphins	
			per day	per tow
22-31 Dec. 1998	42°S-47°S	22-94m	0.000	0.000
1-3 Jan. 1999	41°S-42°S	39-48m	8.333	1.667
4-5 Jan. 1999	40°S-41°S	35-49m	9.000	2.250
6-17 Jan. 1999	39°S-41°S	32-58m	1.545	0.386
Whole trip	39°S-47°S	22-94m	2.308	0.645

Caution should also be exercised when comparing capture rates, given the differences between fishing areas and seasons. At present there is insufficient information to test for this. Most dolphin captures (cases 1-3, 6-8) occurred in the transition zone between the opposing flows of sub-tropical and sub-Antarctic water masses (33°-39°S). By contrast, case 5 was located in an area (south of 39°S) which is more under the influence of sub-Antarctic water masses (Boltovskoy, 1986; Gayoso and Podestá, 1996; Crespo *et al.*, 1998). Thus, some differences may be related to the fishing area where the entanglements took place. Similarly, there is insufficient information to examine for seasonal events. Five cases occurred between October and April ('summer conditions') whilst there is no precise information on season for the remaining cases (Table 1).

Age and sex composition of the catch of common dolphins

Of the 60 animals caught by the FV *Mar Salvaje*, biological information was available for 18 (12 males and 6 females); it is not possible to determine whether these are representative of the 60 animals. The difference in sex ratio was not statistically significant from parity (Binomial test $p=0.238$). The standard length of the females ranged between 174 and 210cm and their weight between 67 and 102kg. The standard length of males ranged between 170 and 219.5cm and their weight between 56 and 138kg (Table 6). With respect to age, the females ranged between 5 and 10 years old, while the males showed a wider range between 2

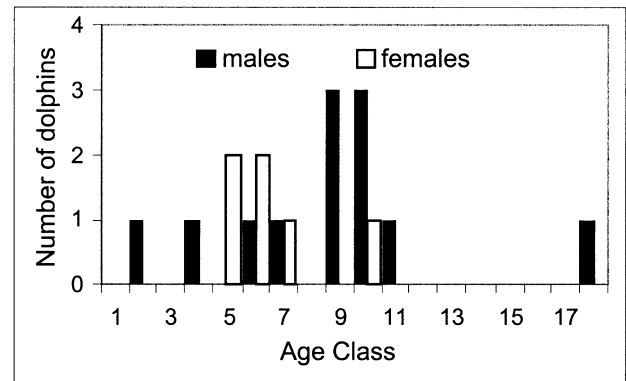


Fig. 2. Age and sex composition of the collected sample of common dolphins ($n=18$) caught in mid-water trawls for southern anchovies by the FV *Mar Salvaje* during January 1999, off northern Patagonia.

and 18 years old (Fig. 2). Within this small sample size there was a higher proportion of males between 9 and 10 years. No foetuses or lactating females were caught and histological analysis revealed no corpora lutea.

Although the sample is small, it does suggest differences in age and sex composition from the dusky dolphins affected by mid-water trawls for Argentine red shrimp. In the latter case, females predominated (around 70%) and their average age was 5.9 ± 2.1 (Crespo *et al.*, 1997; Dans *et al.*, 1997a; b). In the present case no sex predominates in the sample and the age distribution is widely spread.

Table 6

Size and age data of common dolphins incidentally caught by FV *Mar Salvaje* using mid-water trawls for anchovies, in January 1999, in northern Patagonia.

Field number	Sex	St. length (cm)	Weight (kg)	Age (GLGs)
Dd145	F	174	67.65	5
Dd147	F	182	68.10	5
Dd141	F	188.5	79.00	6
Dd138	F	191	86.26	6
Dd143	F	198	90.80	7
Dd135	F	210	102.15	10
Dd149	M	170	56.30	2
Dd142	M	192	79.45	4
Dd146	M	196	95.34	6
Dd148	M	187	86.26	7
Dd137	M	200	113.95	9
Dd136	M	209	90.80	9
Dd134	M	212	117.59	9
Dd139	M	192.5	102.15	10
Dd140	M	197	103.06	10
Dd144	M	206	90.80	10
Dd150	M	219.5	138.47	11
Dd133	M	210	124.85	18

Table 5

Capture rates of dolphins for Cases 6, 7 and 8 (see Table 1).

Case	Vessel	Date	Area	Depth	No. of dolphins	
					per day	per tow
6	<i>Humback</i>	2-13 Apr. 1998	39°S-40°S	50-70m	0.417	0.122
7	<i>Harengus</i>	2-13 Apr. 1998	39°S-40°S	50-70m	0.833	0.227-0.263
8	<i>Mar Salvaje</i>	22 Dec. 1998-17 Jan. 1999	39°S-47°S	22-94m	2.308	0.645
		1-17 Jan. 1999	39°S-42°S	32-58m	3.750	0.896

CONCLUSIONS AND RECOMMENDATIONS

Efforts to monitor marine mammal mortality in trawl fisheries have been considerably less than for other fishing gear (e.g. purse seines, gillnets) and the extent of the problem has probably been underestimated (Fertl and Leatherwood, 1997). In the North Atlantic, Couperus (1997) reported white-sided dolphin (*L. acutus*) catches in the Dutch mid-water trawl fishery for mackerel (*Scomber scombrus*) and Northridge (1984) reported common dolphins caught in mid-water trawls for sardines (*Sardina pilchardus*) and mackerel (*Scomber japonicus*). Thus, the available data suggest that bycatches in mid-water trawls are potentially a serious problem that requires thorough evaluation. This gear appears to affect mainly small cetaceans such as common dolphins and those of the genus *Lagenorhynchus*.

The few events recorded in this paper occurred when the trawl fishery was almost completely directed towards Argentine hake and Argentine red shrimp. Occasionally, in the absence of the main target species and under specific market conditions, the target species changed to Argentine anchovy with pelagic nets. This situation changed in the late 1990s when Argentine hake was depleted and temporal and spatial restrictions were imposed in order to reduce the fishing effort.

Given this background, some fishing companies began to increase catches of Argentine anchovy, which at present is considered an under-exploited resource. Clearly, if mid-water trawl effort for the Argentine anchovy is going to increase, this represents a potential risk to those small cetacean species, such as the dusky and common dolphin, that feed on anchovy.

Therefore, the authorities should seriously consider the possible impact on dolphin populations when developing fishery management models for Argentine anchovy or similar pelagic species, such as the mackerel.

From a management perspective, a number of possible strategies are apparent, e.g.:

- (a) determine whether dolphin schools are present before fishing for Argentine anchovies using mid-water trawls;
- (b) do not deploy the nets if dolphins are present, especially at night;
- (c) if dolphins are entangled, change the fishing area.

With respect to research recommendations, it is clear that the Fishery Agency should begin to systematically collect information on dolphin catches as part of an observer programme and to recover dolphin carcasses for biological studies. In the longer term it is important to establish a research programme in order to assess the impact of bycatches on the relevant cetacean populations (e.g. see Donovan, 1994).

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REFERENCES

- Anonymous. 1999. La captura '98 cayó un 19%. Redes-Letter N°31:11-12.
- Bastida, R., Rodríguez, D., Morón, S., Gerpe, M. and Marcoveccio, J. 1992. Varamientos y capturas incidentales de pequeños cetáceos en el sudeste de la provincia de Buenos Aires (Argentina) en el período 1989-1992. Abstracts of the 5th Reun. Esp. Mamif. Acuát. Am. Sur., 28 September-2 October 1992, Buenos Aires, Argentina. p.8. [Available from the author].
- Boltovskoy, D. 1986. Biogeography of the southwestern Atlantic: Overview, current problems and prospects. In: A.C. Pierrot-Bulls, S. Van der Spoels, B.J. Zahuranec and R.J. Johnson (eds.) *Pelagic Biogeography. Proceedings of an International Conference, The Netherlands, 29 May-5 June 1985*. UNESCO Technical Papers in Marine Sciences 49. UNESCO, Paris.
- Corcuera, J., Monzón, F., Crespo, E.A., Aguilar, A. and Raga, J.A. 1994. Interactions between marine mammals and the coastal fisheries of Necochea and Claromecó (Buenos Aires Province, Argentina). *Rep. int. Whal. Commn* (special issue) 15:283-90.
- Couperus, A.S. 1997. Interactions between Dutch midwater trawl and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) southwest of Ireland. *J. Northwest Atl. Fish. Sci.* 22:209-18.
- Crespo, E.A., Corcuera, J.F. and López Cazorla, A. 1994a. Interactions between marine mammals and fisheries in some coastal fishing areas of Argentina. *Rep. int. Whal. Commn* (special issue) 15:269-81.
- Crespo, E.A., Schiavini, A.C.M., Pérez Macri, G., Reyes, L. and Dans, S. 1994b. Estudios sobre determinación de edad en mamíferos marinos del Atlántico sudoccidental. *An. Reun. Trab. Esp. Mamif. Acuát.* IV:31-9. [In Spanish].
- Crespo, E.A., Pedraza, S.N., Dans, S.L., Koen Alonso, M., Reyes, L.M., García, N.A., Coscarella, M. and Schiavini, A.C.M. 1997. Direct and indirect effects of the high seas fisheries on the marine mammal populations in the northern and central Patagonian Coast. *J. Northwest Atl. Fish. Sci.* 22:189-207.
- Crespo, E.A., Harris, G. and González, R. 1998. Group size and distributional range of the franciscana, *Pontoporia blainvillei*. *Mar. Mammal Sci.* 14(4):845-9.
- Dans, S.L., Crespo, E.A., García, N.A., Reyes, L.M., Pedraza, S.N. and Alonso, M.K. 1997a. Incidental mortality of Patagonian dusky dolphins in mid-water trawling: retrospective effects from the early 80's. *Rep. int. Whal. Commn* 47:669-703.
- Dans, S.L., Crespo, E.A., Pedraza, S.N. and Alonso, M.K. 1997b. Notes on the reproductive biology of the female dusky dolphins (*Lagenorhynchus obscurus*) off the Patagonian coast. *Mar. Mammal Sci.* 13(2):303-7.
- Donovan, G.P. 1994. Developments on issues relating to the incidental catches of cetaceans since 1992 and the UNCED conference. *Rep. int. Whal. Commn* (special issue) 15:609-13.
- Fertl, D. and Leatherwood, S. 1997. Cetacean interactions with trawls: a preliminary review. *J. Northwest Atl. Fish. Sci.* 22:219-48.
- Gayoso, A.M. and Podestá, G. 1996. Surface hydrography and phytoplankton of the Brazil-Malvinas currents confluence. *J. Plankton Res.* 18:941-51.
- Goodall, R.N.P., Schiavini, A.C.M. and Fermani, C. 1994. Net fisheries and net mortality of small cetaceans off Tierra del Fuego, Argentina. *Rep. int. Whal. Commn* (special issue) 15:295-304.
- Hohn, A.A. 1980. Age determination and age related factors in the teeth of western North Atlantic bottlenose dolphins. *Sci. Rep. Whales Res. Inst., Tokyo* 32:39-66.

- International Whaling Commission. 1980. Report of the Workshop on Determining Age of Odontocete Cetaceans, La Jolla, September 1978. *Rep. int. Whal. Commn* (special issue) 3:1-50.
- Koen Alonso, M., Crespo, E.A., García, N.A., Pedraza, S.N. and Coscarella, M. 1998. Diet of dusky dolphins (*Lagenorhynchus obscurus*), in waters of Patagonia, Argentina. *Fish. Bull.* 96(2):366-74.
- Norris, K. 1961. Standardized methods for measuring and recording data on the smaller cetaceans. *J. Mammal.* 42(4):471-6.
- Northridge, S.P. 1984. World review of interactions between marine mammals and fisheries. *FAO Fish. Rep.* 251:1-190.
- Perez-Macri, G. and Crespo, E.A. 1989. Survey of the franciscana, *Pontoporia blainvillei*, along the Argentine coast, with a preliminary evaluation of mortality in coastal fisheries. *Occas. Pap. IUCN SSC* 3:57-63.
- Schiavini, A.C.M., Pedraza, S.N., Crespo, E.A., Gonzales, R. and Dans, S.L. 1999. The abundance of dusky dolphins (*Lagenorhynchus obscurus*) off north and central Patagonia, Argentina, in spring and a comparison with incidental catch in fisheries results from a pilot survey in spring 1995. *Mar. Mammal Sci.* 15(3):828-40.

Population biology, conservation threats and status of Mediterranean striped dolphins (*Stenella coeruleoalba*)

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ABSTRACT

The paper reviews the information available on those aspects of the biology, ecology and effects of human impact that are relevant to the management and conservation of striped dolphins in the Mediterranean Sea. The striped dolphin is common throughout the western Mediterranean, although it shows a preference for open waters beyond the continental shelf. In 1991, the western Mediterranean population was estimated as 117,880 (95% CI = 68,379-214,800), but no comparable estimates are available for the eastern basin. Geographical variation in body length, skull morphometrics and genetic analyses, as well as the geographic range and evolution of the 1990-1992 epizootic, suggest some degree of isolation between dolphins in different regions within the Mediterranean and independence from those in the Atlantic. Growth and reproductive parameters in the Mediterranean are, overall, similar to those of other populations, with the exception of age at sexual maturity, which in both sexes is extremely high (11-12 years). Tissue levels of organochlorine compounds, some heavy metals and selenium are high and exceed threshold levels above which detrimental effects commonly appear in mammals. However, apart from the indication that these levels may have acted as triggering factors in the 1990-1992 epizootic by depressing the immune system of diseased individuals and potential lesions in the ovaries, no information on pollutant-related effects is available. The 1990-1992 epizootic devastated the whole Mediterranean population; over one thousand corpses were examined in the western Mediterranean alone, but the toll was probably much higher. The causative agent of the die-off was a morbillivirus, but the effect of some pollutants and decreased food availability were suggested as triggering factors. Depletion of fish and cephalopod resources is widespread in the Mediterranean and, given that the diet of striped dolphins includes commercial species, this undoubtedly has a potential for limiting population numbers. A number of fishing activities produce an associated striped dolphin bycatch. In particular, the pelagic driftnet fishery for tuna and swordfish, carried out by boats from Italy, Spain and Morocco, produces a significant kill in various locations. Variation in sighting and stranding frequency suggests that striped dolphins may have increased their numbers in recent decades. However, this progressive increase may have run parallel to a reduction in carrying capacity of its habitat. This suggestion is supported by the late age at attainment of sexual maturity observed in the Mediterranean population as compared to other conspecific or even congeneric populations.

KEYWORDS: STRIPED DOLPHIN; FEEDING; REPRODUCTION; LONG-TERM CHANGE; ECOSYSTEM; POLLUTANTS; HEAVY METALS; ORGANOCHLORINES; EPIZOOTIC; HABITAT; TRENDS; FISHERIES; GILLNETS; INCIDENTAL CAPTURES; PURSE-SEINES; FOOD/PREY; MEDITERRANEAN; ATLANTIC OCEAN; EUROPE; AFRICA; DISEASE; CONSERVATION; ABUNDANCE ESTIMATE; SURVEY-VESSEL; GROWTH; DISTRIBUTION; GENETICS; AGE AT SEXUAL MATURITY

INTRODUCTION

Among the various cetacean species that inhabit the Mediterranean Sea, the striped dolphin (*Stenella coeruleoalba*) is generally considered to be the most abundant. However, the potential impact of fishing interactions, high levels of pollution and the drastic toll of an epizootic that afflicted the population during 1990-1992 have recently raised concerns about the capacity of the species to maintain its initial levels of abundance. The striped dolphin inhabits both the eastern and the western basins of the Mediterranean Sea and, although mainly an offshore species, it is also found in inshore waters when conditions are favourable.

This paper reviews the information available on those aspects of biology, ecology and effects of human impact relevant to the management and conservation of striped dolphins in the Mediterranean Sea.

DISTRIBUTION AND ABUNDANCE

The striped dolphin is present throughout the Mediterranean Sea but not at uniform densities. It is common in the western and central Mediterranean and is generally considered to be the most abundant cetacean (Forcada *et al.*, 1994). It is less common in the eastern basin, particularly in the easternmost part, where it is considered rare (Kinzelbach, 1997).

In all areas it shows a preference for highly productive, open waters beyond the continental shelf (Gannier and Gannier, 1993; Notarbartolo di Sciara *et al.*, 1993; Pulcini *et al.*, 1993a; Boutiba, 1994; Forcada *et al.*, 1994; Forcada and Hammond, 1998; Gannier, 1998; Cañadas and Sagarminaga, 1999). Thus, it is particularly abundant in the Ligurian Sea, the Gulf of Lions and the Alboran Sea (see Fig. 1).

Reliable population or density estimates are only available for the western basin and unfortunately they only refer to the period after the 1990-1992 die-off. Thus, in 1991, one year after the main epizootic outbreak in the western Mediterranean, striped dolphin numbers in the whole region (excluding the Tyrrhenian Sea) were estimated as 117,880 individuals (95% CI = 68,379-214,800; Forcada *et al.*, 1994).

Additionally, sightings cruises to estimate numbers and density for particular regions within the western Mediterranean were carried out during 1991-1992 (Forcada *et al.*, 1995; Forcada and Hammond, 1998). The results of these surveys are summarised in Table 1. The highest densities were found in the Ligurian Sea, with 0.2359 dolphins/km² (CV = 0.26; 95% CI = 0.1382-0.4026), and in the Alboran Sea, with 0.1955 dolphins/km² (CV = 0.33; 95% CI = 0.1048-0.3646). These two areas are generally considered to be the most productive in the western Mediterranean (Forcada and Hammond, 1998). Overall, striped dolphins were found to be more abundant in the northern rather than the southern regions, where they share the habitat with common (*Delphinus delphis*) and bottlenose (*Tursiops truncatus*) dolphins, which are also abundant in this region, particularly in inshore waters (e.g. Bayed and Beaubrun, 1987; Boutiba, 1994).

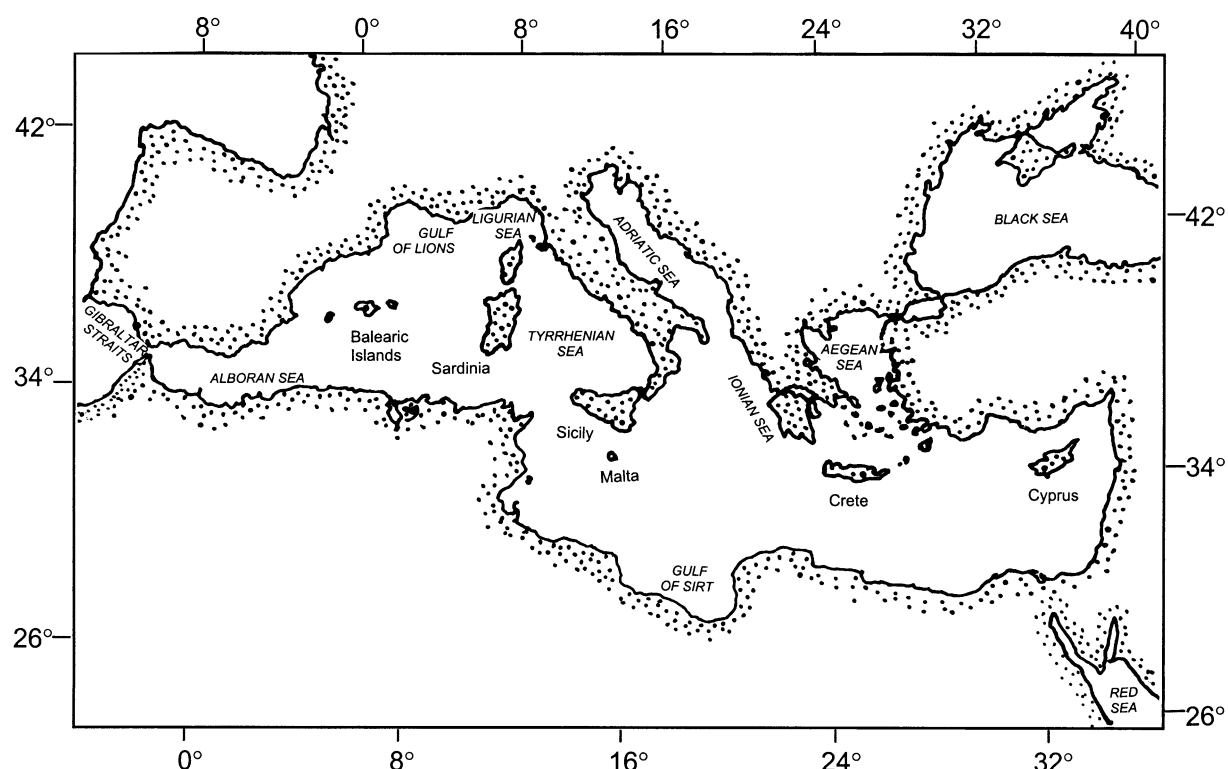


Fig. 1. Map of the Mediterranean Sea showing the locations cited in the text.

No abundance estimates are available for the Tyrrhenian Sea or the eastern Mediterranean. Although striped dolphins are also frequently seen in these areas, their density appears to be lower than in the western region (Marchessaux, 1980; Payne and Selzer, 1986; Marini *et al.*, 1993; 1996; Notarbartolo di Sciara *et al.*, 1993; Öztürk, 1995). The species has not been reported in the Black Sea.

Table 1

Population estimates of striped dolphins from various regions of the western Mediterranean (Forcada and Hammond, 1998).

Area	Point estimate	CV	95% confidence interval
Balearic Sea	5,826	0.36	2,193-15,476
Gulf of Lions	30,774	0.25	17,433-54,323
Ligurian Sea	14,003	0.35	6,305-31,101
South Balearic area	18,810	0.34	8,825-35,940
Alboran Sea	17,728	0.33	9,507-33,059

STOCK IDENTITY

Morphological and genetic studies strongly suggest that the Mediterranean and eastern North Atlantic populations of striped dolphins are isolated from each other, with little or no gene flow across the Gibraltar Straits. Calzada and Aguilar (1995) compared length distributions of stranded striped dolphins from the western Mediterranean and the eastern Atlantic and found that individuals from the two regions differ in maximum body length, with those from the Atlantic being 5-8cm longer. Di Méglia and Romero-Alvarez (1996) compared growth curves from the two regions and although they only found significant differences in asymptotic length for males, the female sample size was probably too small ($n = 18$ in the Atlantic and $n = 22$ in the Mediterranean) to

reveal differences. Similarly, Archer (1997) found that skull size is significantly smaller in Mediterranean striped dolphins than in their neighbouring Atlantic counterparts. Genetic isolation between the two areas was confirmed by García-Martínez *et al.* (1995), who compared the mitochondrial DNA of striped dolphins from the Mediterranean Sea and from the eastern North Atlantic using restriction analysis. The analysis yielded 27 haplotypes, none of which was shared between the two areas. In addition, it should be noted that when the 1990-92 morbillivirus epizootic affected the Mediterranean population (see below), no cases of affected individuals were reported in the neighbouring North Atlantic waters (Aguilar and Raga, 1993).

However, the stock structure of striped dolphins within the Mediterranean Sea is not yet clearly understood. Calzada and Aguilar (1995) showed that in the western Mediterranean, animals from the southern edge of the range are about 3cm longer than their northern conspecifics. The authors attributed this to differences in the intensity of seasonality and population density between the two regions and believed that it probably reflected some restriction in gene flow between sub-populations. In addition, Monaci *et al.* (1998) found that the mercury tissue content differed between dolphins from the Spanish and Italian coasts, again suggesting some degree of isolation between regions. However, García-Martínez *et al.* (1995) analysed mitochondrial DNA variability in a sample of striped dolphins collected along a wide latitudinal range off the Mediterranean coast of Spain and found no evidence of correlation between haplotype frequencies and geographic distribution or other population subdivision.

Information from the eastern Mediterranean is much more limited. Besides the usual *S. coerulealba* morph, Mörzer-Bruyns (1971; 1974) proposed the existence of a

coastal form which had a smaller body, shorter beak and lacked the lateral black stripe. According to the author, this form of 'striped' dolphin inhabited waters around Greece (for which reason he named it the Greek dolphin), southern Italy and east of Sardinia. However, apart from a rather ambiguous morphological description, the author provided no appropriate data to support the existence of such a coastal form. No studies on geographical variation in body length, morphology or genetic composition are available for eastern Mediterranean striped dolphins.

BIOLOGY

Table 2 summarises the biological parameter data available for the western Mediterranean striped dolphin.

Growth and physical maturation

Mediterranean striped dolphins are the smallest of that species in the world. The difference between individuals from the western Pacific population, in which the largest individuals have been identified, and those from the Mediterranean Sea is about 10-11% (Archer, 1997). This is consistent with the previous finding that dolphins living in enclosed, relatively small bodies of water are smaller in body size than their conspecifics inhabiting large oceanic regions (Perrin *et al.*, 1989).

Information on growth and physical maturation parameters (Table 2) is only available for striped dolphins from the northern fringe of the western Mediterranean basin. Aguilar (1991) estimated length at birth at 90-95cm, which corresponds to an average weight of 11.3kg (SD=5.6kg). Calzada *et al.* (1997) studied patterns of growth in a sample of 152 stranded striped dolphins from northern Spain and found that whilst females grow faster than males when they are young, their growth ceases and asymptotic length is attained earlier than in males. However, sex-related differences are small and a smaller sample ($n = 44$) from the neighbouring coast of southern France studied by Di-Mèglio and Romero-Alvarez (1996) did not reveal significant differences associated with sex.

The equations obtained by fitting a Gompertz growth curve to the length-age data by Calzada *et al.* (1997) were:

Males: length = $199.9 (\exp(-0.513 \exp(-0.258 \text{ age})))$ $r^2 = 0.79$
 Females: length = $194.4 (\exp(0.575 \exp(-0.376 \text{ age})))$ $r^2 = 0.72$

They also found that the asymptotic body length was significantly larger in males (200cm) than in females (194cm), which is consistent with the comparison of body length distributions of 208 stranded dolphins from the northwestern Mediterranean, which also indicated a larger maximum body length in males than in females (Calzada and Aguilar, 1995). Again, no sexual differences in asymptotic body length were observed by Di Mèglio and Romero-Alvarez (1996), but this negative result may be a result of the small sample size used ($n = 44$).

Calzada *et al.* (1997) estimated the age at attainment of physical maturity as 13-18 years in females and 15-20 years in males ($n = 121$). This was based on the assumption that the complete fusion of epiphyses to their centra in mid-thoracic vertebrae is indicative of physical maturation of the vertebral column and, therefore, the end of growth. Cranial maturity, as determined by the fusion of the nasal bones and the condition of the distal portion of the premaxillar-maxillar suture, was estimated to be achieved at a similar age, although the sample size was limited ($n = 15$). In the flipper, the ossification of epiphyses shows a decreasing gradient in the proximodistal direction, as is usual in odontocetes. Primary ossification centres are present at birth, while secondary centres generally appear within the first few months after birth. The proximal epiphysis of the humerus becomes evident when the animals are about 100cm long, and the two centres fuse when animals reach about 150cm. Phalangeal epiphyses do not appear to be useful as indicators of skeletal maturity. Physical maturation of the flipper, as assessed by the age and length at which the distal epiphyseal ossification centre fuses to the metaphysis in the radius and ulna, was established at 5-6 years and 160-175cm in females (Table 2) and 8-9 years and 170-181cm in males (Calzada and Aguilar, 1996; Calzada *et al.*, 1997; Di Giancamillo *et al.*, 1998).

Thus available information on sexual dimorphism in maximum body length, growth curves and patterns of physical maturation of the skeleton indicate that females grow faster and reach their asymptotic size earlier than males. This is consistent with comparable parameters determined for striped dolphins from Japanese waters (Miyazaki, 1977; Ito and Miyazaki, 1990) as well as those

Table 2
Summary of biological parameters for the western Mediterranean striped dolphin.
* = data calculated for males and females combined.

Parameter	Male	Female	<i>n</i>	Reference
Asymptotic body length (cm)	200		75	Calzada <i>et al.</i> , 1997
	191		22	Di-Mèglio and Romero-Alvarez, 1996
		194	77	Calzada <i>et al.</i> , 1997
		194	22	Di-Mèglio and Romero-Alvarez, 1996
Neonatal length (cm)	90-95*	90-95*	401	Aguilar, 1991
Neonatal weight (kg)	11.3*	11.3*	4	Aguilar, 1991
Age at physical maturation of the vertebral column (years)	15-20		43	Calzada <i>et al.</i> , 1997
		13-18	42	Calzada <i>et al.</i> , 1997
	13-20*	13-20*	15	Calzada <i>et al.</i> , 1997
	8-9		54	Calzada and Aguilar, 1996
Age at physical maturation of flipper (years)				Calzada <i>et al.</i> , 1997
		5-6	44	Calzada and Aguilar, 1996
				Calzada <i>et al.</i> , 1997
				Calzada <i>et al.</i> , 1996
Length at sexual maturity (cm)	190.4		61	Calzada, 1996
Age at sexual maturity (years)		187	84	Calzada <i>et al.</i> , 1996
	11.3		61	Calzada, 1996
		12	84	Calzada <i>et al.</i> , 1996

for other delphinids (Calzada *et al.*, 1997) and is associated with a higher, more prolonged investment in building a competitive body mass in males than in females (Read *et al.*, 1993).

Reproduction

The only information available is from the northern part of the western basin. In this region, births occur during a single season, extending from late summer to autumn. Calving has been estimated from strandings to peak in mid-October, although it may take place somewhat earlier because of the delay between the death of the dolphin and the report of the stranding (Aguilar, 1991). This coincides with the time of the year in the western Mediterranean when waters are warmest and precedes a peak of productivity (Estrada *et al.*, 1985), therefore providing optimum conditions for lactation.

During the reproductive season, about 25% of the schools carry calves. However, calving appears to take place mainly in the larger dolphin aggregations. Thus, calves are not usually present in schools of less than 10 individuals, while schools of over 30 individuals showed the highest presence of calves (Forcada *et al.*, 1994). This is consistent with the reproductive behaviour observed in striped dolphins from Japan, where calving also takes place in large aggregations known as 'reproductive' schools, which are composed of sexually mature individuals, calves and a few immatures (Miyazaki and Nishiwaki, 1978).

The sex ratio in the adult population is estimated to be 1:1. However, males are more abundant at the foetal stage (1.4:1, $n=12$). The male mortality rate appears to be higher than that of females, because the ratio in calves is 1.11 ($n=95$) and numbers approach unity (1.03, $n=294$) soon after weaning (Aguilar, 1991). This is consistent with the generally observed mammalian pattern (Ralls *et al.*, 1980). The frequency distribution of strandings of calves, with a peak in September-November, suggests that neonatal or early-lactation mortality is much higher than that during the mid or late phases of lactation or at the juvenile stage (Aguilar, 1991).

The attainment of sexual maturity has been estimated to occur when females are about 12 years old and measure about 187cm (Calzada *et al.*, 1996). Comparable figures for males are 11.3 years and 190cm (Calzada, 1996). These estimates (Table 2) are much higher than those for the striped dolphin population from Japanese waters (Kasuya, 1972; 1985) or those of other members of the *Stenella* genus from other areas (Perrin and Reilly, 1984). This may reflect density-dependent variation between populations subject to dissimilar demographic histories as is discussed further below.

Information on seasonal variation in testis weight suggests that mating peaks in August (Calzada, 1996). Considering that births also peak in late summer (Aguilar, 1991), the gestation period is estimated to be about, or slightly over, 12 months.

Feeding

The striped dolphin is an opportunistic feeder, generally exploiting a wide variety of oceanic, pelagic and bathypelagic prey species which form large, dense shoals in the water column. Stomach content analysis of Mediterranean specimens has shown that bony fishes are dominant in numbers, but cephalopods appear to represent an equally, or possibly more, important dietary item because they are of larger size when consumed. Preferred prey include muscular and gelatinous body cephalopods of the families Histioteuthidae, Ommastrephidae,

Enoploteuthidae and Onychoteuthidae, and bony fishes of the families Gadidae, Sparidae and Gonostomiidae. A number of species of shrimp-like crustaceans are also occasionally consumed, but they represent a small proportion of the diet. The size of preferred prey is <130mm body length for fish and <200mm dorsal mantle length for cephalopods (Würtz and Marrale, 1991; Pulcini *et al.*, 1993b; Blanco *et al.*, 1995; Meotti and Podestà, 1997).

POPULATION THREATS

Pollution

The Mediterranean is an enclosed sea surrounded by heavily industrialised countries to the north and predominantly agricultural countries to the south and east. The concentration of a variety of chemical pollutants is known to be high in all trophic levels of the ecosystem (e.g. Ramade, 1993), and since the early 1970s, high heavy metal and organochlorine levels have been recorded in a number of species of small cetaceans inhabiting the region. Research on this subject in Mediterranean striped dolphins has been extensive (Table 3), although mostly restricted to the western basin, where they have been found to carry extremely high levels of DDTs and PCBs (Alzieu and Duguy, 1979; Kannan *et al.*, 1993; Aguilar and Borrell, 1994; Arnoux *et al.*, 1994; Corsolini *et al.*, 1995; Borrell *et al.*, 1996a; b; Marsili and Focardi, 1996; 1997; Marsili *et al.*, 1997) and moderate to high levels of heavy metals, particularly mercury, and selenium (Viale, 1978; Carlini and Fabbri, 1990; André *et al.*, 1991a; b; Di Guardo *et al.*, 1992; Leonzio *et al.*, 1992; Augier *et al.*, 1993; Palmisano *et al.*, 1995; Monaci *et al.*, 1998; Storelli *et al.*, 1998). Recent surveys suggest that DDT and PCB levels in striped dolphins were slowly, but steadily, decreasing during the period 1987-1993 (Borrell *et al.*, 1996b). In the eastern Mediterranean, PCB blubber concentrations are also high, although the limited data available indicate that they are lower than those in the western Mediterranean (Troisi *et al.*, 1998).

The effects of pollutants on marine mammals, particularly in the wild, are not well understood (Reijnders *et al.*, 1999). High levels of organochlorine compounds have been associated with a number of physiological disruptions and pathologies mainly affecting growth (e.g. Zakharov and Yablokov, 1990), reproduction (e.g. Reijnders, 1986; Addison, 1989; Baker, 1989) and the immune system (e.g. Brouwer *et al.*, 1989; De Swart *et al.*, 1995; Ross *et al.*, 1995). Although most of these effects have been shown in pinnipeds, they have been assumed to also occur in cetaceans given the fact that the two taxonomic groups share similar pollutant levels as well as their main biological and ecological traits. Indeed, it has been suggested that these effects may be even more intense in cetaceans given their inability to degrade certain highly toxic forms of PCBs (Tanabe *et al.*, 1988; Tanabe and Tatsukawa, 1992).

Levels of organochlorine compounds and some heavy metals commonly found in Mediterranean striped dolphins (Table 3) far exceed thresholds usually associated with detrimental effects. Indeed, for DDTs and PCBs they are among the highest ever recorded in a living wild mammal and their potential impact on populations is a matter of serious concern. Guitart *et al.* (1996) have suggested that fatty acid composition in the blubber of Mediterranean striped dolphins may have been altered by the high concentrations of PCBs to which this population is exposed. PCBs, sometimes reaching blubber concentrations over 1,000 ppm, have also been suggested to have triggered the

onset and development of the 1990-92 Mediterranean morbillivirus epizootic either by debilitating the immune performance of individuals or by adversely affecting their liver function, in both scenarios making dolphins more susceptible to the infectious disease (Kannan *et al.*, 1993; Aguilar and Borrell, 1994; Borrell *et al.*, 1996a). It has also been proposed that high PCB exposure caused unusual luteinised cystic structures found in the ovaries which impede normal ovulation of striped dolphins from the western Mediterranean (Munson *et al.*, 1998). However, to date, lack of appropriate studies precludes confirmation of these potential cause-effect relationships (e.g. see Kennedy, 1999).

Fishing interactions

Fishing intensity is high in most parts of the Mediterranean and it is extremely diverse with respect to gear used, setting techniques and target species (e.g. Di Natale and Notarbartolo di Sciara, 1994). The potential for direct and indirect conflict between striped dolphins and fishing operations is thus very high. Depletion of fish and cephalopod resources is widespread in the Mediterranean and, given that the diet of striped dolphins includes commercial species (see above), this undoubtedly has the potential to affect population numbers. In addition, a number

of fishing activities are known to result in striped dolphin bycatches. However, most of the information available in this regard has been opportunistically collected and is fragmentary.

Undoubtedly, because of its potential for large bycatches, the fishery that has received most attention is the pelagic driftnet fishery for tuna and swordfish. This fishing is carried out by boats of at least three flags: Italy, Spain and Morocco. The Italian driftnetters, directed to albacore (*Thunnus alalunga*) and swordfish (*Xiphias gladius*), are the largest and best equipped. They number about 650-800, their length ranges from 5- >20m (although the majority range from 12-20m), and the nets they set range between 2.5-14km long. The fleet is based in over one hundred different ports located along the western Italian coast, Sicily and the Ionian coast of Calabria. Most boats operate in waters neighbouring Italy, but in recent years a significant part of the fleet has also been fishing off continental Spain, the Balearic Islands and western Greece. In various locations, the activity of this fleet has been associated with large cetacean bycatches, including striped dolphins. The fishery has been intermittently legal and outlawed, and the gear it uses quite often far exceeds the 2.5km limit set by European regulations (Di Natale and Notarbartolo di Sciara, 1994).

The Spanish driftnet fleet is mainly directed towards swordfish. The fishing grounds are restricted to a small area

Table 3
Tissue concentration of pollutants detected in Mediterranean striped dolphins.

Pollutant	Sampling area	Tissue	n	Mean	SD	Max.	Min.	Units	Reference
DDE	W. Italy	blubber	6			7.05	1.80	mg/kg ??	Di Guardo <i>et al.</i> , 1992
DDTs	N.E. Spain	blubber	142	135.00				mg/kg, lipid weight	Borrell <i>et al.</i> , 1996b
DDTs	N.E. Spain	blubber	10	436.70	378.07	1,200.00	62.00	mg/kg, lipid weight	Kannan <i>et al.</i> , 1993; Corsolini <i>et al.</i> , 1995
DDTs	Italy	blubber*	64	114.27		721.77	5.05	mg/kg, lipid weight	Marsili and Focardi, 1996; Marsili <i>et al.</i> , 1997
DDTs	Ligurian Sea	blubber*	61	45.45	24.32	72.16	26.82	mg/kg, lipid weight	Marsili and Focardi, 1996
PCB	N.E. Spain	blubber	142	240.00				mg/kg, lipid weight	Borrell <i>et al.</i> , 1996b
PCB	N.E. Spain	blubber	72	778.00**				mg/kg, lipid weight	Aguilar and Borrell, 1994
PCB	N.E. Spain	blubber	10	1,197.00	851.18	2,600.00	210.00	mg/kg, lipid weight	Kannan <i>et al.</i> , 1993; Corsolini <i>et al.</i> , 1995
PCB	Italy	blubber*	64	172.59		1,529.44	7.84	mg/kg, lipid weight	Marsili and Focardi, 1996; Marsili <i>et al.</i> , 1997
PCB	Ligurian Sea	blubber*	61	68.18	24.09	97.73	53.18	mg/kg, lipid weight	Marsili and Focardi, 1996
PCB	W. Italy	blubber	6			15.60	8.25	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Cd	N.E. Spain	kidney	39	8.38	6.57			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Cd	Tyrrhenian Sea	kidney	19	44.80		98.8	10.8	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Cd	W. Italy	kidney	86	27.51	31.29			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Cd	W. Italy	liver	6			0.66	0.55	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Cu	N.E. Spain	liver	39	39.24	40.60			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Cu	W. Italy	liver	86	22.01	21.63			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Hg	France	liver	25	346.06	356.27	1,544.00	1.2	mg/kg, fresh weight	André <i>et al.</i> , 1991a,b
Hg	France	liver	13	668.40	588.19	2,271.6	396.8	mg/kg, dry weight	Augier <i>et al.</i> , 1993
Hg	N.E. Spain	liver	39	1,043.14	835.17			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Hg	Tyrrhenian Sea	liver	4	10.37	12.69	29.4	3.67	mg/kg, fresh weight	Carlini and Fabbri, 1990
Hg	Tyrrhenian Sea	liver	19	324.40		4,400.00	12.6	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Hg	W. Italy	liver	86	592.97	1,120.01			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Hg	W. Italy	liver	6			112.00	85.00	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Hg	Adriatic Sea	liver	1	827.60				mg/kg, fresh weight	Carlini and Fabbri, 1990
Hg	Adriatic Sea	liver	30	277.40	246.00	966.31	0.58	mg/kg, fresh weight	Storelli <i>et al.</i> , 1998
Pb	Tyrrhenian Sea	muscle	19	0.66		6.7	0.1	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Pb	W. Italy	liver	6			0.31	0.27	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Se	N.E. Spain	liver	39	100.82	220.21			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Se	Tyrrhenian Sea	liver	4	4.38	2.24	7.4	2.04	mg/kg, fresh weight	Carlini and Fabbri, 1990
Se	Tyrrhenian Sea	liver	19	106.00		960	2.00	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Se	W. Italy	liver	86	265.95	316.45			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Se	Adriatic Sea	liver	30	141.65	104.00	423.98	0.89	mg/kg, fresh weight	Storelli <i>et al.</i> , 1998
Zn	N.E. Spain	liver	39	161.53	57.42			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Zn	Tyrrhenian Sea	liver	19	225.00		387.5	150.00	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Zn	W. Italy	liver	86	111.06	58.87			mg/kg, dry weight	Monaci <i>et al.</i> , 1998

* recalculated from dry weight; ** median.

on both sides of the Gibraltar Straits. The fishery appears to have started in the early 1980s and, from 1988, the number of vessels increased markedly because of the high revenues obtained. In 1990, about 100 Spanish boats based in the harbours of southern Spain were involved in the fishery. In 1991, Spanish regulations outlawed the activity of this fleet, but a limited number of boats continued until 1994, when the fishery finally came to a halt. Given the unregulated nature of the operation in its later years of activity, no data on effort, landings or bycatch are available in the official Spanish fishing statistics. An observer programme developed during the 1993-1994 seasons showed that the fleet was comprised of 27 boats deploying nets 3.5-10.5km long. The bycatch rate of dolphins (common and striped dolphins in similar proportions) was established at about 0.1 individuals per km of net set. The total catch of striped dolphins was estimated at about 170 individuals for the 1993 fishing season and 148 for 1994; the catch was predominantly composed of juvenile males probably because of segregation of different components of the population in the fishing grounds and/or because of sex and age-related differences in behaviour or ability to avoid entanglement (Silvani *et al.*, 1999).

The Moroccan driftnet fishery is poorly understood, with most information arising from casual observations by Spanish observers (Silvani *et al.*, 1999). The fleet is estimated to comprise about 120 boats, most of which are of small tonnage and use shorter nets than the Spanish or the Italian fleets. They also target swordfish, and the fishing grounds appear to overlap those of the Spanish driftnetters.

Reports from other fishing activities are sparse and unsystematically collected. However, they suggest that the pelagic driftnet fishery is not an isolated case and that incidental catches, or even direct catches for human consumption or for use as bait, are widespread and therefore represent a serious toll for the local cetacean populations, including the striped dolphin (Collet, 1983; Duguy *et al.*, 1983; Troncone *et al.*, 1990; Di Natale and Notarbartolo di Sciara, 1994; Mazzola *et al.*, 1995). In particular, purse-seine fishing for surface-schooling fish appears to be associated with significant bycatches in various locations (Di Natale and Notarbartolo di Sciara, 1994; University of Barcelona, 1994).

The 1990-1992 epizootic

An epizootic of complex origin and development began in July 1990 and produced a massive mortality of striped dolphins in the Mediterranean Sea. The first affected dolphins were detected near Valencia (mid-Spain), but after a few months the die-off had extended to most of the western Mediterranean. This outbreak was followed by two subsequent outbreaks, the first in summer 1991, affecting at least southern Italy, Sicily and western Greece, and the second in summer 1992 affecting at least eastern Greece and Turkey (Aguilar and Raga, 1993; Cebrian, 1995).

The primary cause of the die-off was a morbillivirus infection (Domingo *et al.*, 1990) of unknown origin. It was similar, if not identical, to that isolated from harbour porpoises (*Phocoena phocoena*) from the Irish Sea in 1990, and distinct from that which caused the 1987 harbour seal epizootic (Bolt and Blixenkrone-Møller, 1994). The morbillivirus antigens were identical for different parts of the Mediterranean (Van Bressem *et al.*, 1993), indicating that the three outbreaks were caused by the same agent. Dolphins affected by the disease showed respiratory insufficiency and frequent nervous and locomotory

disorders. Pathological studies showed bronchiolo-interstitial pneumonia, non-suppurative meningoencephalitis, lymphoid depletion, necrosis of lymphocytes in spleen and lymph nodes, and formation of multinucleate syncytia in the cortex of lymph nodes (Van Bressem *et al.*, 1991; Domingo *et al.*, 1992; Duignan *et al.*, 1992). These lesions were similar to those caused by morbillivirus in seals and porpoises. After the 1990-92 outbreaks, the virus remained in the population and several later cases were reported. In these cases the systemic infection had apparently disappeared, giving way to chronic infection of the central nervous system. This mainly produced non-suppurative encephalitis, with diffuse gliosis and glial nodules and neuronophagia, and loss of neurons (Domingo *et al.*, 1995). The high mortality observed during the event was taken as an indication that in 1990 the morbillivirus had entered a naive population that had not been exposed to the virus before and therefore had no immunity (Van Bressem *et al.*, 1993).

The tissue concentration of PCBs and other organochlorine pollutants of recognised immunosuppressive effect in dolphins that were victims of the epizootic were found to be much higher than in the 'healthy' population sampled before or after the event. This difference could not be explained by the effect of nutritive condition or by differences in the age or sex composition of the samples (Kannan *et al.*, 1993; Aguilar and Borrell, 1994; Borrell *et al.*, 1996a). In addition, the population component that suffered the largest mortality was that of sexually mature individuals and calves, with juveniles apparently not affected. This mortality pattern is not consistent with the epidemiology of morbillivirus infections previously observed in other mammals (e.g. Calzada *et al.*, 1994).

A number of hypotheses on the key factors in the outbreak (other than pollutants) have been proposed, including:

- (1) behavioural factors increasing susceptibility to the disease in adults;
- (2) the existence of an allopatric geographical distribution of population components;
- (3) decreased food availability (as indicated by poor nutritive condition) and extensive epizootic infection in many of the diseased animals during the early phase of the 1990 outbreak (Aguilar *et al.*, 1991; Aznar *et al.*, 1994).

However, the abnormally high pollutant concentrations found in the stranded dolphins strongly support the hypothesis that pollutants played a role in the onset and spread of the morbillivirus infection and the associated high mortality (Aguilar and Borrell, 1994; Calzada *et al.*, 1994). Despite this, it will always be extremely difficult to identify the precise factors involved in such events (e.g. see Kennedy, 1999).

Although over 1,000 carcasses were recovered during 1990 and 1991 in the western Mediterranean alone (Bortolotto *et al.*, 1992; Aguilar and Raga, 1993), the toll caused by the epizootic could not be reliably assessed for two reasons. Firstly, an unknown proportion of dead dolphins sank before reaching the coast and were therefore not recorded in the statistics. The importance of this was undoubtedly enhanced by the offshore nature of striped dolphin distribution and numerous observations of dead dolphins far from shore were reported. Secondly, efficient monitoring of the shore for carcasses was only undertaken on the western European segment of the coastline, and no mortality numbers are available for the eastern Mediterranean basin or the western Mediterranean coast of

Africa, although substantial mortality of striped dolphins is also known to have occurred in these areas (Aguilar and Raga, 1993).

Forcada *et al.* (1994) found that the mean size of the dolphin schools observed in part of the western Mediterranean decreased from 25.3 (SE=4.7) before the event to only 7.0 (SE=2.3) during the outbreak. One interpretation of this is that at least in that area, the population decreased to less than one third of its initial level of abundance. However, (1) observations during the outbreak were restricted to the area around the Balearic Islands, northeastern Spain and the Gulf of Lions (the region that apparently suffered the greatest mortality), and (2) it is likely that the behaviour of the dolphins was altered by the process of the infectious disease. Thus the observed decrease in mean school size cannot be directly taken as a reliable indication of a parallel reduction in abundance. In 1991, mean school size appeared to return to usual levels, although this was not considered a sign of recovery but merely a regrouping of individuals into schools of a preferred size. It is likely that such regrouping was a response by surviving dolphins to facilitate social activities, foraging or reproduction (Forcada *et al.*, 1994). Reproductive parameters of females examined during the epizootic were profoundly altered, indicating a high frequency of abortions and abandonment of lactating calves. This will have had an extensive deleterious effect on recruitment to the population (Calzada *et al.*, 1996).

Other human-related threats

Given its offshore distribution, local effects of coastal development or human presence in coastal waters probably have limited impact on the striped dolphin. Boat traffic does not appear to represent a problem for this species, which is often attracted to boats, independently of their activity (Angradi *et al.*, 1993).

In January 1998, an abnormally high number of striped dolphins (more than 22 individuals in one a week) washed ashore on a small section of coastline on the French Gulf of Lions. The strandings included individuals of both sexes, adults as well as juveniles. Most dolphins had ulcers of uncertain origin on the lateral and ventral sides of the cephalic region. The cause of this mortality could not be established (Rigollet *et al.*, 1998).

CONCLUSIONS AND POPULATION STATUS

The pattern of the 1990-1992 epizootic, which through three successive outbreaks affected the whole Mediterranean Sea but did not extend to the eastern Atlantic, suggests that striped dolphins from the whole Mediterranean basin form an interconnected collective, separated from that from the Atlantic. The limited information available indicates that some degree of genetic subdivision or stratification occurs within the Mediterranean but considerably more work is required to elucidate stock structure. Therefore, biological parameters from one region should not be extrapolated directly to other regions, particularly if they relate to body size and growth, which have been shown to vary. Stock structure must be taken into account in a management context, particularly when assessing the effects of mortality associated with fishing operations, disease, pollution, habitat destruction or other factors.

Although no information on age-related parameters with respect to physical maturation and growth is available for the eastern Mediterranean, the parameters determined for the west (Calzada and Aguilar, 1996; Calzada *et al.*, 1997) are

similar to those for striped dolphins around Japan (Miyazaki, 1977; Ito and Miyazaki, 1990). The same is not true for reproductive parameters: western Mediterranean striped dolphins show a remarkably high age at attainment of sexual maturity in both sexes when compared to the striped dolphin population of Japan or to other congeneric populations (Miyazaki, 1984; Kasuya, 1985; 1999; Calzada *et al.*, 1996). This variation can be associated with differences in the demographic history of the populations, probably reflecting dissimilar density-dependent effects. Thus, while striped dolphins off Japan have been heavily exploited for a long time with numbers remaining well below the carrying capacity of the habitat (Miyazaki, 1984; Kasuya, 1985; 1999), the available information suggests that the Mediterranean population, at least in the western basin for which we have most information, may in fact have been increasing. Surveys in recent years indicate the presence, particularly in the western basin, of a large population. It is intriguing that until the end of the 1960s the striped dolphin was considered to be relatively rare in the Mediterranean, with most reports referring to the common dolphin as the most abundant small odontocete (Van Bree *et al.*, 1969). However, when in the early 1970s, trained cetologists began to collect strandings and sightings data in the region, the widespread presence of the striped dolphin was immediately recognised (e.g. Van Bree *et al.*, 1969; Duguy *et al.*, 1983). It is unclear whether the apparent scarcity of the species in the first half of the century was true, or whether it reflected the fact that striped dolphins were mistakenly identified as common dolphins (Casinos and Vericard, 1976; Viale, 1985).

Having said that, at least during the period 1970-1995, the common dolphin appears to have decreased throughout the northern part of the western Mediterranean. There has been some speculation that the striped dolphin began to occupy the ecological niche of the common dolphin and, thus, increased its numbers (Viale, 1985) although why competition between these two should have resulted in favour of the striped dolphin is unclear. Both species appear to share a common habitat in a wide portion of their distribution range (Sagarminaga and Cañadas, 1996; Forcada and Hammond, 1998), although no conclusive studies have been made to assess the extent of any competition between them, for example for food. However, data from a limited number of common dolphins do suggest at least a partial overlap in diet (Orsi Relini and Relini, 1993). Although the replacement of one species by another may have occurred to some extent, it is not clear whether the apparent increase in reports of strandings and sightings of striped dolphins was indeed significant, or whether it was partially a consequence of striped dolphins extending their range to the inshore waters traditionally inhabited by common dolphins.

In summary, there is some inconclusive evidence that striped dolphins may have increased in numbers in recent decades. However, this progressive increase may have occurred at a time when its available habitat is decreasing. Würtz and Marrale (1991) found that a single cephalopod species (the red squid, *Todarodes sagittatus*) and a single fish species, (the blue whiting, *Micromesistius poutassou*), comprised over 60% of the food items present in the stomachs of 23 striped dolphins stranded on the coasts of the Ligurian Sea; *Todarodes sagittatus* is also a significant food item of the striped dolphins found on the Spanish Mediterranean coast (Blanco *et al.*, 1995). Both of these species are of prime commercial interest and heavily exploited.

In this context, the extremely old age at attainment of sexual maturity observed in Mediterranean striped dolphins compared with those from Japan and other areas is suggestive of a population with stringent food limitations. Density-dependence theory suggests that in this situation, selection will induce compensatory responses resulting in low survival and pregnancy rates and high age at attainment of sexual maturity (Eberhardt and Siniff, 1977). Although opposite effects may indeed sometimes occur (Trites and York, 1993), it seems possible that the life-history parameters observed in Mediterranean striped dolphins do reflect a population that is at an abundance level close to if not beyond the carrying capacity of its environment. In such circumstances, the occurrence of the 1990-1992 epizootic might be considered more as a density-regulatory mechanism in a population at an excessive population level rather than an exceptional, isolated disaster (Harwood and Hall, 1990).

The implications of these scenarios for the management and conservation of the western Mediterranean population of striped dolphins are quite different and thus urgent research is required to assess: (1) long-term demographic changes in the population, mainly in its abundance and gross reproductive rates; (2) effects of chemical pollutants on reproductive rates and immunocompetence; (3) diet composition and potential overlapping with the catch of the main fishing activities in the region; and (4) the overall nutritive condition of the dolphins.

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REFERENCES

- Addison, R.F. 1989. Organochlorines and marine mammal reproduction. *Can. J. Fish. Aquat. Sci.* 46(2):360-8.
- Aguilar, A. 1991. Calving and early mortality in the western Mediterranean striped dolphin, *Stenella coeruleoalba*. *Can. J. Zool.* 69(5):1,408-12.
- Aguilar, A. and Borrell, A. 1994. Abnormally high polychlorinated biphenyl levels in striped dolphins (*Stenella coeruleoalba*) affected by the 1990-1992 Mediterranean epizootic. *Sci. Total Environ.* 154(2-3):237-47.
- Aguilar, A. and Raga, J.A. 1993. The striped dolphin epizootic in the Mediterranean Sea. *Ambio* 22(8):524-8.
- Aguilar, A., Borrell, A., Calzada, N. and Grau, E. 1991. The nutritive condition of striped dolphins (*Stenella coeruleoalba*) affected by the western Mediterranean epizootic. *Eur. Res. Cetaceans* [Abstracts] 5:84-6.
- Alzieu, C. and Duguy, R. 1979. Teneurs en composés organochlorés chez les cétacés et pinnipèdes fréquentant les côtes françaises. *Oceanol. Acta.* 2(1):107-20. [In French].
- André, J.M., Boudou, A. and Ribeyre, F. 1991a. Mercury accumulation in Delphinidae. *Water Air Soil Pollut.* 56:187-201.
- André, J.M., Boudou, A., Ribeyre, F. and Bernhard, M. 1991b. Comparative study of mercury accumulation in dolphins (*Stenella coeruleoalba*) from French Atlantic and Mediterranean coasts. *Sci. Total Environ.* 104:191-209.
- Angradi, A.M., Consiglio, C. and Marini, L. 1993. Behaviour of striped dolphins (*Stenella coeruleoalba*) in the central Tyrrhenian Sea in relation with commercial ships. *Eur. Res. Cetaceans* [Abstracts] 7:77-9.
- Archer, F.I. 1997. Osteological variation in striped dolphins (*Stenella coeruleoalba*). Paper SC/49/SM28 presented to the IWC Scientific Committee, October 1997 (unpublished). 30pp. [Paper available from the Office of this Journal].
- Arnoux, A., Augier, H., Monod, J.L. and Mialon, S. 1994. Polychlorinated biphenyl concentrations in striped dolphins *Stenella coeruleoalba* beached along the Provencal French Sea coast. *Eur. Res. Cetaceans* [Abstracts] 8:214-21.
- Augier, H., Park, W.K. and Ronneau, C. 1993. Mercury contamination of the striped dolphin, *Stenella coeruleoalba*, Meyen from the French Mediterranean coasts. *Mar. Poll. Bull.* 26(6):306-10.
- Aznar, F.J., Balbuena, J.A. and Raga, J.A. 1994. Are epizootes biological indicators of a western Mediterranean striped dolphin die-off? *Dis. Aquat. Org.* 18(3):159-63.
- Baker, J.R. 1989. Pollution-associated uterine lesions in grey seals from the Liverpool Bay area of the Irish Sea. *Vet. Rec.* 125:303.
- Bayed, A. and Beaubrun, P.-C. 1987. Les mammifères marins du Maroc: inventaire préliminaire. *Mammalia* 51(3):437-46. [In French].
- Blanco, C., Aznar, J. and Raga, J.A. 1995. Cephalopods in the diet of *Stenella coeruleoalba* (Meyen, 1833) from the Western Mediterranean during an epizootic in 1990. *J. Zool., Lond.* 237:151-8.
- Bolt, G. and Blixenkrone-Møller, M. 1994. Nucleic acid hybridization analyses confirm the presence of a hitherto unknown morbillivirus in Mediterranean dolphins. *Vet. Microbiol.* 41(4):363-72.
- Borrell, A., Aguilar, A., Corsolini, S. and Focardi, S. 1996a. Evaluation of toxicity and sex related variation of PCB levels in Mediterranean striped dolphins affected by an epizootic. *Chemosphere* 32:2359-69.
- Borrell, A., Aguilar, A. and Pastor, T. 1996b. Organochlorine compound levels in striped dolphins from the western Mediterranean during the period 1987-1993. *Eur. Res. Cetaceans* [Abstracts] 10:281-5.
- Bortolotto, A., Casini, L. and Stanzani, L.A. 1992. Dolphin mortality along the southern Italian coast (June-September 1991). *Aquat. Mamm.* 18(2):56-60.
- Boutiba, Z. 1994. Bilan de nos connaissances sur la présence des cétacés le long des côtes Algériennes. *Mammalia* 4:613-22. [In French].
- Brouwer, A., Reijnders, P.J.H. and Koeman, J.H. 1989. Polychlorinated biphenyl (PCB)-contaminated fish induces vitamin A and thyroid hormone deficiency in the common seal (*Phoca vitulina*). *Aquat. Toxicol.* 15:99-106.
- Calzada, N. 1996. Biología del delfín listado (*Stenella coeruleoalba*) del Mediterráneo occidental. PhD Thesis, University of Barcelona. 161pp.
- Calzada, N. and Aguilar, A. 1995. Geographical variation of body size in Western Mediterranean striped dolphins (*Stenella coeruleoalba*). *Z. Säugetierkd* 60:257-64.
- Calzada, N. and Aguilar, A. 1996. Flipper development in the Mediterranean striped dolphin (*Stenella coeruleoalba*). *Anat. Rec.* 245:708-14.
- Calzada, N., Lockyer, C.H. and Aguilar, A. 1994. Age and sex composition of the striped dolphin die-off in the western Mediterranean. *Mar. Mammal Sci.* 10(3):299-310.
- Calzada, N., Aguilar, A., Sorensen, T.B. and Lockyer, C. 1996. Reproductive biology of female striped dolphin (*Stenella coeruleoalba*) from the western Mediterranean. *J. Zool., London.* 240:581-91.
- Calzada, N., Aguilar, A., Lockyer, C. and Grau, E. 1997. Patterns of growth and physical maturity in the western Mediterranean striped dolphin, *Stenella coeruleoalba* (Cetacea:Odontoceti). *Can. J. Zool.* 75:632-7.
- Cañadas, A. and Sagarminaga, R. 1999. A comparative study on the distribution and behaviour of the common dolphin (*Delphinus delphis*) and the striped dolphin (*Stenella coeruleoalba*) along the south-eastern coast of Spain. *Eur. Res. Cetaceans* [Abstracts] 12:334.
- Carlini, R. and Fabbri, F. 1990. Indagine preliminari sul contenuto in mercurio, metilmercurio e selenio in Odontoceti spiaggiati lungo le coste italiane (Mammalia Cetacea). *Atti. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano* 130(20):261-66. [In Italian].
- Casinos, A. and Vericard, J.-R. 1976. The cetaceans of the Spanish coasts: a survey. *Mammalia* 40:267-89.
- Cebrian, D. 1995. The striped dolphin *Stenella coeruleoalba* epizootic in Greece. 1991-1992. *Biol. Conserv.* 74(2):142-5.
- Collet, A. 1983. Report of the sub-committee on small cetaceans, Appendix 3. Directed and incidental catch of small cetaceans by French fishing vessels in the North Atlantic and Mediterranean. *Rep. int. Whal. Commn* 33:169.
- Corsolini, S., Focardi, S., Kannan, K., Tanabe, S., Borrell, A. and Tatsukawa, R. 1995. Congener profile and toxicity assessment of

- polychlorinated biphenyls in dolphins, sharks and tuna collected from Italian coastal waters. *Mar. Environ. Res.* 40(1):33-53.
- De Swart, R.L., Ross, P.S., Timmerman, H.H., Vos, H.W., Reijnders, P.J.H., Vos, J.G. and Osterhaus, A.D.M.E. 1995. Impaired cellular immune response function in harbour seals (*Phoca vitulina*) feeding on environmentally contaminated herring. *Clin. Exper. Immunol.* 101:480-6. [Copy in Publications 1995, Erasmus Universiteit Rotterdam, Zeehondenrecreatiepieterburen.]
- Di Giancamillo, M., Rattegni, G., Podestà, M., Cagnolaro, L., Cozzi, B. and Leonardi, L. 1998. Postnatal ossification of the thoracic limb in striped dolphins (*Stenella coeruleoalba*) (Meyen, 1833) from the Mediterranean Sea. *Can. J. Zool.* 76(7):1,286-96.
- Di Guardo, G., Ubaldi, A., Agrimi, U., Cozzani, R., Teracciano, G., Carnevale, M. and Kennedy, S. 1992. Policlorobifenili (PCBs) e metalli pesanti in organi e tessuti di stenelle (*Stenella coeruleoalba*) rinvenute spiaggiate sulle coste laziali e toscane: rilievi chimico-analitici, istomorfologici ed ultrastrutturali. *Atti. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano* 46:787-91. [In Italian].
- Di Méglia, N. and Romero-Alvarez, R. 1996. Growth comparison in striped dolphins, *Stenella coeruleoalba*, from the Atlantic and Mediterranean coasts of France. *Aquat. Mamm.* 22(1):11-21. [In French].
- Di Natale, A. and Notarbartolo di Sciarra, G. 1994. A review of the passive fishing nets and trap fisheries in the Mediterranean Sea and of the cetacean bycatch. *Rep. int. Whal. Commn* (special issue) 15:189-202.
- Domingo, M., Ferrer, L., Pumarola, M. and Marco, A. 1990. Morbillivirus in dolphins. *Nature, Lond.* 348:21.
- Domingo, M., Visa, J., Pumarola, M., Marco, A.J., Ferrer, L., Rabanal, R. and Kennedy, S. 1992. Pathologic and immunocytochemical studies of morbillivirus infection in striped dolphins (*Stenella coeruleoalba*). *Vet. Pathol.* 29:1-10.
- Domingo, M., Vilafranca, M., Visa, J., Prats, N., Trudgett, A. and Visser, I. 1995. Evidence for chronic morbillivirus infection in the Mediterranean striped dolphin (*Stenella coeruleoalba*). *Vet. Microbiol.* 44(2-4):229-39.
- Duguy, R., Besson, J., Casinos, A., di Natale, A., Filella, S., Raduan, A., Raga, J. and Viale, D. 1983. L'impact des activités humaines sur les cétacés de la Méditerranée occidentale. *Rapp. Comm. Int. Mer Médit.* 28(5):219-22. [In French].
- Duignan, P.J., Geraci, J.R., Raga, J.A. and Calzada, N. 1992. Pathology of morbillivirus infection in striped dolphins (*Stenella coeruleoalba*) from Valencia and Murcia, Spain. *Can. Vet. J. Res.* 56(3):242-8.
- Eberhardt, L.L. and Siniff, D.B. 1977. Population dynamics and marine mammal management policies. *J. Fish. Res. Bd Can.* 34(2):183-90.
- Estrada, M., Vives, F. and Alcaraz, M. 1985. Life and productivity in the open sea. pp. 148-97. In: R. Margalef (ed.) *Key Environments: Western Mediterranean*. Pergamon Press, Oxford.
- Forcada, J. and Hammond, P.S. 1998. Geographical variation in abundance of striped and common dolphins of the western Mediterranean. *J. Sea. Res.* 39:313-25.
- Forcada, J., Aguilar, A., Hammond, P.S., Pastor, X. and Aguilar, R. 1994. Distribution and numbers of striped dolphins in the western Mediterranean Sea after the 1990 epizootic outbreak. *Mar. Mammal Sci.* 10(2):137-50.
- Forcada, J., Notarbartolo di Sciarra, G. and Fabbri, F. 1995. Abundance of fin whales and striped dolphins summering in the Corso-Ligurian basin. *Mammalia* 59(1):127-40.
- Gannier, A. 1998. Seasonal variation of the bathymetric distribution of cetaceans in the Liguro-Provençal basin (Western Mediterranean). *Vie Milieu* 48(1):25-34.
- Gannier, A. and Gannier, O. 1993. Striped dolphin abundance estimate in the Liguro-Provençal basin: preliminary study. *Eur. Res. Cetaceans* [Abstracts] 7:139-43.
- Garcia-Martinez, J., Barrio, E., Raga, J.A. and Latorre, A. 1995. Mitochondrial DNA variability of striped dolphins (*Stenella coeruleoalba*) in the Spanish Mediterranean waters. *Mar. Mammal Sci.* 11(2):182-99.
- Guitart, R., Guerrero, X., Silvestre, A.M., Gutierrez, J.M. and Mateo, R. 1996. Organochlorine residues in tissues of striped dolphins affected by the 1990 Mediterranean epizootic: Relationships with the fatty acid composition. *Arch. Environ. Contam. Toxicol.* 30(1):79-83.
- Harwood, J. and Hall, A.J. 1990. Mass mortality in marine mammals: its implications for population dynamics and genetics. *Trends Ecol. Evol.* 5(8):254-7.
- Ito, H. and Miyazaki, N. 1990. Skeletal development of the striped dolphin (*Stenella coeruleoalba*) in Japanese waters. *J. Mammal. Soc. Jpn* 14(2):79-96.
- Kannan, K., Tanabe, S., Borrell, A., Aguilar, A., Focardi, S. and Tatsukawa, R. 1993. Isomer-specific analysis and toxic evaluation of polychlorinated biphenyls in striped dolphins affected by an epizootic in the western Mediterranean Sea. *Arch. Environ. Contam. Toxicol.* 25(2):227-33.
- Kasuya, T. 1972. Growth and reproduction of *Stenella coeruleoalba* based on the age determination by means of dentinal growth layers. *Sci. Rep. Whales Res. Inst., Tokyo* 24:57-79.
- Kasuya, T. 1985. Effect of exploitation on reproductive parameters of the spotted and striped dolphins off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 36:107-38.
- Kasuya, T. 1999. Review of biology and exploitation of striped dolphins off Japan. *J. Cetacean Res. Manage.* 1(1):81-100.
- Kennedy, S. 1999. Morbilliviral infections in marine mammals. *J. Cetacean Res. Manage.* (special issue 1):267-73.
- Kinzelbach, R. 1997. A record of striped dolphin *Stenella coeruleoalba* (Meyen, 1833) from the Turkish Mediterranean Sea coast. *Zool. Middle East* 15(0):15-8.
- Leonzio, C., Focardi, S. and Fossi, C. 1992. Heavy metals and selenium in stranded dolphins of the northern Tyrrhenian (NW Mediterranean). *Sci. Total Environ.* 119:77-84.
- Marchessaux, D. 1980. A review of the current knowledge of the cetaceans in the eastern Mediterranean Sea. *Vie Marine* 2:59-66.
- Marini, L., Consiglio, C., Catalano, B. and Valentini, T. 1993. Cetaceans in the Central Tyrrhenian Sea: third (and last?) year of sightings. Preliminary results. *Eur. Res. Cetaceans* [Abstracts] 7:148-50.
- Marini, L., Carpentieri, P. and Consiglio, C. 1996. Presence and distribution of the cetological fauna of the Aegean Sea: preliminary results. *Eur. Res. Cetaceans* [Abstracts] 9:99-101.
- Marsili, L. and Focardi, S. 1996. Organochlorine levels in subcutaneous blubber biopsies of fin whales *Balaenoptera physalus* and striped dolphins *Stenella coeruleoalba* from the Mediterranean Sea. *Environ. Pollut.* 91(1):1-9.
- Marsili, L. and Focardi, S. 1997. Chlorinated hydrocarbon HCB, DDTs and PCBs levels in cetaceans stranded along the Italian coasts: An overview. *Environ. Monitoring and Assessment* 45(2):129-80.
- Marsili, L., Casini, C., Marini, L., Regoli, A. and Forcardi, S. 1997. Age, growth and organochlorines (HCB, DDTs and PCBs) in Mediterranean striped dolphins *Stenella coeruleoalba* stranded in 1988-1994 on the coasts of Italy. *Mar. Ecol. Prog. Ser.* 151(1-3):273-82.
- Mazzola, S.B., A. Guerrini, A., Patti, B. and Giusto, G.B. 1995. Preliminary study on census data about the interaction between dolphins and fishing activity in the Sicilian fisheries. *Eur. Res. Cetaceans* [Abstracts] 9:256-9.
- Meotti, C. and Podestà, M. 1997. Stomach contents of striped dolphins, *Stenella coeruleoalba* (Meyen 1833), from the western Ligurian Sea (Cetacea, Delphinidae). *Atti. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano* 137:5-15.
- Miyazaki, N. 1977. On the growth and reproduction of *Stenella coeruleoalba* off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 29:21-48.
- Miyazaki, N. 1984. Further analyses of reproduction in the striped dolphin, *Stenella coeruleoalba*, off the Pacific coast of Japan. *Rep. int. Whal. Commn* (special issue) 6:343-53.
- Miyazaki, N. and Nishiwaki, M. 1978. School structure of the striped dolphin off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 30:65-116.
- Mörzer-Bruyns, W.F.J. 1971. *Field Guide of Whales and Dolphins*. C.A. Meese, Amsterdam. 258pp.
- Mörzer Bruyns, W.F.J. 1974. On sight-records of the Euphrosune dolphin, *Stenella coeruleoalba* (Meyen, 1833), in the Mediterranean. *Mammalia* 38(3):503-7.
- Monaci, F., Borrell, A., Leonzio, C., Marsili, L. and Calzada, N. 1998. Trace elements in striped dolphins (*Stenella coeruleoalba*) from the western mediterranean. *Environ. Pollut.* 99(1):61-8.
- Munson, L., Calzada, N., Kennedy, S. and Sorensen, T.B. 1998. Luteinized ovarian cysts in Mediterranean striped dolphins. *J. Wildl. Dis.* 34(3):656-60.
- Notarbartolo di Sciarra, G., Venturino, M.C., Zanardelli, M., Bearzi, G., Borsani, F.J. and Cavalloni, B. 1993. Cetaceans in the central Mediterranean Sea: distribution and sighting frequencies. *Boll. Soc. Zool. Ital.* 60:131-38.
- Öztürk, B. 1995. Marine mammal inventory of Turkey. *Eur. Res. Cetaceans* [Abstracts] 9:96-8.
- Orsi Relini, L. and Relini, M. 1993. The stomach content of some common dolphins (*Delphinus delphis* L.) from the Ligurian Sea. *Eur. Res. Cetaceans* [Abstracts] 8:99-102.
- Palmisano, F., Cardellicchio, N. and Zamboni, P.G. 1995. Speciation of mercury in dolphin liver: A two-stage mechanism for the

- demethylation accumulation process and role of selenium. *Mar. Environ. Res.* 40(2):109-21.
- Payne, P.M. and Selzer, L.A. 1986. Marine mammals, seabirds and marine turtles in the Gulf of Maine and Massachusetts Bay with special emphasis on the locations of the foul-area disposal site and the Cape Arundel disposal site. Report presented to Stanford Ecological Services Inc. (unpublished). 212pp. [Available from the author].
- Perrin, W.F. and Reilly, S.B. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. *Rep. int. Whal. Commn* (special issue) 6:97-133.
- Perrin, W.F., Miyazaki, N. and Kasuya, T. 1989. A dwarf form of the spinner dolphin (*Stenella longirostris*) from Thailand. *Mar. Mammal Sci.* 5(3):213-27.
- Pulcini, M., Angradi, A.M. and Sanna, A. 1993a. Distribution and frequency of cetaceans in the Ligurian-Provençal Basin and in the North Tyrrhenian Sea (Mediterranean Sea). *Eur. Res. Cetaceans* [Abstracts] 7:144-7.
- Pulcini, M., Angradi, A.M. and Sanna, A. 1993b. Stomach contents of striped dolphins (*Stenella coeruleoalba*) from the south-Central Tyrrhenian coast. *Eur. Res. Cetaceans* [Abstracts] 6:37-9.
- Ralls, K., Brownell, R.L. and Ballou, J. 1980. Differential mortality by sex and age in mammals, with specific reference to the sperm whale. *Rep. int. Whal. Commn* (special issue) 2:233-43.
- Ramade, F. 1993. Environmental and ecotoxicological problems in the Mediterranean countries. *Sci. Total Environ.* (Suppl.) 3:97-107.
- Read, A.J., Wells, R.S., Hohn, A.A. and Scott, M.D. 1993. Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. *J. Zool., London.* 231:107-23.
- Reijnders, P.J.H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. *Nature, Lond.* 324:456-7.
- Reijnders, P.J.H., Donovan, G.P., Aguilar, A. and Bjørge, A. 1999. Report of the Workshop on Chemical Pollution and Cetaceans, March 1995, Bergen, Norway. *J. Cetacean Res. Manage.* (special issue 1):1-42.
- Rigollet, V., Muller, M. and Oliver, G. 1998. Quelle est donc cette 'étrange maladie' qui rouge les dauphins? *Courr. Nat.* 171:8-9. [In French].
- Ross, P.S., De Swart, R.L., Reijnders, P.J.H., Loveren, H.V., Vos, J.G. and Osterhaus, A.D.M.E. 1995. Contaminant related suppression of delayed-type hypersensitivity and antibody responses in harbour seals fed herring from the Baltic Sea. *Environ. Health Perspect.* 103(2):162-7.
- Sagarminaga, R. and Cañadas, A. 1996. Studying a possible competition for ecological niche between the common dolphin, *Delphinus delphis*, and striped dolphin, *Stenella coeruleoalba*, along the southeastern coast of Spain. *Eur. Res. Cetaceans* [Abstracts] 9:114-7.
- Silvani, L., Gazo, M. and Aguilar, A. 1999. Spanish driftnet fishing and incidental catches in the western Mediterranean. *Biol. Conserv.* 90:79-85.
- Storelli, M.M., Ceci, E. and Marcotrigiano, G.O. 1998. Comparison of total mercury, methylmercury, and selenium in muscle tissues and in the liver of *Stenella coeruleoalba* (Meyen) and *Caretta caretta* (Linnaeus). *Bull. Environ. Contam. Toxicol.* 61(4):541-7.
- Tanabe, S. and Tatsukawa, R. 1992. Chemical modernization and vulnerability of cetaceans: increasing toxic threat of organochlorine contaminants. pp. 161-79. In: C.H. Walker and D.R. Livingstone (eds.) *Persistent Pollutants in Marine Mammals*. SETAC Special Publications Series. 1st. Edn. Pergamon Press, Oxford, New York, Seoul, Tokyo.
- Tanabe, S., Watanabe, S., Kan, H. and Tatsukawa, R. 1988. Capacity and mode of PCB metabolism in small cetaceans. *Mar. Mammal Sci.* 4(2):103-24.
- Trites, A.W. and York, A.E. 1993. Unexpected changes in reproductive rates and mean age at first birth during the decline of the Pribilof northern fur seal (*Callorhinus ursinus*). *Can. J. Fish. Aquat. Sci.* 50(4):858-64.
- Troisi, G.M., Haraguchi, K., Simmonds, M.P. and Mason, C.F. 1998. Methyl sulphone metabolites of polychlorinated biphenyls (PCBs) in cetaceans from the Irish and the Aegean Seas. *Arch. Environ. Contam. Toxicol.* 35(1):121-8.
- Troncone, A., Marano, G., Marcotrigiano, G.O., Rositani, L. and Zizzo, N. 1990. The stranding of cetaceans along the coasts of Puglia: connections with fishing. General Fisheries Council for the Mediterranean, Expert Consultation on the Evaluation of Stocks of Large Pelagic Fishes in the Mediterranean Area. Bari, Italy, 21-27 June 1990. 6pp.
- University of Barcelona. 1994. SUROESTE: A survey of interactions between marine mammals and fisheries in the southwestern waters of the EC. Contract Report, DGXIV-C-1, Commission of the European Communities. 113pp.
- Van Bree, P.J.H., Mizoule, R. and Petit, G. 1969. Sur trois spécimens de *Stenella euphrosyne* (Gray, 1846) (Cetacea, Delphinidae) de Méditerranée (région de Banyuls-sur-mer, France). *Vie Milieu* 20(2A):447-60. [In French].
- Van Bressem, M.F., Visser, I.K.G., Van de Bilt, M.W.G., Teppema, J.S., Raga, J.A. and Osterhaus, A.D.M.E. 1991. Morbillivirus infection in Mediterranean striped dolphins (*Stenella coeruleoalba*). *Vet. Rec.* 129:471-2.
- Van Bressem, M.F., Visser, I.K.G., De Swart, R.L., Orvell, C., Stanzani, L., Androukaki, E., Siakavara, K. and Osterhaus, A.D.M.E. 1993. Dolphin morbillivirus infection in different parts of the Mediterranean Sea. *Arch. Virol.* 129:235-42.
- Viale, D. 1978. Evidence for metal pollution in Cetacea of the western Mediterranean. *Ann. Inst. Océanogr.* 54(1):5-16.
- Viale, D. 1985. Cetaceans in the northwestern Mediterranean: their place in the ecosystem. *Oceanogr. Mar. Biol. Ann. Rev.* 23:491-571.
- Würtz, M. and Marrale, D. 1991. On the stomach contents of striped dolphins *Stenella coeruleoalba* from the Ligurian coast, central Mediterranean sea. *Eur. Res. Cetaceans* [Abstracts] 5:62-4.
- Zakharov, V.M. and Yablokov, A., V. 1990. Skull asymmetry in the Baltic grey seal - effects of environmental pollution. *Ambio* 19(5):266-9.

Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques

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ABSTRACT

The distribution and relative abundance of groups of striped dolphins (*Stenella coeruleoalba*) in the Ligurian Sea cetacean sanctuary, based on acoustic surveys carried out in the summers of 1994–1996, is presented. Abundance indices based on acoustic detections were adjusted for covariates likely to influence the detectability of dolphin vocalisations, such as wind speed, background noise and sea state. Dolphin vocalisation rates were shown to vary diurnally, being higher at night, and this effect was also modelled and removed. Results showed that dolphin groups were fairly evenly distributed throughout the sanctuary, but they were more abundant in offshore waters, peaking at water depths between 2,000–2,500m. Preliminary sightings results also indicated larger-sized groups in offshore regions. Relative abundance does not appear to vary significantly over the summer months. Sperm whales (*Physeter macrocephalus*) were detected at 4% of monitoring stations, representing at least 61 different group encounters. Although not common, they appeared to be widely distributed in deep water throughout the study area.

KEYWORDS: MEDITERRANEAN; SANCTUARIES; INDEX OF ABUNDANCE; MONITORING; SURVEY-ACOUSTIC; OCEANOGRAPHY; ACOUSTICS

INTRODUCTION

On 22 March 1993, 96,000km² of the northwestern Mediterranean Sea, extending between the French and Italian Riviera, Corsica and Northern Sardinia, and centred on the Ligurian Sea, was declared a sanctuary for the protection of whales and dolphins by Ministers from Italy, Monaco and France. The sanctuary finally came into existence on 25 November 1999, when the formal Agreement was signed by those countries. In undertaking this action, these Governments recognised that this was a particularly important area of distribution for cetaceans, which are under threat in many parts of the Mediterranean. Article 9 of the Declaration states that the signatories should encourage and stimulate research programmes aimed at monitoring the effect of the measures implemented in the framework of the Declaration.

In response to this, scientific teams from the International Fund for Animal Welfare (IFAW), the Tethys Research Institute (TRI) and Group de Recherche sur les Cétacés (GREC) established a collaborative programme to investigate ways of monitoring cetacean populations in the new sanctuary that are compatible with their existing cetacean research in the area. This paper presents information on the relative abundance of striped dolphins (*Stenella coeruleoalba*) in the Ligurian Sea, and the effect of certain environmental variables on their distribution, based on a cooperative acoustic survey. The intention of this work was to provide information on distribution and population trends that will be useful in managing the sanctuary, and

results that would be complementary to line transect surveys. Some less detailed results of sperm whale (*Physeter macrocephalus*) detections are also presented.

Striped dolphins are by far the most commonly encountered cetacean in the Ligurian Sea. They face a number of threats in the Mediterranean, including entanglement in driftnets, overfishing and pollution (Aguilar, 2000). The striped dolphin is the cetacean species that suffers the largest mortality in driftnets within the Mediterranean (Di Natale and Notarbartolo di Sciara, 1994). Although the exact size of the striped dolphin bycatch is not known, the level of mortality exceeds ‘the safe take limit’ of 2% for the western Mediterranean population, and is unsustainable (IWC, 1994).

Between 1990 and 1992 a massive die-off of striped dolphins occurred in the Mediterranean Sea, spreading eastward from the Catalanian coasts to the Aegean Sea. This was due to an outbreak of a morbillivirus infection (Aguilar and Raga, 1993). It has been suggested that high PCB concentrations found in Mediterranean striped dolphins and other Mediterranean cetaceans may have depressed the dolphin’s immune system, contributing to the morbillivirus outbreak (Kannan *et al.*, 1993).

Previous line transect studies conducted during the summer months have indicated population sizes of 117,880 for the entire western Mediterranean (Forcada *et al.*, 1994), with an estimate of 25,614 individuals for the Corsican-Ligurian Basin in 1992 (Forcada *et al.*, 1995). Gannier (1998b) obtained a similar estimate for the sanctuary area based on a smaller scale summer survey in

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1996. On the basis of both genetic and morphometric data, Archer (1996) concluded that populations of striped dolphins in the Mediterranean are isolated from those in the North Atlantic.

The teams involved in this research decided to experiment with passive acoustic techniques for this study because, provided that standardised techniques and equipment are used, these should allow several independent research groups, operating from different vessels of similar type, to collect consistent data. In addition, acoustic methods would allow data to be collected during periods when the teams' primary cetacean research activities were not possible (for example, at night, during passage and when weather conditions were poor).

The range at which cetacean vocalisations can be detected will be affected by a variety of factors including the levels of background noise in masking frequency bands, and the propagation properties of the medium. In addition, some behavioural variation may be expected in the vocalisation rates of the animals. During a survey, variations in these conditions arise with or without a random survey design, leading to imprecision and possible bias. The methods used here attempt to make adjustments for some of the varying conditions that influence detectability during surveys (Robel *et al.*, 1969) using generalised linear models (e.g. Nicholls, 1989). After this adjustment, the effects of other factors on dolphin distribution, such as bathymetric variables, can be better examined.

METHODS

Survey methods

Surveys were conducted over three summers in 1994-1996, from motor sailing vessels, ranging in size from 12-20m, towing identical hydrophone arrays on 100m of cable. Each array consisted of two *Benthos* AQ4 hydrophones, each with a *Magrec* preamplifier, mounted 3m apart in the centre of a 10m long, 25mm diameter, oil-filled polythene tube. The preamplifiers were designed with high-pass filters, which suppressed noise below 200Hz by 6dB per octave. This reduced the levels of lower frequency background noise, while still allowing effective monitoring of odontocete vocalisations.

Survey tracks were chosen to provide a more-or-less even coverage of the area, although sometimes tracks were dictated by logistical considerations, e.g. for the survey vessel to make a passage to a port. Knowledge of, or assumptions about, cetacean distributions were not allowed to influence the designation of survey tracks. Survey effort was suspended if the vessel diverted to close with cetaceans encountered during the day.

While vessels were conducting acoustic surveys, hydrophones were monitored and one-minute recordings were made at regular intervals. If the boat was sailing fast it would be slowed down at monitoring stations, and if it was motoring, the engine would be put out of gear to facilitate efficient acoustic detection. On the IFAW research vessel, *Song of the Whale*, hydrophones were monitored every 15 minutes. Such frequent monitoring was not compatible with the work routine on other vessels. On the *Tethys* vessel, *Gemini Lab*, hydrophones were monitored every 20 minutes, while on the GREC vessel a 20-25 minute schedule was adopted.

Monitoring personnel were required to score the strength, on a scale between 0 (not heard) and 5 (very loud), of dolphin clicks or whistles, and sperm whale clicks. They also scored the strength of background water noise, background ship

noise, noise generated by their own vessel as well as recording their own vessel's speed and whether or not its engine was on. All monitoring personnel listened to a training tape that gave examples of different types and strengths of vocalisations and background noises. Field workers were also encouraged to compare how they scored particular sessions throughout the season to improve consistency.

The location of each monitoring station was recorded and environmental conditions were noted each hour. Where possible, data were entered directly into the *LOGGER* data collection program, in other cases records were made on pre-prepared sheets and transcribed to computer files later.

On one occasion, an experiment was undertaken to assess the range over which dolphins could be heard with the hydrophone equipment used during these surveys. A field worker was dropped off in a dinghy with a tape recorder and hydrophone equipment similar to that used during this study. The main research vessel then followed a group of dolphins as they swam away, while the fieldworker in the dinghy listened and made a continuous tape recording. The range between the main research vessel, which was close to the dolphins and the dinghy, was determined by using the vessel's radar.

Data used

The analysis described here uses only the data recorded in the field; no analysis of the tape recordings made at listening stations has been carried out.

The response data used for analysis of dolphin distribution were binary outcomes denoting presence or absence of dolphin groups at listening stations, where independent groups were determined *post hoc* as explained below. Typically, dolphins would be heard at several consecutive stations, and it seemed likely that the boat was within acoustic range of the same dolphin group during such periods. To obtain data on independent encounters with groups, consecutive positive detections were considered to be part of the same group encounter until no dolphins had been detected for at least 40 minutes. The time, location and associated covariates of each group encounter were taken at the midpoint of these strings of detections. Forty minutes was chosen as the critical time interval because, with a survey speed of 5 knots, a vessel would have travelled over 1.5 miles in that time, which was greater than the acoustic range observed for dolphins in this area during this work.

As with dolphin detections, strings of positive stations were considered to be encounters with a single sperm whale group. Detections were considered to be from a new group when no sperm whales had been detected for at least one hour. An hour was chosen as the time interval for determining a new encounter based on knowledge of sperm whale acoustic behaviour. Feeding sperm whales usually show a predictable pattern of behaviour. They make long dives that can extend for 30-50 minutes or more, interspersed by periods of 8-12 minutes at the surface (Gordon and Steiner, 1992; Watkins *et al.*, 1999). During dives, sperm whales click almost continuously, with only short pauses of less than a minute. Clicking usually starts within a few minutes of leaving the surface and ceases several minutes before whales reach the surface. While at the surface they are usually silent (Gordon *et al.*, 1992). Thus, typical silent periods for diving whales are of the order of 20 minutes or less, and if sperm whales are heard during a survey after an hour or more with no detections, it is likely that a new group has been encountered.

Audibility covariates

At each listening station a set of ‘audibility’ covariates relating to detectability were collected. These are shown in Table 1.

Table 1

Covariates recorded at listening stations, their type (number of levels given in parentheses for discrete variables) and their means of assessment.

Variable	Variable type	Method of assessment
wind speed	continuous	anemometer
boat speed	continuous	speedometer
engine state (on/off)	discrete (0-1)	switch
sea-state	discrete (0-10)	visual
time-of-day	continuous	GPS
self-noise	discrete (0-5)	aural
water-noise	discrete (0-5)	aural
ship-noise	discrete (0-5)	aural

Those variables not assessed aurally were considered important *a priori* because they were unambiguous and could be reliably measured. Sea state and wind speed are well known to affect ambient noise conditions in the ocean (Urick, 1983). If the research boat’s engine was on it would contribute to background masking noise, and would also be likely to be the primary means by which dolphins would be alerted to the presence of the boat. It was expected that dolphin vocalisation rates would vary diurnally, based on previous experience (e.g. Gordon, 1987).

The variables assessed aurally are more subjective (more inter- and intra-observer variation) than other data and the masking effect of these noises will depend on a number of factors, including their spectra, which were not measured.

Environmental covariates

Two ‘environmental’ variables expected to relate to the distribution of dolphins were acquired post-survey for each listening station: water depth and angle of bottom slope, calculated by interpolation between the closest contours. These calculations were performed using routines in Atlas GIS and specially written MATLAB programs. Data on coastlines and depth contours were exported from the GEBCO 97 Digital Atlas (BODC, Proudman Laboratory, Birkenhead, Merseyside, L43 7RA, UK).

Modelling methods

The relationship between presence/absence of dolphin groups and other predictive variables was determined using generalised linear models (GLMs). These are appropriate for data with a combination of categorical and continuous predictor variables. The link function was a logit, suitable for binomial responses. This type of model is asymptotic so that fitted values cannot fall outside the interval [0,1], and uses maximum likelihood estimators appropriate for binomially distributed variables (McCullagh and Nelder, 1983).

The GLMs in the present study were of the form:

$$\text{logit}(p_i) = \text{intercept} + \alpha_1 x_{i1} + \dots + \alpha_n x_{in} + \beta_1 y_{i1} + \dots + \beta_m y_{im} + \gamma_1 \sin(\omega \cdot t_i) + \gamma_2 \cos(\omega \cdot t_i)$$

where, for listening station i :

- p_i is the regression estimate of the detection rate;
- α_j is the coefficient of discrete term x_{ij} (e.g. sea state) with $j = 1, \dots, n$;
- β_k is the coefficient of continuous term y_{ik} (e.g. wind speed or depth) with $k = 1, \dots, m$;

γ_1 and γ_2 are the coefficients of the two temporal terms, and t_i the time-of-day.

$\gamma_1 \sin(\omega t) + \gamma_2 \cos(\omega t)$ represents the temporal variation as a phased sinusoid, using the relationship:

$$\gamma_1 \cdot \sin(\omega t) + \gamma_2 \cdot \cos(\omega t) = \gamma_3 \cdot \sin(\omega t + \phi)$$

where ϕ is the phase constant, ω the angular frequency, and t_1, t_2 and t_3 are amplitude terms.

Models examined included hierarchical subsets of the above terms. Two models were compared by their change in ‘deviance’ (twice the log likelihood ratio). The degree of improvement from the introduction of new parameters was assessed, and a superior model selected. Specifically, the reductions in deviance brought about firstly by the audibility variables, and secondly by other environmental variables after adjustment for these audibility variables, were examined. This analysis used the ‘logistic regression’ procedure in SPSS 7.0 (Norušis, 1990).

In the model selection of the audibility variables, those covariates recorded by non-aural means (Table 1) were included by default. The aurally-assessed covariates were considered less reliable, and for this reason, these covariates were included in the model by forward stepwise selection. Some of the audibility predictor variables are highly correlated, for example, wind-speed and sea state. One potential effect of this collinearity is to give misleading significance values; however, optimum model-selection was not a prime concern. The parameter values of the selected model were examined and found to be of sensible magnitude and sign.

In some cases, the teams collected and measured covariates differently and the scoring of the more subjective factors is also likely to be more consistent within a single group’s data (because observers compared their rating systems) than between them. For these reasons, the effects of covariates on detection probability were modelled separately for each organisation’s dataset.

Relative abundance of striped dolphins

For each listening station i , we have:

- d_i a binary response indicating presence/absence of a dolphin group.
- p_i an estimate, provided by the GLM, for the expected probability of detecting dolphin groups given the audibility conditions and time-of-day at the survey station.

To examine geographical distributions, data were assigned to cells in a grid comprised of 25 n.mile squares. For each sub-area j , there is a set of listening stations \mathbf{j} with associated response data \mathbf{d}_j and predictor data \mathbf{p}_j . Our estimate of relative abundance for area j is $\bar{\mathbf{r}}_j = \bar{\mathbf{d}}_j / \bar{\mathbf{p}}_j$.

If we assume that the audibility covariates affect detectability independently of the environmental covariates (only the latter being causally related to the underlying distribution of the animals), then adjusting for audibility conditions should give reduced bias and improved precision for relative abundance.

Group sizes from sightings were compared between two bathymetric regions: the area of water of depth greater than 2,000m was designated ‘offshore’, and the area of shallower water ‘onshore’. The 2,000m contour was chosen as a convenient but arbitrary boundary because approximately half the stations were in each of the two areas.

Relative abundance of sperm whales

The total number of sperm whale detections was too small to allow a GLM approach to investigate factors affecting sperm whale audibility and distribution (but see Gordon *et al.*, 1998, for an example of this method applied to sperm whales for a dataset with more acoustic detections). Here, only general data on sperm whale detections are presented to provide a qualitative impression of distribution and abundance.

RESULTS

During the period of this study, virtually all of the visual encounters of dolphin groups by all three research teams were of striped dolphins. For example, during its 1994 season *Song of the Whale* logged 100 encounters with striped dolphins and only single encounters with bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*) and pilot whales (*Globicephala melas*). The vocalisations of Risso's dolphins and pilot whales are rather dissimilar to those of striped dolphins. Examples of both species were provided on the training tape and it is likely that they would have been distinguished by monitoring personnel in the field. However, even if they were not, the sightings records suggest that they would have made an insignificant contribution to the overall dataset and it seems reasonable to consider that the vast majority of acoustic encounters were with striped dolphins.

A total of 5,428 acoustic monitoring stations were completed. Table 2 shows how this effort was distributed between different research teams and over time, while Figs

1a and 1b show the geographic distributions of survey effort within the sanctuary area. Most of the area of the sanctuary was well covered by the survey. Some areas, such as the corridor between San Remo in Italy and Calvi in northern Corsica, received particularly high coverage.

Table 2
Distribution of monitoring effort: number of monitoring stations by year and by organisation.

Year	IFAW	TETHYS	GREC	Total
1994	2,696	739	-	3,435
1995	-	-	422	422
1996	-	696	875	1,571
Total	2,696	1,435	1,297	5,428

Effects of audibility covariates

The effects of the audibility covariates were generally as expected. For example, detection rate fell with increasing wind speed, sea state and levels of background noise. Fig. 2 shows examples for the IFAW *Song of the Whale* data. The model chi-square statistics for the audibility covariates without time-of-day are shown in Table 3. In this table, the chi-square value approximates the reduction in deviance of a model with the predictor variable(s) included compared to a model without. The change in deviance is highly significant for both IFAW and TETHYS data (indicating rejection of the

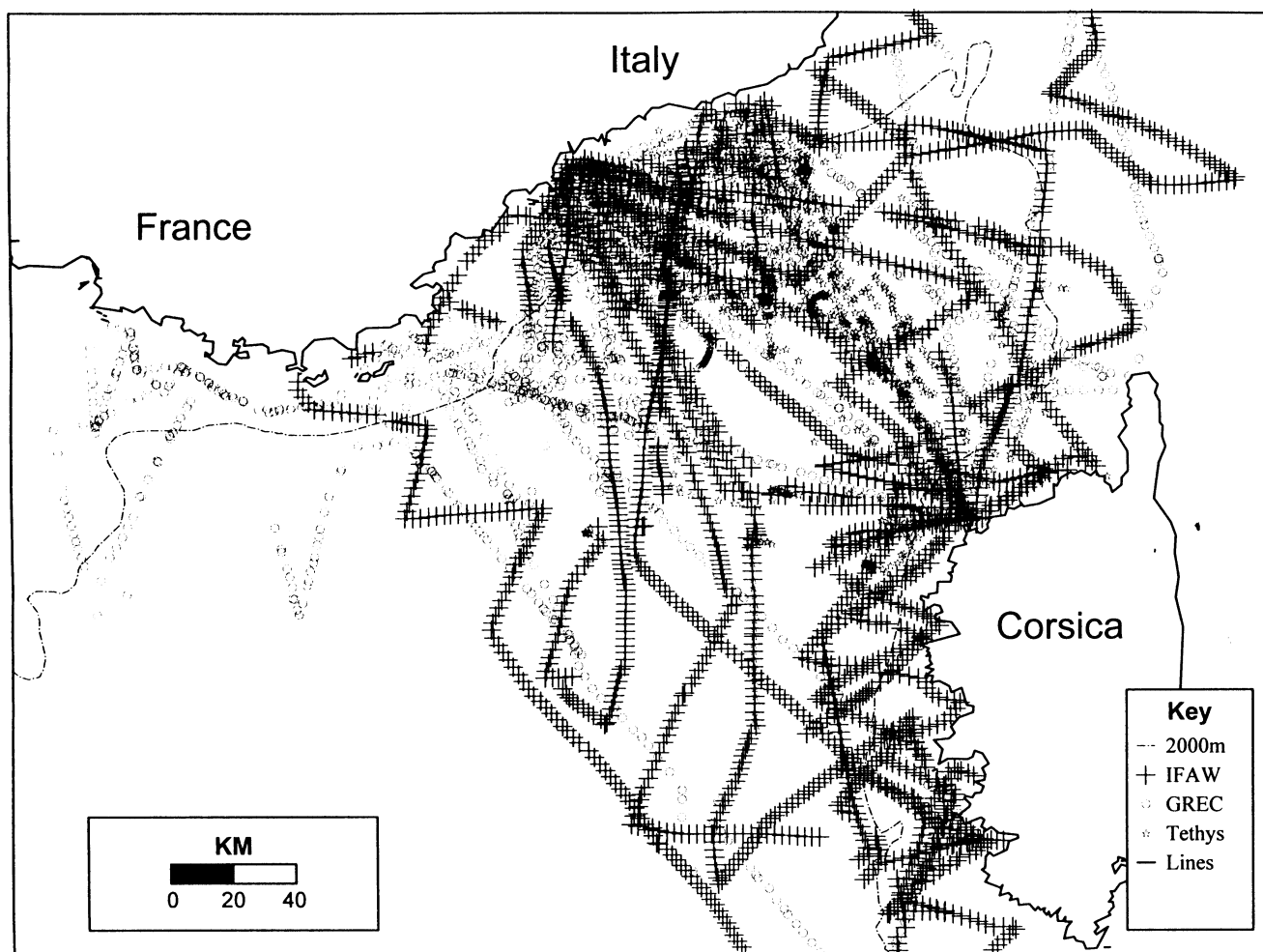


Fig. 1a. Distribution of acoustic stations monitored by each organisation.

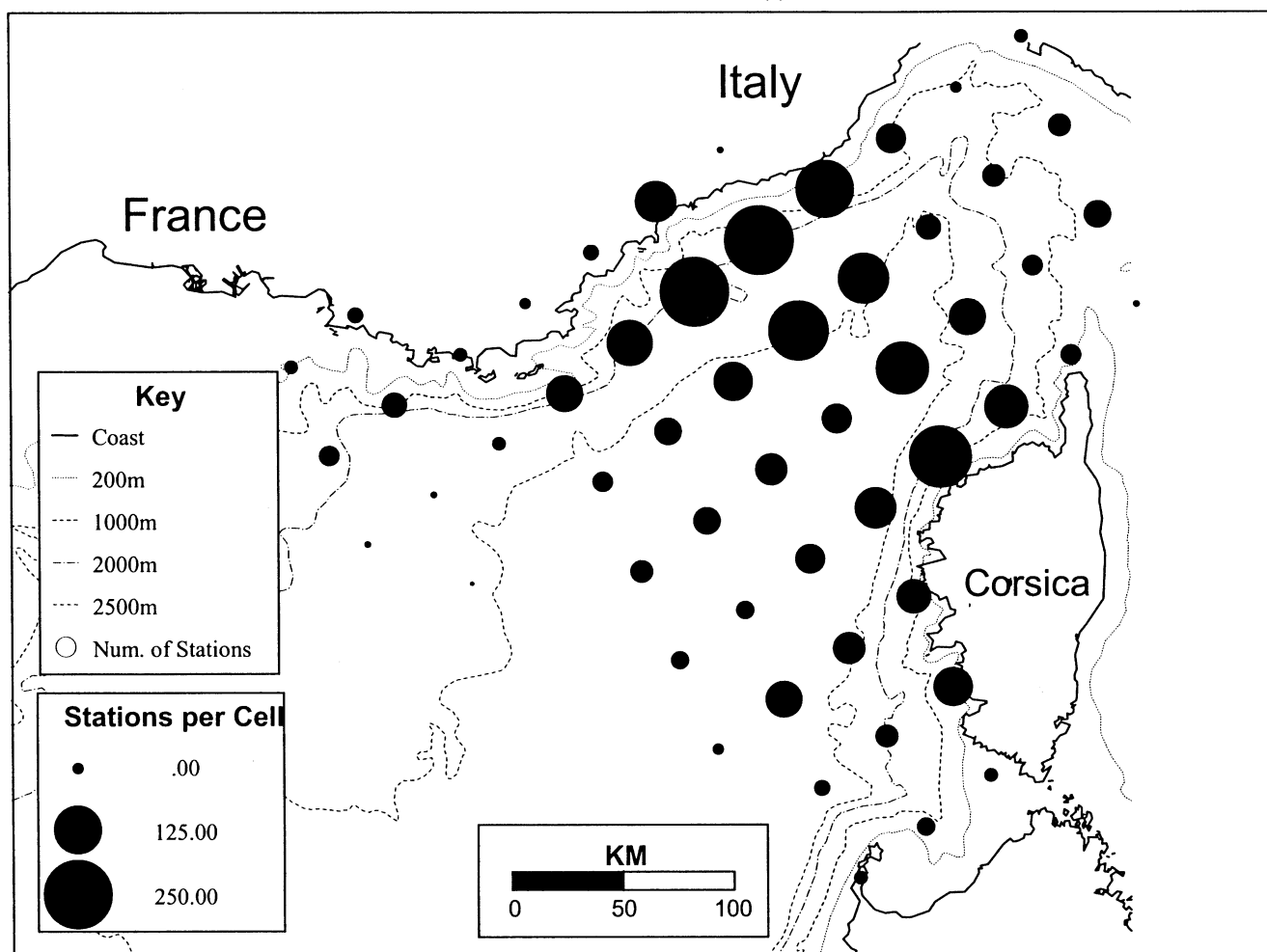


Fig. 1b. Distribution of acoustic monitoring effort in a 25 n.mile square grid.

null hypothesis that all model coefficients are zero); GREC did not record this information using the standard procedure.

Initially, the audibility covariates were incorporated into models without time-of-day. A marked diurnal variation in detection rate, which seems to represent a diurnal change in dolphin vocal behaviour, was evident (Fig. 3). The introduction of temporal terms to the model was significant for all three organisations' data (Table 3).

Distribution and relative abundance of striped dolphins

Seasonal and spatial variation was investigated, after adjustment for audibility covariates. Geographical distribution of adjusted detection rates is indicated in Fig. 4. Adjustments have been made for all audibility and temporal covariates. (These maps were plotted and compared for unadjusted detection rates, and showed a somewhat similar picture.) Dolphins are distributed throughout the sanctuary, but seem to be more abundant in offshore regions and in the northern part of the Ligurian Sea.

The relationship between detection rate and certain geographic variables (range to coast, depth and bathymetric slope) were investigated more thoroughly for the IFAW data, which was the largest of the three datasets. Fig. 5 shows detection rate against depth. A marked increase in detection rates, peaking in the 2,000 and 2,500m depth zone, is evident. Table 4 shows statistical results for models with linear and quadratic terms. Of these three, the depth model is the best predictor of detection rate. As discussed above,

sequential acoustic detections are considered as encounters with single dolphin schools. Dolphin density will be a product of group density and group size. Although group size could not be assessed acoustically with the techniques used in these surveys, some visual data on group size were collected. The visually estimated sizes of 161 groups of striped dolphins (96 encountered by IFAW and 65 by GREC) were compared for groups encountered in 'offshore' and 'inshore' waters. Table 5 summarises these data. Group size was significantly higher in offshore waters (Mann-Whitney U test, $P = 0.042$). However, we do not feel that group sizes were estimated sufficiently accurately during encounters for these data to be used to estimate the relative density of individuals. Despite this, it should be noted that if group sizes are larger offshore, as these data indicate, this will enhance the observed pattern of higher detection rates of groups in offshore waters.

Distribution of sperm whales

Sperm whales were detected at 220 of 5,428 stations (4%) and these represented at least 61 separate group encounters. The number of whales heard at each station ranged from 1-3 with an overall mean of 1.5. The distribution of monitoring stations at which whales were and were not detected is shown in Fig. 6. Although not abundant, sperm whales were widely distributed throughout the area. The observed frequencies of sperm whale group encounters in different depth zones (<1,000m; 1,000-2,000m; 2,000-2,500m; >2,500m) were compared with expected values (based on number of monitoring stations in each depth zone) using a chi-squared test. Encounters were less frequent than

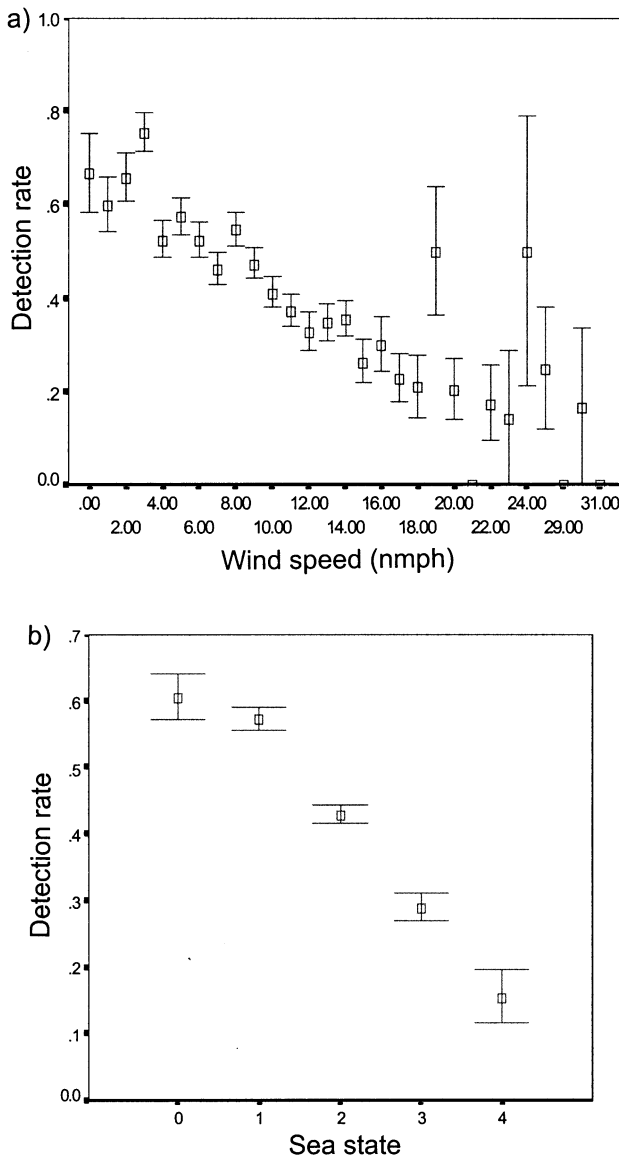


Fig. 2. Detection rate versus (a) wind speed and (b) sea state (IFAW data). Bars are standard errors assuming binomial distributions.

expected in waters $< 1,000\text{m}$ than in waters $> 1,000\text{m}$ ($\chi^2 = 5.27$, $df = 1$, $P = 0.02$). However, the frequency of encounters was not significantly different from expected between all depth zones ($\chi^2 = 5.917$, $df = 3$, $P = 0.116$) or between the bands greater than $1,000\text{m}$ depth ($\chi^2 = 0.562$, $df = 2$, $P = 0.755$).

DISCUSSION

Distribution and relative abundance of striped dolphins

The deep water and offshore distribution of striped dolphins indicated by this work is consistent with this species' generally oceanic habit (Jefferson *et al.*, 1993), although it is

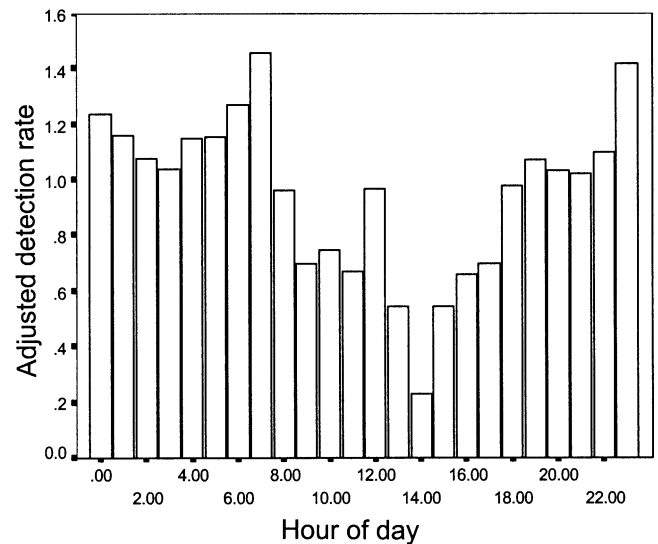


Fig. 3. Detection rates by time of day (IFAW data) after adjustment for 'audibility' covariates.

notable that in this area, dolphin density seems to fall beyond the $2,500\text{m}$ contour. These observations broadly agree with those of Gannier (1998a) who found that a very low relative abundance of dolphins in waters less than 500m increased continuously through the $2,000\text{--}2,500\text{m}$ depth stratum.

A prominent oceanographic feature in the Ligurian Sea is the Ligurian Sea Front. This lies between a peripheral, less saline coastal zone, and a more saline central zone of mainly Levantine water. Off Cape Ferrat (France), the front is found approximately 12 miles from the coast (Boucher *et al.*, 1987; Fig. 7). Coastal currents flow within the peripheral zone: a north-bound current flows along the west coast of Corsica and joins the Ligurian current to the north of the island; together these move across the northern end of the Ligurian Sea and turn to flow in a south-westerly direction along the French-Italian Riviera coast (Millot, 1987). Nutrients are brought to the surface in the frontal zone making it an area of increased biological activity, with maximum concentrations of both chlorophyll biomass and zooplankton being found here. Boucher *et al.* (1987) found that, for many species, the frontal zone was an area where they were localised during their growing and spawning phases. Downwelling transport of organic matter from the euphotic zone to deep levels also occurs here, supporting populations of midwater plankton (Baussant *et al.*, 1992).

Fig. 7 shows that, for much of its length, the Ligurian Sea Front occurs in water depths between $2,000$ and $2,500\text{m}$. It is possible, therefore, that the peak in dolphin abundance at these depths indicated here could reflect an association with the more productive frontal zone. A front is a dynamic structure and its position is likely to vary with time. It would thus be interesting to compare dolphin distribution and behaviour with direct, up-to-date observations of the front's location, e.g. provided by satellite imagery.

Table 3

Model statistics for audibility covariates

Added variables	Given variables	IFAW			TETHYS			GREC		
		df	χ^2	P	df	χ^2	P	df	χ^2	P
Audibility (not time of day)	-	18	260.6	0.0000	34	271	0.0000	n/a	n/a	n/a
Time of day	Audibility (not time of day)	2	183.3	0.0000	2	81.2	0.0000	2	25.7	0.0000

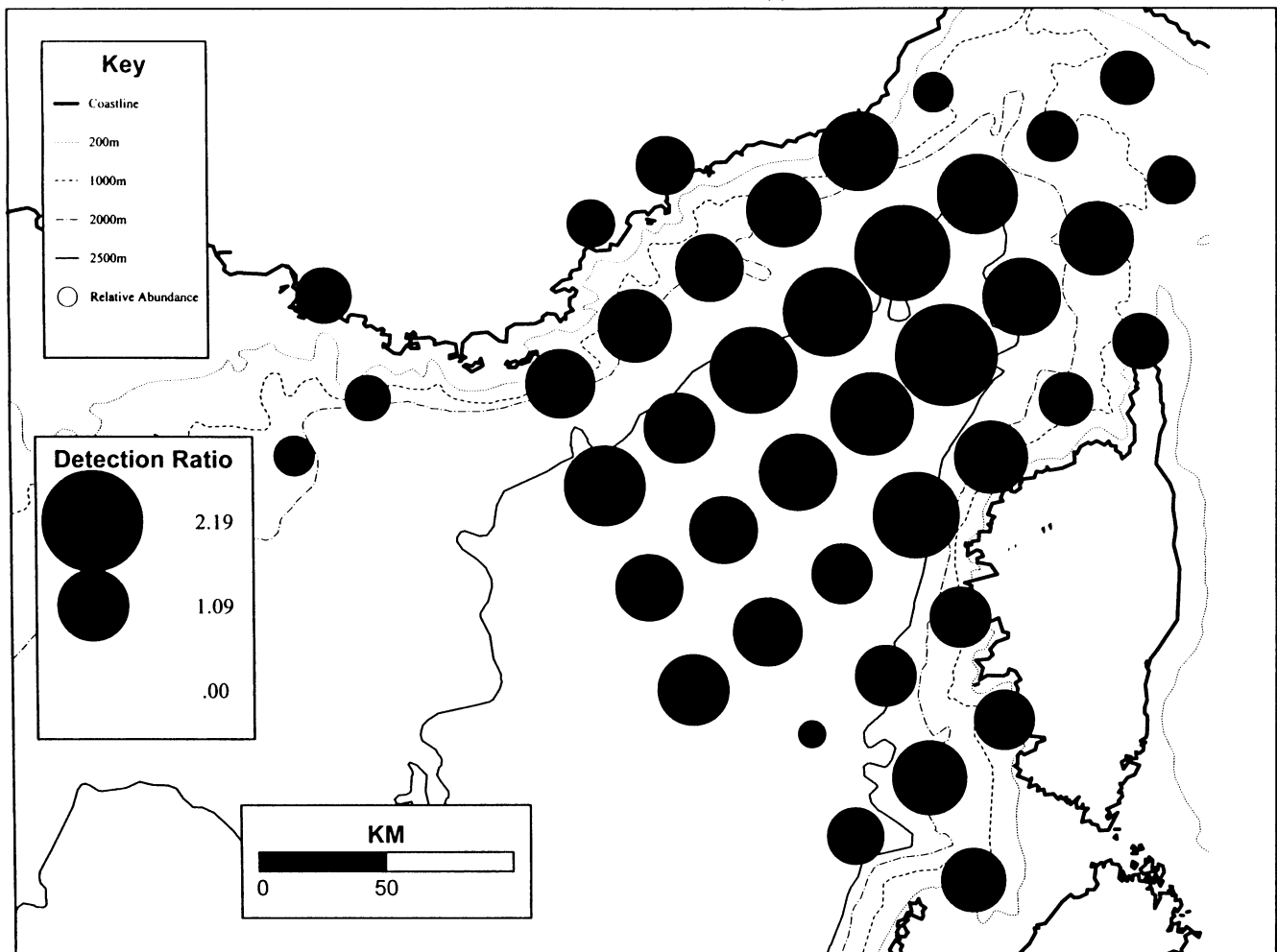


Fig. 4. Rates of detection of dolphins in different 25 n.mile grid cells. Detection ratio is the observed detection rate/predicted detection rate (based on modelled covariates).

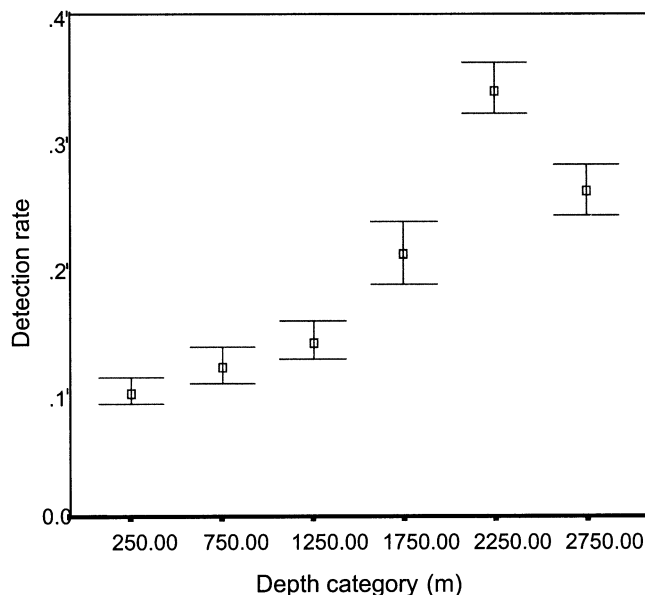


Fig. 5. Mean detection rate for dolphin groups against water depth (IFAW data).

Striped dolphin densities within the sanctuary appeared to remain fairly constant throughout the summer months (June-September) when this work was carried out. To date, most cetacean survey work has been confined to the summer. Gannier and Gannier (1997) showed a marked reduction in

relative abundance of dolphins in the winter months, though sightings conditions were also poor at this time of year. Acoustic methods, which are less affected by bad weather than visual techniques, could be used to improve knowledge of seasonal abundance.

The marked diurnal variation in vocalisation rates, shown here, suggests that striped dolphins may be more active at night. It is possible that, like other oceanic dolphins (e.g. spinner dolphins, Norris and Dohl, 1980; and dusky dolphins, Würsig *et al.*, 1991), they feed mainly on fish and cephalopods that migrate towards the surface at night. This suggestion is supported by Gannier (1999) who showed that, off the French Ligurian coast, dolphins move inshore and produce echolocation signals at higher rates, suggestive of foraging activity, at night.

Acoustic detection rates, which are assumed here to be a proxy for dolphin density, will be affected by propagation conditions. Through the summer months (*ca* May to September), a stable thermocline develops in the Ligurian Sea at a depth of ~30-60m with a sound velocity minimum at around 60-80m (Mediterranean Ocean Database <http://modb.oce.ulg.ac.be/>). In these conditions, sound will tend to be refracted away from the surface, reducing the potential for long range propagation of dolphin vocalisations produced near the surface. The thermocline is stable day and night so it is unlikely that diurnal variation in propagation conditions could explain the diurnal changes in acoustic detection rates demonstrated during this study. In the frontal region, upwelling of cold water results in a less pronounced thermocline at a shallower depth, and in some cases this

Table 4
Model statistics for environmental variables (IFAW data).

Added variables	Given variables	df	χ^2	<i>P</i>	exp(B)
Day of year depth d (m)	Audibility	1	0.88	0.347	0.9972
	Audibility	2	46.43	0.0000	d 1.0009
					d ² 1.0000
Distance to coast r (nm)	Audibility	2	29.08	0.0000	r 1.0841
					r ² 0.9988
					s 0.8383
Slope s	Audibility	2	16.98	0.0000	s ² 1.0063

Table 5
Comparison of sizes of striped dolphin groups observed in offshore and onshore waters.

Depth	No.	Mean	Median
<2000m (onshore)	37	13.1	6
>2000m (offshore)	124	21.5	12
Overall	161	19.6	10

could result in different propagation patterns, theoretically resulting in better sound propagation. The relatively high frequency sound of dolphin whistles will be heavily attenuated by absorption effects however, so that even here there is limited scope for long range propagation of these signals. We feel that it is unlikely that the potential for

improved acoustic propagation in the frontal zone explains the more general distribution of detection rates revealed here. Nevertheless, during future acoustic surveys' attempts to measure propagation conditions and effective range throughout the survey area should be made.

Some shortcomings of the work described here should be noted. For example, it would have been useful to measure the accuracy with which different workers from different teams scored recordings of a series of standard monitoring sessions on different occasions. The analysis was weaker, and made more complicated, by a lack of consistency in the data collection protocols followed by the different partners. In particular, certain predictors found to be significant in the data from one organisation were not recorded by other organisations. Clearly, in the future, it is essential that all collaborators should collect the same data on the same schedule in exactly the same way.

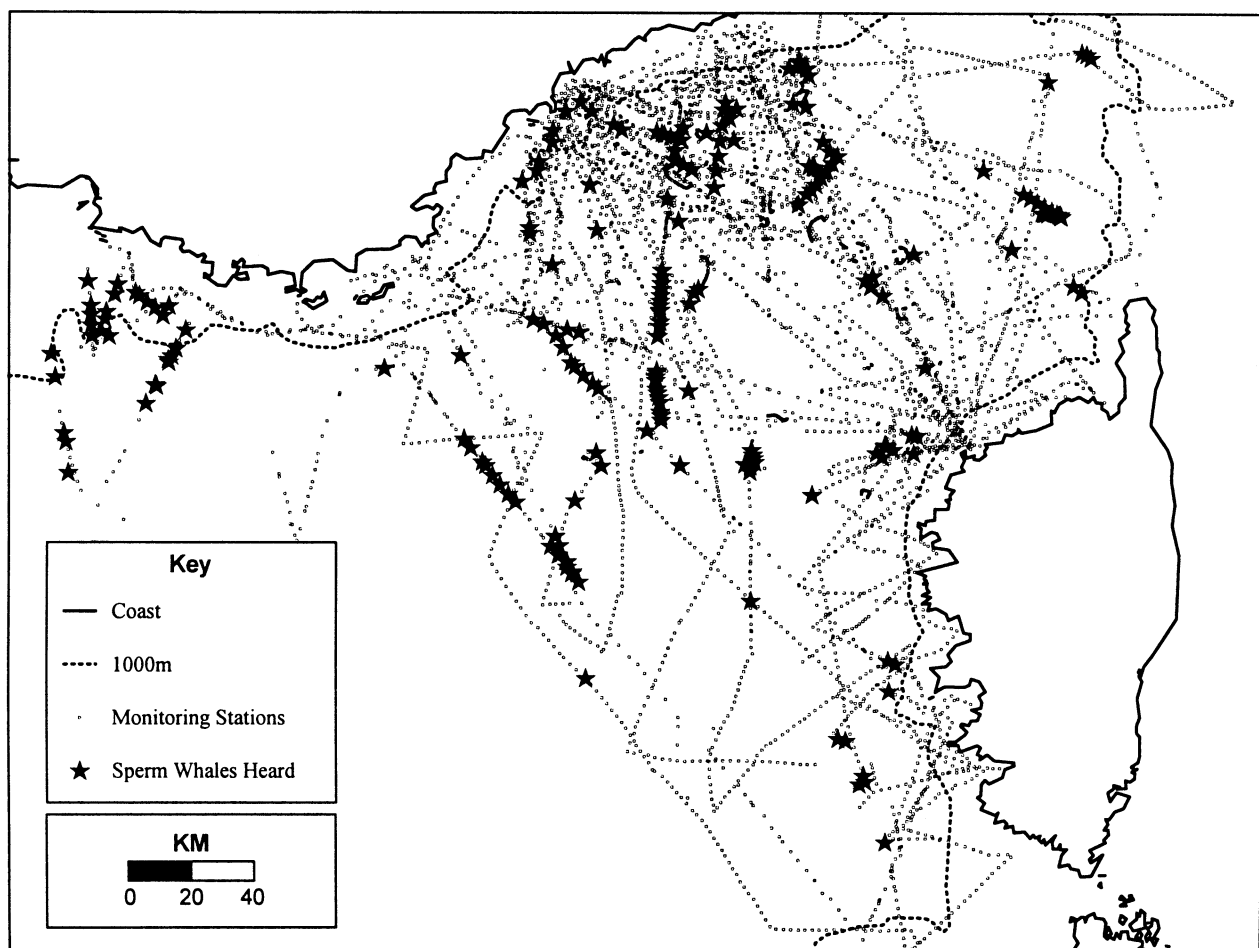


Fig. 6. Distribution of stations at which sperm whales were heard during the survey.

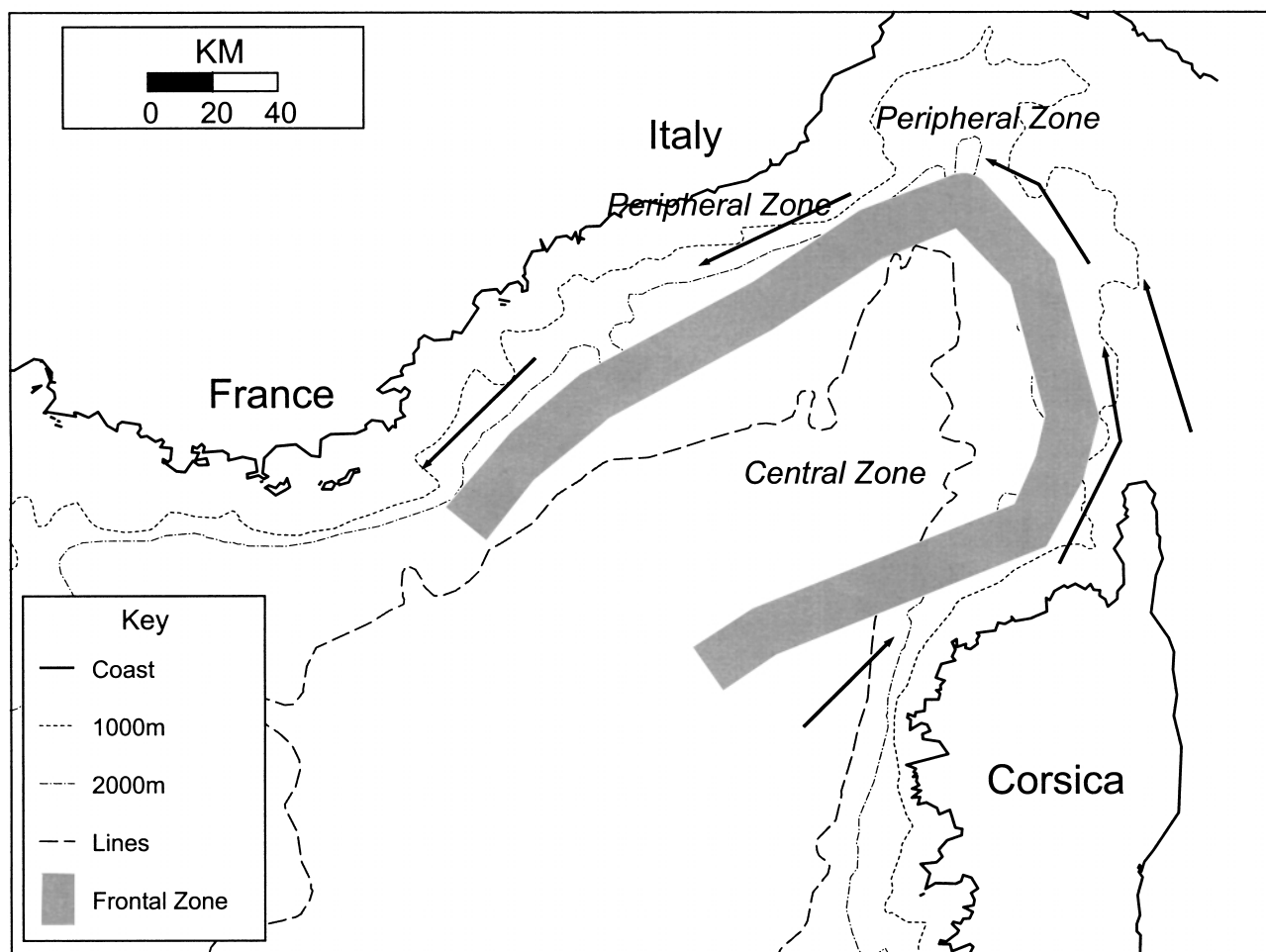


Fig. 7. Typical location of Ligurian Sea Front and coastal currents (indicated by arrows) after Boucher *et al.*, (1987).

Future development

By using identical acoustic equipment, three different research groups were able to collaborate to collect a substantial amount of data on the distribution and vocal behaviour of striped dolphins in the Ligurian Sea sanctuary. These data provide a robust measure of relative abundance that has been useful in indicating geographical distribution, and may, if extended into the future, reveal trends in population abundance. The data provided by this technique are best used in conjunction with other visually-collected data for such variables as group size. One of the ways in which data on seasonal and geographical distributions provided by acoustic techniques would be useful is in planning the geographical allocation of effort in large-scale dedicated sightings surveys and identifying areas of higher abundance and greater sensitivity.

Two refinements to the analysis techniques used are given below.

- (1) Logistic regression efficiently models relationships of a sigmoid form, but is not well-suited to the complex and often patchy distributions of animals. Methods based on Generalised Additive Models (Hastie and Tibshirani, 1990) provide flexibility in this respect, by incorporating non-parametric, smoothed functions with forms suggested by the data itself.
- (2) The collapsing of detection series to single group detections, as was done here, is simple to understand and easy to apply. However, an alternative approach, more consistent with a modelling framework and providing interpretable quantitative information, would be to incorporate an autoregressive component in the model.

This would allow adjustment to be made for the serial correlation in detections before testing other explanatory variables.

So far, only the data on vocalisations and noise levels noted in the field have been investigated. Analysis of the tape recordings made at the monitoring stations might yield improved results, especially if spectra of both signals and noise were to be measured. In the case of very characteristic signals, such as whistles, there are good prospects for using computer algorithms to detect and measure the signals (see e.g. Sturtivant and Datta, 1995). Although such machine methods are unlikely to be as sensitive as the human ear at detecting quiet signals, they do offer the very significant advantage of removing the element of human variability.

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REFERENCES

- Aguilar, A. 2000. Population biology, conservation threats and status of Mediterranean striped dolphins (*Stenella coeruleoalba*). *J. Cetacean Res. Manage.* 2(1):17-26. [This volume].
- Aguilar, A. and Raga, J.A. 1993. The striped dolphin epizootic in the Mediterranean Sea. *Ambio* 22(8):524-8.
- Archer, F.I. 1996. Morphological and genetic variation of striped dolphins (*Stenella coeruleoalba*, Meyen 1833). PhD Thesis, University of California, San Diego. 185pp.

- Baussant, T., Ibanez, F., Dallot, S. and Etienne, M. 1992. Diurnal mesoscale patterns of 50kHz scattering layers across the Ligurian Sea front (NW Mediterranean Sea). *Oceanol. Acta*. 15:3-12.
- Boucher, J., Ibanez, F. and Prieur, L. 1987. Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. *J. Mar. Res.* 45:133-73.
- Di Natale, A. and Notarbartolo di Sciara, G. 1994. A review of the passive fishing nets and trap fisheries in the Mediterranean Sea and of the cetacean bycatch. *Rep. int. Whal. Commn* (special issue) 15:189-202.
- Forcada, J., Aguilar, A., Hammond, P.S., Pastor, X. and Aguilar, R. 1994. Distribution and numbers of striped dolphins in the western Mediterranean Sea after the 1990 epizootic outbreak. *Mar. Mammal Sci.* 10(2):137-50.
- Forcada, J., Notarbartolo di Sciara, G. and Fabbri, F. 1995. Abundance of fin whales and striped dolphins summering in the Corso-Ligurian basin. *Mammalia* 59(1):127-40.
- Gannier, A. 1998a. Seasonal variation of the bathymetric distribution of cetaceans in the Liguro-Provençal basin (western Mediterranean). *Vie Milieu* 48(1):25-34.
- Gannier, A. 1998b. Une estimation de l'abundance du dauphin bleu et blanc *Stenella coeruleoalba* (Meyen 1833) dans le futur Sanctuaire Marin International de Méditerranée nord-occidentale. *Rev. Ecol. Terre Vie* 53:255-72.
- Gannier, A. 1999. Diel variations of the striped dolphin distribution off the French Riviera (Northwestern Mediterranean Sea). *Aquat. Mamm.* 25(3):123-34.
- Gannier, A. and Gannier, O. 1997. New results on the seasonal variation of cetaceans in the Liguro-Provençal basin. *Eur. Res. Cetaceans* [Abstracts] 11:91-4.
- Gordon, J.C.D. 1987. The behaviour and ecology of sperm whales off Sri Lanka. PhD Thesis, University of Cambridge. 347pp.
- Gordon, J. and Steiner, L. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. *Rep. int. Whal. Commn* 42:561-5.
- Gordon, J., Leaper, R., Hartley, F.G. and Chappell, O. (eds.). 1992. *Effects of Whale-Watching Vessels on the Surface and Underwater Acoustic Behaviour of Sperm Whales off Kaikoura, New Zealand. Science and Research Series* 52. 1st Edn. Department of Conservation, Wellington. 63pp.
- Gordon, J., Moscrop, A., Carlson, C., Ingram, S., Leaper, R., Matthews, J. and Young, K. 1998. Distribution, movements and residency of sperm whales off the Commonwealth of Dominica, Eastern Caribbean: implications for the development and regulation of the local whalewatching industry. *Rep. int. Whal. Commn* 48:551-7.
- Hastie, T.J. and Tibshirani, R.J. 1990. *Monographs on Statistics and Applied Probability*. 43. *Generalized Additive Models*. Chapman & Hall, London. 335pp.
- International Whaling Commission. 1994. Report of the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps. *Rep. int. Whal. Commn* (special issue) 15:1-71.
- Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. *FAO Species Identification Guide. Marine Mammals of the World*. FAO, Rome. 320pp.
- Kannan, K., Tanabe, S., Borrell, A., Aguilar, A., Focardi, S. and Tatsukawa, R. 1993. Isomer-specific analysis and toxic evaluation of polychlorinated biphenyls in striped dolphins affected by an epizootic in the western Mediterranean Sea. *Arch. Environ. Contam. Toxicol.* 25(2):227-33.
- McCullagh, P. and Nelder, J.A. 1983. *Generalized Linear Models*. Chapman and Hall, London. 261pp.
- Millot, C. 1987. Circulation in the Western Mediterranean Sea. *Oceanol. Acta*. 10:143-9.
- Nicholls, A.O. 1989. How to make biological surveys go further with generalised linear models. *Biol. Conserv.* 50:51-75.
- Norris, K.S. and Dohl, T.P. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Bull.* 77(4):821-49.
- Norušis, M.J. 1990. *SPSS/PC+ Advanced Statistics 4.0*. SPSS Inc., Chicago.
- Robel, R.J., Dick, D.J. and Krause, G.F. 1969. Regression coefficients used to adjust quail whistle counts. *J. Wildl. Manage.* 33(3):662-7.
- Sturtivant, C. and Datta, S. 1995. Techniques to isolate dolphin whistles and other tonal sounds from background noise. *Acoustic Letters* 18:189-93.
- Urick, R.J. 1983. *Principles of Underwater Sound*. 3rd Edn. McGraw Hill, Baskerville, New York. xiv+423pp.
- Watkins, W.A., Daher, M.A., DiMarzio, N.A., Samuels, A., Wartzk, D., Frstrup, K.M., Gannon, D.P., Howey, P.W., Maiefski, R.R. and Spraldin, T.R. 1999. Sperm whale surface activity from tracking by radio and satellite tags. *Mar. Mammal Sci.* 15:1158-80.
- Würsig, B., Cipriano, F. and Würsig, M. 1991. Dolphin movement patterns: information from radio and theodolite tracking studies. pp. 79-111. In: K. Pryor and K.N. Norris (eds.) *Dolphin Societies, Discoveries and Puzzles*. University of California Press, Oxford. LFS. 397pp.

Geographic and temporal comparison of skulls of striped dolphins off the Pacific coast of Japan

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ABSTRACT

Skulls of striped dolphins taken by the drive fishery off the Pacific coast of Japan in 1958-79 and 1992, and those taken by research vessels in offshore waters of the northwestern North Pacific in 1992 were examined to study the geographic and temporal differences that are expected to suggest the identity of stocks exploited by the fishery. Coastal specimens collected in 1958-79 showed distinct sexual dimorphism in rostral width, while no dimorphism was found in recent (1992) coastal specimens. Females showed more obvious variation among samples, and recent coastal specimens were distinct from others. The present results provide some support for the view that the drive fishery has exploited dolphins from plural coastal stocks, and that coastal dolphins currently taken by the Taiji fishery and offshore dolphins ranging east of 145°E do not belong to the same stock. The need to obtain larger sample sizes is stressed.

KEYWORDS: STRIPED DOLPHIN; DIRECT CAPTURE; MORPHOMETRICS; STOCK IDENTITY; NORTH PACIFIC

INTRODUCTION

Striped dolphins (*Stenella coeruleoalba*) have a long history of exploitation along the Pacific coast of Japan (e.g. Miyazaki, 1983; Kishiro and Kasuya, 1993). They were taken in large numbers by a drive fishery at the Izu Peninsula (Shizuoka Prefecture) during the 1960s, with over 10,000 animals killed each year (Kasuya, 1999). The catch had declined drastically by the 1980s and it is thought that the fishery may have depleted the population to below 10% of its size in the 1950s (IWC, 1993; Kishiro and Kasuya, 1993). The drive fishery at Taiji, which began in 1973 and which had been taking a few thousand striped dolphins each year, has also shown a recent decline (Kishiro and Kasuya, 1993).

At least three stocks of striped dolphins in the western North Pacific have been proposed from sightings surveys (Kasuya and Miyashita, 1989; Miyashita, 1993; 1997): (1) south of 30°N; (2) from 145°E to at least 180° and north of 30°N; and (3) in Japanese coastal waters between 30° and 42°N. Kasuya and Miyashita (1989) suggested that the latter two stocks are distinct, since a drastic decline in catch would not have occurred if the two had been a single stock. The International Whaling Commission's Scientific Committee agreed that the available data supported the existence of a coastal stock (IWC, 1993).

This paper compares the skull morphology of animals taken from inshore and offshore areas to determine whether there are morphological differences that support the stock differentiation proposed by Kasuya and Miyashita (1989) and Miyashita (1993). In addition, specimens taken by the Japanese drive fishery from 1958-1979 (i.e. from the peak of the catch to its decline) were examined to see whether there is any temporal variation in skull morphology that may indicate historical changes in exploited stocks.

MATERIALS AND METHODS

Samples

Recent (1982) specimens from the drive fishery were collected by researchers from the National Research Institute of Far Seas Fisheries (NRFSF) (Iwasaki and Kasuya, 1993).

Sixteen offshore specimens were obtained from dolphins harpooned during the research cruise of the *Shinhoyo-maru* from July to September 1992 (Fig. 1). Twenty-four coastal specimens were collected under scientific supervision from the dolphins driven at Taiji (Iwasaki and Kasuya, 1993). Skulls were selectively taken from larger dolphins (body length 216-257cm). All of these specimens were prepared and deposited at the National Science Museum, Tokyo (NSMT).

Fifty-six striped dolphin skull specimens stored in the NSMT and the Museum of Comparative Zoology, Harvard University (MCZ) were also examined. Five of these were collected in the offshore area of the northwestern North Pacific between 1982 and 1984. Assuming there was no temporal variation in the proposed offshore group, these animals were added to that group. The other skulls were collected at the Izu Peninsula between 1958 and 1970, and at Taiji between 1969 and 1979, from when the drive fishery was at its peak through to the decline in captures.

For the coastal 1958-79 group, a comparison of measurements between localities (i.e. Izu vs. Taiji) and between year groups yielded no significant heterogeneity among them, apart from the fact that sexual dimorphism in rostrum width was more distinct in the 1978-79 Taiji sample. No significant sexual dimorphism was found in the other samples, but it is possible that the small sample sizes affected the analyses. In this study, all the 1958-79 coastal samples have been pooled into a single group.

A total of 74 specimens had teeth and the age of these animals was obtained following the method given in Kasuya (1976). Ito and Miyazaki (1990) stated that skull growth of this species ceases around three years of age, and therefore only specimens older than three years were used in the analyses. Fifteen specimens whose teeth were not available were included as they had obviously reached adult size and exhibited distal fusion of premaxilla and maxilla.

The age composition of each of the three groups (coastal 1958-79; coastal 1992; offshore) was comparable in females but not in males. The coastal 1958-79 males were older than those in the offshore sample (Kruskal-Wallis test, $p < 0.05$).

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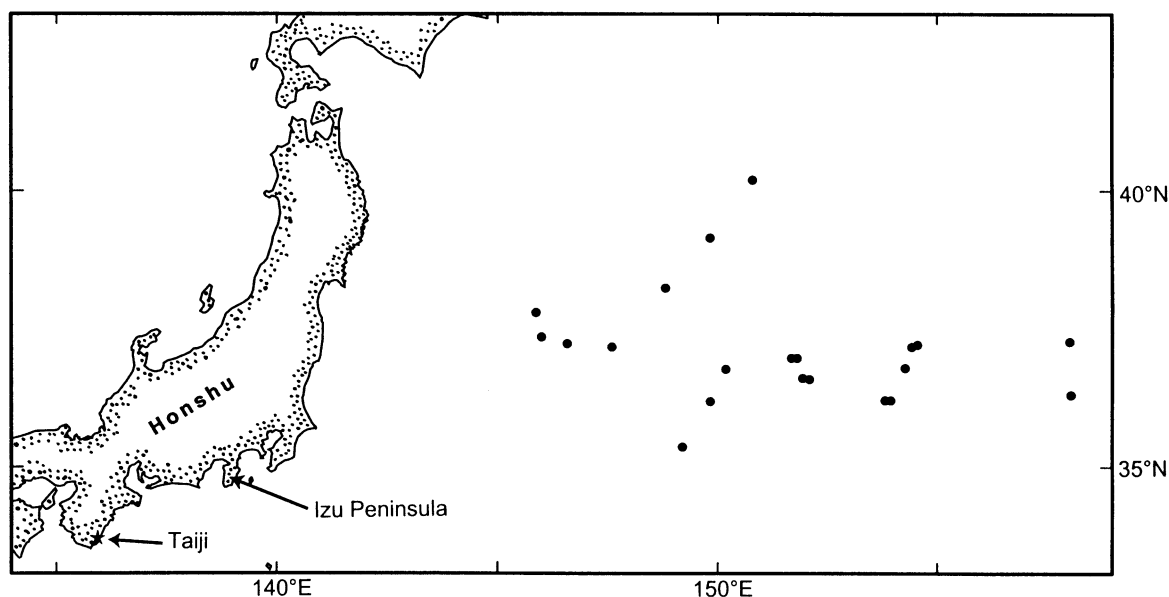


Fig. 1. Sampling localities of striped dolphins.

Twenty-five specimens lacked gender data. This was determined using sexual differences in the supraoccipital crest (Ito and Miyazaki, 1990); the supraoccipital protrudes forward over the frontal and its upper surface is smooth in adult females, whereas in adult males the surface of the vertex is rough and the overhang of the supraoccipital appears fused and indistinct. This approach was tested with 64 known-sex specimens and all specimens were correctly identified to sex.

All specimens examined are listed in Appendix Table 1. The available sample sizes by sex for each group are summarised in Table 1.

Table 1

Sample sizes used in this study. Note: not all skull characters could be measured in each specimen.

Group	Females	Males	Total
Coastal, 1958-79	19	25	44
Coastal, 1992	10	14	24
Offshore	8	13	21

Characters

A total of 39 characters were measured (Table 2). The rostra of most specimens were more or less separated distally, and although the measurements were taken with the rostrum laterally compressed, the distal measurement (WRT) did not seem to be appropriately corrected. Under these circumstances, the width of the gap on the palatal surface at one third of the length of the rostral length was measured, and a corrected WRT obtained by subtraction of this width.

Analyses

Skull measurements of the three groups (coastal 1958-79; coastal 1992; offshore) were compared using the non-parametric Mann-Whitney test and Kruskal-Wallis test with Tukey-type multiple comparison methods (Zar, 1996), in order to reduce the effect of small sample sizes. Analysis of covariance (ANCOVA) with the condylobasal length as a

covariate was also carried out with *post hoc* comparisons utilising non-parametric methods. Canonical discriminant analysis after stepwise character selection was carried out for each sex using the STEPDISC and CANDISC procedures (SAS Inst. Inc., 1989).

RESULTS

Sexual dimorphism

Sexual dimorphism was found in a number of characters, although this varied among the three samples (Table 3, Appendix Table 2). Distinct sex-related differences in the distal width of the rostrum were found in the coastal 1958-79 group by both univariate tests and ANCOVAs. No significant correlations between any rostral width measurements and age were found in any individual group or in all groups combined (Kendall's rank correlation, $p > 0.05$; Fig. 2).

Temporal and geographic variation

Significant differences among groups were found in the rostrum of females in both absolute and relative comparisons (Tables 4 and 5). Animals in the 1958-79 coastal group have narrower rostra than those in the 1992 coastal group. The width of the rostrum at half-length differed absolutely and relatively in both sexes, being wider in the coastal 1992 group than the coastal 1958-79 group.

Although the sample size was small, 1992 coastal females were almost completely separate on the first canonical variate axes (Fig. 3). Animals from the 1958-79 coastal and offshore groups could not be distinguished. The overlap was greater for males, although each group showed some degree of dispersion from each other (Fig. 3). No canonical discriminant scores showed significant correlations with age (Kendall's rank correlation, $p > 0.05$).

DISCUSSION

Distinct sexual dimorphism in the width of the rostrum was found in the 1958-79 coastal group, supporting the finding of Ito and Miyazaki (1990). Geographical/temporal comparisons revealing a narrower rostral width in the 1958-79 coastal females suggested that sexual dimorphism

Table 2
Skull measurements of striped dolphins.

1	Condylbasal length - from tip of rostrum to hindmost margin of occipital condyles (CBL)
2	Length of rostrum - from tip to line across hindmost limits of antorbital notches (LR)
3	Width of rostrum at base - along line across hindmost limits of antorbital notches (WRB)
4	Width of rostrum at 60mm anterior to line across hindmost limits of antorbital notches (WR6)
5	Width of rostrum at mid-length (WRH)
6	Width of premaxillaries at mid-length of rostrum (WPH)
7	Width of rostrum at $\frac{3}{4}$ length, measured from posterior end (WRT)
8	Distance from tip of rostrum to external nares - to mesial end of anterior transverse margin of right nares (TE)
9	Distance from tip of rostrum to internal nares - to mesial end of posterior margin of right pterygoid (TI)
10	Greatest pre-orbital width (PROW)
11	Greatest post-orbital width (POOW)
12	Least supra-orbital width (SOW)
13	Greatest width of external nares (WEN)
14	Greatest width across zygomatic processes of squamosal (ZW)
15	Greatest width of premaxillaries (GWP)
16	Greatest parietal width, within post-temporal fossae (PW)
17	Internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline (LBC)
18	Greatest length of post-temporal fossa, measured to external margin of raised suture (LPTF)
19	Greatest width of post-temporal fossa at right angles to greatest length (WPTF)
20	Length of left orbit - from apex of preorbital process of frontal to apex of post-orbital process (LOB)
21	Length of antorbital process of left lacrimal (LLA)
22	Greatest width of internal nares (WIN)
23	Greatest length of bulla of left tympanoperiotic (LB)
24	Greatest length of periotic of left tympanoperiotic (LP)
25	Length of upper left tooth row - from hindmost margin of hindmost alveolus to tip of rostrum (LUTR)
26	Number of teeth - upper left (NTUL)
27	Number of teeth - upper right (NTUR)
28	Number of teeth - lower left (NTLL)
29	Number of teeth - lower right (NTLR)
30	Length of lower left tooth row - from hindmost margin of hindmost alveolus to tip of mandible (LLTR)
31	Greatest length of left ramus (LRAM)
32	Greatest height of left ramus at right angles to greatest length (HRAM)
33	Length of left mandibular fossa, measured to mesial rim of internal surface of condyle (LMF)
34	Length of basihyal along midline (LBH)
35	Greatest width of basihyal (WBH)
36	Greatest width of left thyrohyal proximally (WTH)
37	Greatest length of left thyrohyal (LTH)
38	Greatest width of left stylohyal (WSH)
39	Greatest length of left stylohyal (LSH)

Table 3

Significantly different skull measurements (mm, log-transformed; $p < 0.05$) between sexes of striped dolphins from the western North Pacific revealed by analysis of covariance with Mann-Whitney test using condylbasal length as a covariate.

Measurements	Coastal, 1958-79					Coastal, 1992					Offshore, 1992				
	Female		Male		<i>p</i>	Female		Male		<i>p</i>	Female		Male		<i>p</i>
	N	Mean	N	Mean		N	Mean	N	Mean		N	Mean	N	Mean	
4 WR6	19	1.870	24	1.887	0.017	-	-	-	-	-	8	1.881	13	1.903	0.023
5 WRH	19	1.780	24	1.797	0.009	-	-	-	-	-	-	-	-	-	-
6 WPH	19	1.468	24	1.508	0.001	-	-	-	-	-	8	1.490	13	1.530	0.008
7 WRT	17	1.647	23	1.672	0.046	-	-	-	-	-	-	-	-	-	-
8 TE	19	2.508	24	2.504	0.046	-	-	-	-	-	-	-	-	-	-
19 WPTF	18	1.632	24	1.659	0.029	-	-	-	-	-	-	-	-	-	-
22 WIN	-	-	-	-	-	-	-	-	-	-	8	1.793	13	1.808	0.046
34 LBH	15	1.647	13	1.683	0.048	10	1.666	12	1.703	0.006	-	-	-	-	-
36 WTH	-	-	-	-	-	10	1.369	13	1.389	0.032	-	-	-	-	-

in the 1958-79 coastal group was a result of a narrower rostrum in females, rather than a wider rostrum in males. Although the 1992 offshore group showed significant differences in two of the rostral width measurements (WRH and WPH), all of the measurements had smaller means for females, and it is possible that additional significant differences would be detected if the sample size was larger. The 1992 coastal group showed no sexual differences in the rostrum (Table 3).

It is possible that ontogenetic variation affected the above difference in females, since the recent specimens were taken selectively from larger dolphins. However, the ages of recent coastal specimens were not significantly greater than earlier

animals. In addition, no significant correlations were found between rostral measurements and age. It seems reasonable to conclude that sexual dimorphism in the rostrum was present in the striped dolphins taken off the Pacific coast of Japan between the 1950s and 1970s, but appeared to be absent in those taken in 1992. However, the possibility that the small recent sample size was responsible for this cannot be completely ruled out. Why such a difference may have occurred is an interesting question.

Archer (1996) reported clear sexual dimorphism in the rostrum width of striped dolphins from the eastern Pacific and the western Pacific. He also found statistically significant sexual differences between the eastern Atlantic

and Mediterranean striped dolphins. In the eastern tropical Pacific, *Stenella attenuatata* and *S. longirostris* are also sexually dimorphic (Perrin, 1975; Schnell *et al.*, 1985; Douglas *et al.*, 1986; 1992). Females of both species were reported to possess attenuated rostra. This suggests a similar selective pressure in these species, which may be related to partitioning of feeding habits or male-male competition.

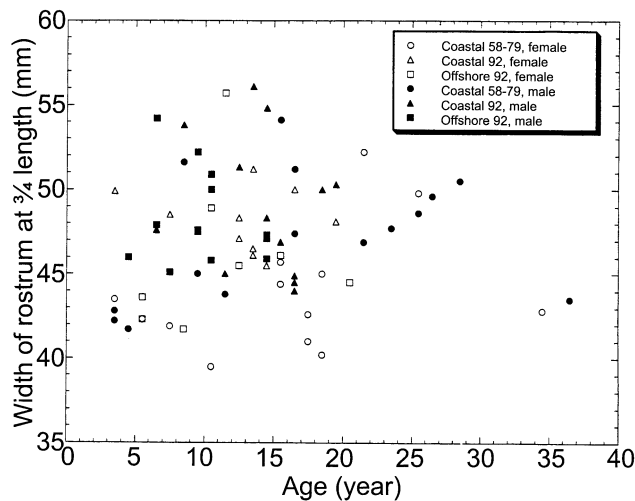


Fig. 2. Relationships between age and width of rostrum at $\frac{3}{4}$ length of striped dolphins from the northwestern North Pacific.

Geographic/temporal differences were more obvious in females than males. This is illustrated on the scatterplots of canonical variates, in which most of the 1992 female coastal specimens could be identified from the others on the first axis that had a large WPH and WIN component (Fig. 3, Table 6). By contrast, males showed less variation and considerable overlap. However, even in males the measurements of rostral width were larger in the 1992 coastal group than in the 1958-79 group (Tables 2, 4, 5).

Clear differences were found between the 1958-79 and 1992 coastal groups, particularly for females. At least two potential explanations present themselves: (1) that the populations exploited by the drive fishery off the Pacific coast of Japan differed at the peak of the catch and in recent years; (2) that the same population has been exploited over time, but its morphology has changed with the decline in the population. For striped dolphins from the Izu Peninsula, the age at sexual maturity in females in the catch declined and the calving interval shortened between the 1950s and 1970s; it has been suggested that this was a density-dependent effect caused by improvement in nutritional condition with population depletion (Kasuya, 1985). There were insufficient specimens in the present sample to examine for temporal trends over the 1958-79 period. However, it seems unlikely that the widening of the rostrum in females, which would require strong selective pressure, could occur over such a short period. It is more plausible that the drive fishery has exploited more than one population over the last four decades. This is consistent with the view of Kasuya (1999),

Table 4

Significantly different skull measurements (mm, $p < 0.05$) among three groups of striped dolphins from the western North Pacific revealed by Kruskal-Wallis test.

Measurements	Coastal, 1958-79		Coastal, 1992		Offshore, 1992		<i>p</i>	Direction of difference*
	N	Mean	N	Mean	N	Mean		
Females								
4 WR6	19	74.2	10	79.7	8	75.8	0.007	CR>CO
5 WRH	19	60.3	10	66.6	8	62.1	<0.001	CR>CO
6 WPH	19	29.5	10	34.1	8	30.9	<0.001	CR>CO, O
7 WRT	17	44.5	10	48.1	8	46.0	0.016	CR>CO
22 WIN	19	61.5	10	65.3	8	61.9	0.028	CR>CO
27 NTUR	15	46.1	8	45.3	7	48.6	0.018	O>CR
35 WBH	15	49.2	10	52.5	8	47.9	0.026	CR>O
Males								
6 WRH	24	62.8	14	66.9	13	65.3	0.008	CR>CO
21 LLA	25	57.5	14	61.1	13	58.8	0.033	CR>CO

* CO, coastal 1958-79; CR, coastal 1992; O, offshore samples.

Table 5

Significantly different skull measurements (mm, log-transformed; $p < 0.05$) among three groups of striped dolphins from the western North Pacific revealed by analysis of covariance with Kruskal-Wallis test using condylobasal length as a covariate.

	Coastal, 1958-79		Coastal, 1992		Offshore, 1992			Direction of difference*
Measurements	N	Mean	N	Mean	N	Mean	<i>p</i>	
Females								
4 WR6	19	1.872	10	1.899	8	1.877	0.011	CR>CO
5 WRH	19	1.781	10	1.822	8	1.791	<0.001	CR>CO
6 WPH	19	1.468	10	1.531	8	1.488	<0.001	CR>CO, O
7 WRT	17	1.648	10	1.681	8	1.661	0.031	CR>CO
35 WBH	15	1.691	10	1.718	8	1.680	0.020	CR>O
Males								
5 WRH	24	1.800	14	1.822	13	1.813	0.035	CR>CO
8 TE	24	2.510	14	2.512	13	2.517	0.018	O>CO
17 LBC	24	2.063	14	2.064	13	2.053	0.003	CR>O

*CO, coastal 1958-79; CR, coastal 1992; O, offshore samples.

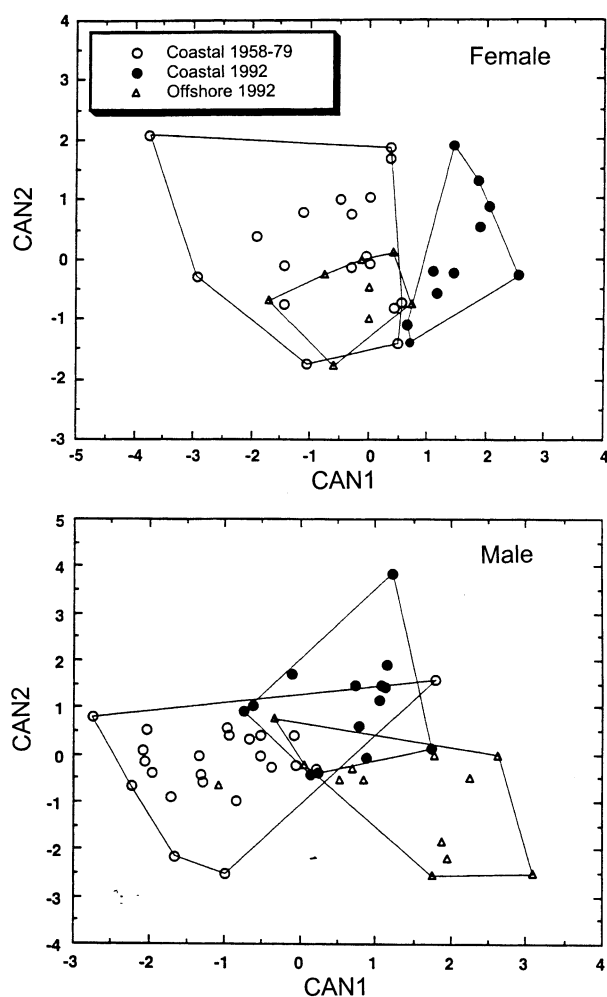


Fig. 3. Scatter plots of the first and second canonical variates for the three samples of striped dolphins off the Pacific coast of Japan.

Table 6

Standardised canonical coefficients for the first and second canonical axes.

Measurements	CAN1	CAN2
Females		
6 WPH	0.917	-0.355
17 LBC	-0.114	0.979
22 WIN	0.817	0.313
32 HRAM	-0.584	-0.663
Males		
2 LR	-2.103	1.535
5 WRH	0.449	0.626
8 TE	2.596	-2.035
14 ZW	0.769	0.065
16 PW	-0.945	0.212
17 LBC	-0.697	0.334
20 LOB	-0.038	0.586
21 LLA	0.550	0.606
22 WIN	-0.115	-0.819

who reviewed the available information and suggested that at least two coastal populations were taken in the drive fishery at Taiji. Loganathan *et al.* (1990) compared the organochlorine residue levels between animals taken in the drive fishery in 1978-79 and 1986 and found that the PCB and DDT levels remained similar while HCHs and HCB declined significantly. Although this may reflect a decline of HCHs and HCB in the environment, HCHs are thought to be removed slowly from the open ocean (Tanabe and

Tatsukawa, 1983), and the differences in the levels of HCHs and HCB may indicate inter-population differences and not temporal trends.

The stock identity of the dolphins taken in the present Taiji fishery is of particular importance for management (IWC, 1993). Two genetic studies using the same sample sets as the present study failed to find a significant difference between offshore and Taiji dolphins in the mitochondrial DNA control region (RFLP, Sasaki and Numachi, 1997; sequence analysis, Yoshida and Iwasaki, 1997). This may reflect small sample sizes compared to the number of haplotypes found and, whilst significant differences in genetic data reveal different populations, the absence of detected differences cannot be assumed to imply a single stock. Although the present study implies that the striped dolphins taken recently at Taiji do not belong to the same stock as dolphins sighted in offshore waters east of 145°E, the small sample size precludes firm conclusions being drawn. The present results are not in conflict with the hypothesis that they may be members of the southern stock normally found south of 30°N (Kasuya and Miyashita, 1989; Miyashita, 1993) that is expanding northwards due to the decline of northern coastal stocks as suggested by Kasuya (1999).

Based on sightings data, Miyashita (1997) suggested that the offshore stock may move southwestwards into the Izu fishing ground from autumn to winter. This could not be investigated here as all recent specimens were from Taiji. If Kasuya and Miyashita (1989) are correct in suggesting that the catch in Izu decreased too drastically for the coastal stock to range far offshore, the offshore stock must not have been involved in the coastal drive fisheries. Further studies using genetic as well as morphological comparisons with larger sample sizes are required to answer the question of the stock identity of dolphins taken in the drive fishery.

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REFERENCES

- Archer, F.I. 1996. Morphological and genetic variation of striped dolphins (*Stenella coeruleoalba*, Meyen 1833). Ph.D. Thesis, University of California, San Diego. 185pp.
- Douglas, M.E., Schnell, G.D. and Hough, D.J. 1986. Variation in spinner dolphins (*Stenella longirostris*) from the eastern tropical Pacific Ocean: sexual dimorphism in cranial morphology. *J. Mammal.* 67:537-44.
- Douglas, M.E., Schnell, G.D., Hough, D.J. and Perrin, W.F. 1992. Geographic variation in cranial morphology of spinner dolphins *Stenella longirostris* in the Eastern Tropical Pacific Ocean. *Fish. Bull.* 90(1):54-76.
- International Whaling Commission. 1993. Report of the Scientific Committee, Annex G. Report of the sub-committee on small cetaceans. *Rep. int. Whal. Commn* 43:130-45.
- Ito, H. and Miyazaki, N. 1990. Skeletal development of the striped dolphin (*Stenella coeruleoalba*) in Japanese waters. *J. Mammal. Soc. Jpn* 14(2):79-96.

- Iwasaki, T. and Kasuya, T. 1993. Biological information of striped dolphins off Japan taken for research purposes in 1992. Paper SC/45/SM5 presented to the IWC Scientific Committee, April 1993 (unpublished). 12pp. [Paper available from the Office of this Journal].
- Kasuya, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. *Sci. Rep. Whales Res. Inst., Tokyo* 28:73-106.
- Kasuya, T. 1985. Effect of exploitation on reproductive parameters of the spotted and striped dolphins off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 36:107-38.
- Kasuya, T. 1999. Review of biology and exploitation of striped dolphins off Japan. *J. Cetacean Res. Manage.* 1:81-100.
- Kasuya, T. and Miyashita, T. 1989. Japanese dolphin fisheries and stock management. *Sai. Shi. [Coll. Breed.]* 51(4):154-60. [In Japanese].
- Kishiro, T. and Kasuya, T. 1993. Review of Japanese dolphin drive fisheries and their status. *Rep. int. Whal. Commn* 43:439-52.
- Loganathan, B.G., Tanabe, S., Tanaka, H., Watanabe, S., Miyazaki, N., Amano, M. and Tatsukawa, R. 1990. Comparison of organochlorine residue levels in the striped dolphin from western North Pacific, 1978-79 and 1986. *Mar. Poll. Bull.* 21(9):435-9.
- Miyashita, T. 1993. Abundance of dolphin stocks in the western North Pacific taken by the Japanese drive fishery. *Rep. int. Whal. Commn* 43:417-37.
- Miyashita, T. 1997. Seasonal distribution changes of striped dolphins in the western North Pacific. Paper SC/49/SM14 presented to the IWC Scientific Committee, September 1997, Bournemouth (unpublished). 12pp. [Paper available from the Office of this Journal].
- Miyazaki, N. 1983. Catch statistics of small cetaceans taken in Japanese waters. *Rep. int. Whal. Commn* 33:621-31.
- Perrin, W.F. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. *Bull. Scripps Inst. Oceanogr. Univ. Calif.* 21:1-206.
- Sasaki, H. and Numachi, K. 1997. Genetic examination of population structure of striped dolphins distributed in the coastal and offshore waters of Japan. Paper SC/49/SM38 presented to the IWC Scientific Committee, September 1997, Bournemouth (unpublished). 9pp. [Paper available from the Office of this Journal].
- SAS Inst. Inc. 1989. *SAS/STAT User's Guide, Version 6*. 4th Edn. SAS Institute Inc, Cary, NC. 846pp.
- Schnell, G.D., Douglas, M.E. and Hough, D.J. 1985. Sexual dimorphism in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. *Mar. Mammal Sci.* 1(1):1-14.
- Tanabe, S. and Tatsukawa, R. 1983. Vertical transport and residence time of chlorinated hydrocarbons in the open ocean water column. *J. Oceanogr. Soc. Jpn.* 39:53-62.
- Yoshida, H. and Iwasaki, T. 1997. A preliminary analysis of mitochondrial DNA in striped dolphins off Japan. Paper SC/49/SM41 presented to the IWC Scientific Committee, September 1997, Bournemouth (unpublished). 7pp.
- Zar, J.H. 1996. *Biostatistical Analysis, 3rd Edition*. Prentice-Hall, Inc., New Jersey. 662pp.

Appendix 1

Table 1
Specimens examined.
NSMT - National Science Museum, Tokyo; MCZ - Museum of Comparative Zoology, Harvard University.

Coastal 1958-79	
NSMT	M19774, M19775, M19776, M19777, M19778, M19779, M19780, M19781, M19782, M19785, M19786, M19787, M19789, M19790, M19791, M21389, M21392, M21393, M24620, M24621, M24622, M24640, M24644, M24645, M24650, M24700, M24704, M24705, M24706, M24744, M24833, M24834, M24838, M24839, M24844, M24916, TK326(not registered)
MCZ	52310, 52311, 52312, 52313, 52314, 52315, 52316, 52319
Coastal 1992	
NSMT	M29739, M29740, M29741, M29742, M29743, M29744, M29745, M29746, M29747, M29748, M29749, M29750, M29751, M29752, M29753, M29754, M29755, M29756, M29757, M29758, M29759, M29760, M29761, M29762
Offshore 1992	
NSMT	M25187, M26235, M26236, M26237, M26239, M29721, M29722, M29723, M29724, M29725, M29727, M29729, M29730, M29731, M29732, M29733, M29734, M29735, M29736, M29737, M29738

Table 2

Measurement values for skull morphology of three samples of striped dolphins from the northwestern North Pacific, with sexually dimorphic characters (Mann-Whitney test, $p < 0.05$) indicated.

Measurements	N	Mean	Female		N	Mean	Male		Difference <i>p</i>
			SD	Range			SD	Range	
Coastal, 1958-79									
1. CBL	19	456.6	16.08	422.7-486.8	24	458.1	17.05	429.6-504.4	0.013
2. LR	19	267.8	11.57	239.9-292.4	24	266.8	12.40	239.3-293.2	
3. WRB	19	113.4	5.97	103.4-124.3	25	114.7	5.70	102.0-124.4	
4. WR6	19	74.2	3.88	67.3-82.9	25	77.3	3.46	72.0-82.9	
5. WRH	19	60.3	3.18	56.0-68.8	24	62.8	2.84	58.2-68.5	0.007
6. WPH	19	29.5	3.24	20.4-34.5	24	32.3	1.67	29.0-35.9	0.001
7. WRT	17	44.5	3.61	39.5-52.2	23	47.1	3.67	41.7-54.1	0.033
8. TE	19	321.3	13.51	289.5-347.2	24	320.2	14.74	289.7-353.2	0.042
9. TI	19	328.3	12.76	300.6-354.0	22	327.1	16.00	291.2-361.9	
10. PROW	19	201.5	9.11	186.0-221.0	25	203.1	8.46	189.5-218.0	
11. POOW	19	221.4	8.84	205.7-237.5	25	224.4	9.63	208.2-249.9	
12. SOW	19	198.5	8.45	183.4-214.6	25	201.0	7.98	189.5-217.0	
13. WEN	19	48.8	2.64	44.8-53.6	25	48.3	2.02	42.7-50.7	
14. ZW	19	217.0	8.09	202.5-232.8	25	219.5	9.72	202.7-243.2	
15. GWP	19	86.4	4.38	78.5-96.4	25	86.4	3.68	79.1-93.3	
16. PW	18	189.1	7.58	171.4-199.0	24	189.3	7.41	176.8-207.9	
17. LBC	19	114.6	4.48	107.8-124.7	25	115.1	3.28	109.2-122.6	
18. LPTF	18	67.1	5.68	57.9-79.5	25	70.5	4.80	63.2-81.7	
19. WPTF	18	43.0	4.15	36.1-54.4	25	45.6	4.65	38.9-56.5	
20. LOB	19	58.6	3.42	52.5-64.4	25	58.8	3.73	53.6-66.6	
21. LLA	19	57.4	4.84	48.5-64.4	25	57.5	3.39	51.1-65.0	
22. WIN	19	61.5	3.03	56.6-66.6	25	63.1	3.17	57.0-70.5	
23. LB	13	32.1	1.14	29.8-33.7	14	32.0	1.63	29.9-36.1	
24. LP	13	29.6	1.17	27.6-31.6	14	30.3	1.34	28.8-33.2	
25. LUTR	18	234.4	11.68	207.4-255.3	24	232.8	10.76	206.9-257.0	
26. NTUL	16	46.6	1.93	43-50	18	49.2	2.65	45-56	0.005> <i>p</i> >0.002
27. NTUR	15	46.1	2.10	43-50	18	48.9	2.40	45-54	0.005> <i>p</i> >0.002
28. NTLL	17	45.4	1.67	43-49	20	48.0	2.58	43-52	0.005> <i>p</i> >0.002
29. NTLR	18	45.8	1.77	42-49	21	48.1	2.59	44-53	0.006
30. LLTR	17	232.5	7.66	216.4-245.0	23	231.8	12.78	210.5-253.0	0.05> <i>p</i> >0.02
31. LRAM	18	393.3	14.02	357.9-419.5	23	391.7	17.17	365.8-426.8	
32. HRAM	18	70.2	2.87	63.4-75.0	23	70.9	3.68	65.0-80.3	
33. LMF	18	129.9	6.37	118-144.4	23	130.2	7.85	115.7-145.1	
34. LBH	15	44.5	4.35	38.0-52.7	13	48.5	4.89	39.4-54.5	
35. WBH	15	49.2	4.91	42.0-58.5	13	50.4	6.24	41.8-63.4	
36. WTH	15	23.3	2.37	20.0-28.6	13	23.4	2.64	19.0-28.0	
37. LTH	15	69.3	6.14	55.0-80.4	13	69.2	6.51	61.0-81.0	
38. WSH	13	17.5	1.75	15.8-21.4	13	17.4	1.77	15.0-20.4	
39. LSH	13	88.1	6.66	77.3-100.1	13	86.1	5.31	78.0-96.2	
Coastal, 1992									
1. CBL	10	462.2	17.73	425.0-488.1	14	467.2	9.27	451.0-485.0	
2. LR	10	271.0	11.48	246.8-287.3	14	272.7	8.93	256.9-292.9	
3. WRB	10	117.3	3.88	112.1-123.8	14	115.7	4.57	107.3-122.5	
4. WR6	10	79.7	3.18	74.0-84.4	14	80.1	4.42	73.9-91.2	
5. WRH	10	66.6	2.18	63.6-70.8	14	66.9	4.70	57.7-75.4	
6. WPH	10	34.1	1.62	32.0-37.0	14	34.2	3.10	29.6-40.0	
7. WRT	10	48.1	1.86	45.5-52.1	13	49.0	4.08	44.0-56.1	
8. TE	10	325.9	14.73	292.7-343.7	14	329.0	11.51	306.8-354.1	
9. TI	10	328.4	16.57	293.3-351.6	14	330.0	8.53	311.0-343.9	
10. PROW	10	208.3	5.83	196.9-214.7	14	207.7	5.45	197.1-218.9	
11. POOW	10	228.1	6.58	214.9-235.1	14	227.6	5.87	219.3-244.4	
12. SOW	10	205.1	6.59	191.9-211.9	14	204.0	5.84	195.8-220.1	
13. WEN	10	50.3	2.03	47.0-53.2	14	50.1	2.57	46.4-54.0	
14. ZW	10	223.4	6.84	210.1-230.5	14	225.8	6.84	216.8-241.4	
15. GWP	10	87.4	3.97	82.5-94.1	14	89.1	2.92	84.3-96.0	
16. PW	10	192.6	6.21	184.0-202.3	14	189.3	7.62	176.2-207.0	
17. LBC	10	114.7	4.08	110.5-121.7	14	116.7	3.66	110.0-121.4	
18. LPTF	10	69.2	4.43	61.2-75.8	14	69.3	5.04	61.8-80.9	
19. WPTF	10	45.0	3.73	39.5-51.4	14	44.3	3.74	37.9-50.4	
20. LOB	10	59.5	2.71	56.0-63.2	14	60.2	2.77	55.9-66.0	
21. LLA	10	60.0	6.05	51.1-70.1	14	61.1	4.26	54.2-69.1	
22. WIN	10	65.3	3.57	60.4-71.4	14	63.3	2.53	59.0-68.8	
23. LB	10	32.1	1.53	30.2-35.0	13	31.9	1.35	29.5-35.2	

continued

Table 2 cont.

Measurements	Female				Male				Difference <i>p</i>
	N	Mean	SD	Range	N	Mean	SD	Range	
24. LP	10	29.7	1.04	28.5-32.0	14	30.0	1.24	28.3-32.4	0.05> <i>p</i> >0.02
25. LUTR	10	233.7	10.41	212.7-245.2	14	238.1	7.72	225.0-251.1	
26. NTUL	8	45.8	2.38	42-50	14	48.7	2.73	44-54	
27. NTUR	8	45.3	2.49	43-50	14	48.0	2.80	43-53	
28. NTLL	10	44.9	2.81	42-49	14	46.9	2.73	41-52	
29. NTLR	10	44.6	2.95	41-50	14	47.0	2.75	42-51	0.005> <i>p</i> >0.002
30. LLTR	10	234.0	14.22	207.7-256.1	14	235.4	8.67	215.8-249.9	
31. LRAM	10	398.0	16.37	363.2-419.3	14	399.9	9.07	382.2-415.1	
32. HRAM	10	69.8	3.26	64.5-74.2	14	72.1	2.62	67.0-76.1	
33. LMF	10	132.2	5.45	121.5-138.9	14	132.8	8.94	120.0-149.6	
34. LBH	10	46.5	3.14	41.3-50.3	12	50.5	2.90	43.0-53.8	0.05> <i>p</i> >0.02
35. WBH	10	52.5	3.32	49.0-60.0	12	51.0	4.52	42.7-57.8	
36. WTH	10	23.3	1.76	20.6-26.7	13	24.6	1.31	22.0-27.6	
37. LTH	10	71.3	4.85	63.2-77.9	13	72.3	4.41	65.8-81.2	
38. WSH	10	17.9	1.24	16.1-20.0	14	17.3	1.30	15.6-19.8	
39. LSH	10	89.2	4.86	82.2-94.9	14	91.0	6.17	81.1-101.0	
Offshore, 1992									
1. CBL	8	461.1	11.8	446.8-481.4	13	465.2	15.85	442.0-510.9	0.05> <i>p</i> >0.02
2. LR	8	272.3	11.64	257.9-293.3	13	273.5	10.27	261.4-302.0	
3. WRB	8		5.87	105.8-122.0	13	116.0	6.45	108.1-127.7	
4. WR6	8	75.8	5.67	71.1-88.2	13	80.5	4.71	75.7-89.0	
5. WRH	8	62.1	4.76	55.8-71.0	13	65.3	3.11	60.5-70.8	
6. WPH	8	30.9	1.88	27.2-33.7	13	34.1	2.38	30.2-37.5	0.005> <i>p</i> >0.002
7. WRT	8	46.0	4.52	41.7-55.7	13	48.3	2.75	45.1-54.2	
8. TE	8	327.7	10.85	314.6-345.6	13	331.2	12.25	317.7-366.0	
9. TI	8	332.1	10.41	318.6-353.1	13	332.2	12.54	314.9-368.0	
10. PROW	7	203.4	7.33	193.0-213.8	13	206.6	6.88	197.0-221.2	
11. POOW	8	222.4	5.08	214.4-231.2	13	227.2	9.41	209.6-244.1	
12. SOW	8	199.0	6.66	188.8-208.7	13	203.6	8.36	190.0-220.8	
13. WEN	8	48.7	1.11	46.5-50.0	13	49.4	2.86	45.0-53.8	
14. ZW	8	218.6	5.35	212.0-226.9	13	224.1	8.43	209.0-237.7	
15. GWP	8	84.8	4.92	77.7-90.7	13	88.8	4.34	81.3-96.1	
16. PW	8	186.5	7.48	174.4-196.3	13	186.4	5.33	175.9-192.1	
17. LBC	8	112.5	3.33	106.0-117.3	13	113.4	3.98	104.9-119.7	
18. LPTF	8	69.5	3.12	66.3-74.0	13	71.6	3.45	65.7-76.5	
19. WPTF	8	44.6	2.74	40.0-48.6	13	45.0	3.86	37.6-51.5	
20. LOB	8	56.7	2.14	53.3-60.5	13	58.2	2.89	52.2-62.1	
21. LLA	8	57.3	1.87	54.6-61.0	13	58.8	2.61	54.9-62.1	
22. WIN	8	61.9	2.55	57.9-65.0	13	64.5	2.07	61.6-68.3	
23. LB	8	32.0	1.01	30.5-33.7	13	32.8	1.48	29.4-35.9	
24. LP	8	29.9	1.42	28.7-32.9	13	30.4	1.55	27.2-32.7	
25. LUTR	8	238.4	8.87	228.7-255.9	13	238.3	9.44	228.0-266.2	
26. NTUL	7	48.1	2.12	46-52	13	47.7	2.50	43-52	
27. NTUR	7	48.6	1.27	47-51	13	48.0	2.48	43-53	
28. NTLL	7	48.0	2.31	45-51	13	46.8	2.41	43-51	
29. NTLR	7	47.7	2.43	45-52	13	46.8	2.19	43-51	
30. LLTR	8	231.8	7.23	223.1-243.0	13	234.5	8.08	222.9-255.0	
31. LRAM	8	393.4	7.90	380.0-406.0	13	396.5	13.18	378.2-431.0	
32. HRAM	8	70.7	3.10	66.7-74.2	13	71.2	2.81	65.5-76.0	
33. LMF	8	131.0	3.57	127.9-138.9	13	129.9	8.08	120.1-144.0	
34. LBH	8	45.1	3.41	40.6-51.3	10	46.8	4.37	39.6-52.7	
35. WBH	8	47.9	2.04	45.6-51.3	10	46.8	4.29	40.6-53.1	
36. WTH	8	23.1	2.02	21.1-26.8	11	23.1	2.67	19.5-28.4	
37. LTH	8	69.6	4.03	63.2-75.9	11	67.2	5.8	58.6-75.4	
38. WSH	7	18.2	2.38	14.8-21.5	11	16.4	2.38	12.7-21.6	
39. LSH	7	89.1	5.79	82.4-97.8	11	87.5	7.78	73.0-100.2	

Capture-recapture estimation of bowhead whale population size using photo-identification data

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ABSTRACT

Statistical models and maximum likelihood methods are developed for estimating bowhead whale population size from photo-identification data. These are tested on both simulated data and actual data from 1985 and 1986 photographic studies. Initially a multinomial model that accounts for unmarked whales is used. Variance is estimated using the parametric bootstrap. In the cases considered, the variance estimators perform similarly to previously used delta method based estimators in terms of confidence interval coverage, as long as log-normal rather than symmetric confidence intervals are used for the latter. Further models are developed to account for heterogeneity in capture probabilities (highly marked whales are more likely to be captured than moderately marked) and non-random sampling caused by age segregation. These models, particularly the latter, perform better than the multinomial model on simulated data that incorporate these violations of standard capture-recapture assumptions. All three models are applied to actual bowhead whale data. The resulting estimates of the 1+ population size (animals 1 year old or older) in 1985–86 range from 4,719 (using the non-random sampling model on the small dataset in which lengths are available for all whales so that age class can be determined) to 7,331 (using the heterogeneity model on the full dataset). Standard errors are comparable to those obtained from the ice-based census in years with sub-optimal environmental conditions. All confidence intervals include the ice-based census estimates for 1985 and 1986, as well as the corresponding values of 1+ population size in the most likely trajectory from a Bayesian synthesis analysis. These most likely values – 6,649 and 6,820 – incorporate the ice-based census estimates and additional data on bowhead whale population dynamics.

KEYWORDS: ABUNDANCE ESTIMATE; ARCTIC; BOWHEAD WHALE; MARK-RECAPTURE; PHOTO-ID

1. INTRODUCTION

Most estimates of the size of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) have been based on the ice-based visual and acoustic counts of whales conducted at Point Barrow during the spring migration. These population estimates have formed the basis of management advice by the International Whaling Commission (IWC) Scientific Committee (e.g. IWC, 2000). However, at least since Rugh (1990) made the first attempt to compute a population estimate from photo-identification data, researchers involved in aerial photography of bowhead whales have been interested in obtaining an independent population size estimate from such data.

This paper describes three capture-recapture models developed to permit bowhead population size estimation from aerial photographs and presents results obtained using those models on real and simulated bowhead data. The models address problems caused by unmarked whales, heterogeneity in capture probabilities (highly marked whales are more likely to be captured in good photographs than whales that are only moderately marked) and non-random sampling resulting from age segregation. The study arose out of difficulties encountered when applying existing approaches to bowhead photo-identification data, and thus the data themselves are described below.

The actual bowhead data

Aerial photographs of bowhead whales suitable for identification of individuals using their natural markings have been collected in the Bering, Chukchi and Beaufort

Seas since 1976. Most of the photographs have been collected by LGL Ltd. (LGL), the National Marine Mammal Laboratory (NMML) and Cascadia Research Collective (CRC). The collections are housed at LGL and NMML. Rugh *et al.* (1992) described how the photographs are taken, summarised the methods used initially for organising and scoring the collection for photo-identification and explained how individuals are identified. The use of capture-recapture techniques to estimate whale population parameters from these data was not envisaged in the early years of the studies, so a single score that combined quality and identifiability was assigned to each photograph.

Inadequate quality screening of photographs can lead to violations of assumptions required for capture-recapture estimation. For example, Hammond (1986), Hammond *et al.* (1990) and subsequent authors have recognised that if photographs are included in a sample on the basis of identifiability rather than photographic quality, heterogeneity of capture probabilities is inevitable, with well-marked whales more likely to be included in a sample. This violates a basic assumption of many capture-recapture analyses. The assumption that all marks are reported on recovery is a particular problem with aerial photographs of bowhead whales, because not all of the whale (from the tip of the rostrum to the tip of the tail) is visible in the majority of such photographs. This is because of water depth as a whale dives, splash, whale motion, sea ice, glare or mud on the whale, each potentially obscuring parts of a whale. Marks on a particular part of a whale cannot be reported on recovery of the whale in a subsequent photograph if the part of the

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whale that has the marks is not visible. In addition, it is possible that a whale would not be recognised because of changes in marks over time. Based on examinations of photographs of the same whales taken many years apart (Miller *et al.*, 1992), it is considered unlikely that large scars disappear. However, smaller marks may be disguised by new marks, and they are also more likely than large marks or groups of marks to be obscured in a photograph.

Another problem of greater importance for the bowhead whale than for several other whale species is the large number of unmarked whales in the population. Many young bowhead whales, in particular, are a uniform black colour and have not yet acquired distinctive scars that would permit them to be re-identified in aerial photographs. Because the majority of bowhead whales are not well enough marked to be re-identified, they cannot be considered 'marked' animals and therefore cannot be 'recaptured' (i.e. re-identified) even if they are photographed at a later time. Rugh *et al.* (1998) recognised that unmarked bowhead whales must be accounted for in any attempt to estimate population size using photo-identification data and capture-recapture techniques.

Rugh *et al.* (1998) developed a revised scoring system for aerial photographs of bowhead whales that addressed these problems. Because the largest available samples of photographs were collected in 1985, they suggested basing a population estimate on the 1985 data, with the photographs collected near Point Barrow during the spring migration providing the initial captures and the photographs taken a few months later in the Beaufort Sea providing the recaptures. However, only a few whales identified in the spring 1985 sample were recaptured in the summer sample, so it was clear that two years of data would need to be used to obtain a reliable estimate. Rugh (1990) and Whitcher *et al.* (1996) both noted that the 1986 samples also provided usable data. The 1985 and 1986 photographs, re-scored using the revised system, provided the data for the estimates of Section 5.

Only photographs in which the mid-back region was of good quality were used, so that whales with identifying marks in that region would be recognised when they were photographed on more than one sampling occasion. A whale had to be at least moderately marked on the mid-back to be treated as marked in the analyses; others were treated as unmarked even if they had identifying marks on other parts of their bodies. The scoring system has sufficiently stringent requirements for categorising a whale as moderately marked to ensure that a whale photographed on one occasion will be recognised if photographed again on a subsequent occasion, even if some changes in markings occur in between, provided that the photographs are of good quality. Three of us (WK, GM, DR) had to agree that two photographs were of the same whale to call the second a recapture, virtually eliminating the possibility of false recaptures.

Simulated dataset

Simulated data were used to develop and test the models and methods. A great deal is known about the bowhead whale population, making realistic simulations possible.

A total of four sampling occasions were considered in the simulation; two intra-year occasions (spring and summer) in 1985 and 1986. The output of the simulation includes: the capture history of the marked whales; the total number of photographs of both marked and unmarked whales at each sampling occasion; and the number of captured marked whales at each occasion. For the intra-year occasions the population is considered closed. However, inter-year

additions and deletions were allowed for. Two kinds of deletions were considered: those caused by aboriginal hunting and natural mortalities.

Values of parameters used in the simulations were gathered from several sources, including papers and monographs describing the photographic surveys conducted by NMML and LGL, results of the scoring test described by Rugh *et al.* (1998) and papers on bowhead population size and dynamics. Important sources of information on characteristics (e.g. age composition) of the bowhead population are summarised by Givens (1993) and Raftery *et al.* (1995), who present a Bayesian synthesis approach for making inferences about characteristics of interest given different sources of information which are linked by a deterministic population dynamics model. A number of the parameters used here came from the most likely population trajectory in a Bayesian synthesis analysis carried out by Givens (pers. comm.).

According to the most likely trajectory, the age structure of the population (average 1978-1992) is 42% mature, 53% immature (aged 1-17 years) and 5% calves. Calves are not considered here because they have no identifying markings and are thus never part of the marked population. They are also excluded from the real data. Thus the population size estimates are for the 1+ population, i.e. age ≥ 1 year, the population generally considered in population dynamics models used by the IWC Scientific Committee (e.g. IWC, 2000). According to the most likely trajectory, the 1+ population sizes for the years 1985 and 1986 were 6,649 and 6,820 individuals respectively. Survival rates were based on the input parameters that produced the most likely trajectory: 0.9445 for the youngest 20% of the immature whales and 0.9853 for the rest. Natural deaths were determined by these rates, and 19 individuals killed in the subsistence harvest between the summer 1985 and spring 1986 samples were accounted for. Additions to the population, assumed to occur among the unmarked immature whales, were determined as the number needed to obtain the 1986 population size given the number of deaths.

Information about proportions of marked and unmarked bowhead whales was extracted from the datasets used in the evaluation of the new scoring system (Rugh *et al.*, 1998). The datasets contained information about photograph quality and identifiability for several regions of the whale, including rostrum, mid-back, lower-back and fluke. Identifiability is scored as **H+**, **H-**, **M+**, **M-**, **U+**, **U-**, and **X** and constituted the information used to estimate the proportions of highly (**H**) and moderately marked (**M**) bowhead whales as well as the proportion of the unmarked whales (**U**) in the population. The notation **X** stands for the photographs whose quality is so poor that it is impossible to determine whether the whale is marked. Quality is scored on a five-point scale (1+, 1-, 2+, 2-, 3), indicating how much of the area is visible: 1+ represents the highest and 3 the lowest quality. Only the mid-back region is considered here since Rugh *et al.* (1998) found that it had the largest number of marked whales in photographs of good quality (2- or better). The values used to generate the simulated data were 72.8% unmarked, 18.6% moderately marked and 8.6% highly marked whales in the 76.7% of the photographs of the mid-back region assumed to be of good quality. Because the photographs used by Rugh *et al.* (1998) did not include those from 1985 and 1986, the older dataset used by Whitcher *et al.* (1996) was used to determine the number of individuals photographed at each sampling occasion for the simulations. In the case of bowhead whales, it is not possible to know how many individuals were photographed, since the unmarked

individuals cannot be recognised. For simulation purposes, these numbers were determined as the total number of good photographs taken at each occasion divided by the number of good quality photographs per marked individual. The resulting number of individuals photographed ranged from a low of 401 in spring 1986 to a high of 1,069 in summer 1985.

The simulated data for some of the models used here must specify the number of good photographs taken of each marked whale captured. These numbers were generated from a zero truncated Poisson distribution; see da Silva (1999) for details.

2. ACCOUNTING FOR UNMARKED WHALES: MULTINOMIAL MODEL

Background

Since the majority of bowhead whales are unmarked and therefore un-catchable using photo-identification techniques, it is essential to account for unmarked whales in estimating population size. Some previous work has been done on estimating population size when only part of the population is catchable. Seber (1982, p.72) gave an estimate

$$\hat{N} = \hat{N}^m / \hat{p}^* \quad (1)$$

where \hat{N}^m is the estimated number of individuals in the catchable population and \hat{p}^* is the estimated proportion of the population that is catchable. Using the delta method, he derived a variance expression under the assumption that \hat{N}^m and \hat{p}^* are statistically independent.

Williams *et al.* (1993), working with bottlenosed dolphin photo-identification data, used equation (1) with \hat{N}^m the estimated number of marked individuals in the population and \hat{p}^* the proportion of the photographs that were of marked individuals. Their estimated variance expression

$$V(\hat{N}) = \hat{N}^2 \left(\frac{V(\hat{N}^m)}{(\hat{N}^m)^2} + \frac{1 - \hat{p}^*}{n \hat{p}^*} \right) \quad (2)$$

matches that given by Seber (1982) when binomial sampling is used to obtain \hat{p}^* ; n is the number of photographs on which the estimate \hat{p}^* is based, and \hat{N}^m and \hat{p}^* are used to approximate their expected values. Williams *et al.* (1993) obtained 95% confidence intervals by multiplying the square root of the variance estimate (equation 2) by 1.96.

This approach is simple and intuitively appealing. However, it can be criticised on several grounds. First, Williams *et al.* (1993) used photographs from the same studies to obtain \hat{N}^m and \hat{p}^* , so the assumption of statistical independence of these estimates on which the delta method variance is based does not hold. Covariance between the estimates is not taken into account in equation (2). Second, numerous authors (e.g. Burnham *et al.*, 1987; Garthwaite and Buckland, 1990; Cormack, 1992) have noted that capture-recapture estimates of population size have a skewed distribution, so the symmetric intervals used by Williams *et al.* (1993) are unsatisfactory. This paper develops alternative interval estimates of population size from photo-identification data when the population includes unmarked animals and this approach is compared with that of Williams *et al.* (1993) using simulated bowhead data.

Darroch's multiple recapture model for closed populations

Here we generalise the multiple recapture model of Darroch (1958) for closed populations. The notation and assumptions of the model used to define our likelihood functions are introduced below.

- (1) N is the population size;
- (2) t is the number of sampling occasions;
- (3) u_i is the number of individuals caught in the i^{th} sample but not otherwise, u_{ij} is the number caught in the i^{th} and j^{th} samples but not otherwise, etc.;

Let w be a subset of the integers 1, ..., t and

$$r = \sum_w u_w = \sum_i u_i + \sum_{i < j} u_{ij} + \dots + u_{12\dots t}$$

be the total number of different individuals caught in the complete experiment. Let $n_i = \sum_{w \ni i} u_w$ be the size of the i^{th}

sample. For example, $n_2 = u_2 + u_{12} + u_{23} + u_{24} + u_{123} + u_{124} + u_{234} + u_{1234}$ if $t = 4$.

The probability distribution of $\{u_w\}$ assumed by Darroch (1958) is a multinomial distribution with parameters N and P_w , where P_w is the probability of an individual with capture history w being caught. Let $p_i = 1 - q_i$ be the probability that any individual is caught in the i^{th} sample. The probability of any individual escaping capture throughout the experiment is $\prod_i q_i = Q$. The probability of being caught in samples $i, \dots, 1$ and no others is $\frac{p_i}{q_i} \dots \frac{p_1}{q_1} Q = P_{i\dots 1}$. Therefore, the probability density of $\{u_w\}$ is multinomial, i.e.

$$P(\{u_w\}) = \frac{N!}{(N-r)! \prod_w u_w!} Q^{N-r} \prod_w P_w^{u_w} \quad (3)$$

where $0 \leq u_w \leq N$ subject to $\sum_w u_w \leq N$. Darroch (1958) shows that equation (3) can also be written as:

$$P(\{u_w\}) = \frac{N!}{(N-r)! \prod_w u_w!} \prod_i p_i^{n_i} q_i^{N-n_i} \quad (4)$$

The above development requires several assumptions:

- (1) the population is closed, i.e. it remains constant throughout the experiment;
- (2) all individuals are equally likely to be members of any given sample, regardless of their previous capture history or of what other individuals are in the sample, although capture probabilities may differ between samples;
- (3) all captured animals are marked and are correctly identified on recapture.

Generalisation of Darroch's model to bowhead whales

Let us now consider how to generalise the above model to a situation in which animals are captured and recaptured photographically, natural markings are used to identify individuals on recapture, and some individuals in the population lack identifying markings. Although this section focuses on bowhead whales, the same considerations apply to similar situations involving any species.

As noted in Section 1, it is necessary to use data from two different years for bowhead whales. It is therefore clear that the closed population assumption does not strictly apply since whales are born and die between samples. However, bowhead whales have high survival rates (Whitcher *et al.*, 1996; George *et al.*, 1999) and relatively low fecundity rates (Miller *et al.*, 1992). Therefore, rather than generalising to an open population model, the closed population assumption is retained and simulated data are used to determine whether its failure is problematic in this case.

For bowhead photo-identification, capture probabilities differ between samples because of differences in photographic effort between sampling occasions. There should be no behavioural response to capture; the whales are not trapped, handled, harmed or treated in any sense. Since in the case of the bowhead whales a *capture* means that a good quality photo of a whale was taken, the only source of some behavioural response could be if the animal felt annoyed or threatened by the noise of the aeroplane flying over it. However, no systematic diversions have been observed during the photographic sessions. It therefore seems reasonable to assume that an individual's previous capture history should not affect its capture probability on a given sampling occasion. In this section, it is assumed that by restricting consideration to photographs of adequate quality, heterogeneity in capture probabilities between highly and moderately marked whales on a given occasion is avoided. It is further assumed that the capture of a particular individual does not make capture of a different individual more or less likely, since no long-term affiliations have been observed among bowhead whales photographed during the 1981-94 studies (Koski *et al.*, 1988; Richardson *et al.*, 1995). In short, it appears reasonable to assume that the second assumption in the previous section holds.

However, the third assumption clearly does not hold for bowhead whales. Whales that lack natural markings remain unmarked even when they are captured in a photograph and they cannot be identified on recapture. Restricting consideration to photographs of adequate quality makes it possible to assume that all marked animals are correctly identified on recapture. Thus it is reasonable to assume that the assumptions of Darroch's model hold for marked whales, but unmarked whales, the majority of bowhead whales, must be accounted for outside of that model. As in Williams *et al.* (1993), the photographs of the unmarked whales are used to do this.

Let:

- X_i^u equal the number of good photographs of unmarked whales taken at time i ;
- X_i^m equal the number of good photographs of marked whales taken at time i ;
- X_i equal the total number of good photographs taken at time i ;
- n_i^m equal the number of individual marked whales captured at time i ;
- r equal the total number of individual marked whales captured over the study; and
- $\{u_w\}$ equal a set which includes the number of individuals with capture history w .

The following relationship is observed:

$$X_i = X_i^u + X_i^m$$

The parameters in the model are:

$N = N^m + N^u$, the total number of individuals in the population;

- N^u , the total number of unmarked individuals in the population;
- N^m , the total number of marked individuals in the population; and
- p_i , the probability that a given whale is photographed at sampling occasion i .

The distribution of X_i^m is assumed to be binomial with parameters

$$\left(X_i, \frac{N^m}{N}\right)$$

and the distribution of $\{u_w\}$ is multinomial given by Darroch's model (equation 3). The joint distribution of these variables is

$$\begin{aligned} P(\{u_w\}, \{X_i^m\}) &= P(\{X_i^m\} | \{u_w\}) P(\{u_w\}) \\ &= \left[\prod_{i=1}^t P(X_i^m | n_i^m) \right] P(\{u_w\}) \end{aligned}$$

The distribution of $(X_i^m | n_i^m)$ is truncated binomial because $X_i^m \geq n_i^m$.

Since the estimation of N^u and N^m is restricted by the relationship $N = N^m + N^u$, it is natural to write N^u as being proportional to N^m with proportionality constant γ , say, and write $N^u = \gamma N^m$. Therefore, $N = N^m (1 + \gamma)$. Further development of the model is simplified by this relationship. It is implicitly assumed that both N and N^m remain constant over time when γ is treated as a constant. Photographs of the same whale taken many years apart suggest that marks are not acquired frequently, so it is assumed that the closed population model is adequate for the marked as well as the total population over the two-year time period being considered.

The distribution of $(X_i^m | n_i^m)$ is expressed by:

$$P(X_i^m | n_i^m) = \frac{\binom{X_i}{X_i^m} \left[\frac{1}{1+\gamma} \right]^{X_i^m} \left[\frac{\gamma}{1+\gamma} \right]^{X_i^u} I\{(X_i^u, X_i^m) \in B\}}{\sum_{j=n_i^m}^{X_i} \binom{X_i}{j} \left[\frac{1}{1+\gamma} \right]^j \left[\frac{\gamma}{1+\gamma} \right]^{X_i-j}} \quad (5)$$

where $B = \{(X_i^u, X_i^m) : n_i^m \leq X_i^m \leq X_i\}$ and $I\{(X_i^u, X_i^m) \in B\}$ is an indicator function for pairs (X_i^u, X_i^m) that belong to the set B .

The likelihood function is given by

$$\begin{aligned} L &= \left\{ \prod_{i=1}^t P(X_i^m | n_i^m) \right\} P(\{u_w\}) \\ &= \prod_{i=1}^t \left[\frac{\binom{X_i}{X_i^m} \left[\frac{1}{1+\gamma} \right]^{X_i^m} \left[\frac{\gamma}{1+\gamma} \right]^{X_i^u} I\{(X_i^u, X_i^m) \in B\}}{\sum_{j=n_i^m}^{X_i} \binom{X_i}{j} \left[\frac{1}{1+\gamma} \right]^j \left[\frac{\gamma}{1+\gamma} \right]^{X_i-j}} \right] \\ &\quad \times \frac{N^m!}{(N^m - r)!} \prod_w u_w! \prod_{i=1}^t p_i^{n_i^m} q_i^{N^m - n_i^m} \quad (6) \end{aligned}$$

The maximum likelihood estimators for p_i and N^m are given by:

$$\hat{p}_i = \frac{n_i^m}{\hat{N}^m}; \quad i = 1, \dots, t \quad (7)$$

\hat{N}^m is obtained by solving the equation

$$\prod_{i=1}^t (N^m - n_i^m) = (N^m)^{t-1} (N^m - r) \quad (8)$$

as in Darroch (1958). This equation is solved iteratively using the technique of Robson and Regier (1968). Starting values are based on recommendations by Chapman (1952) or, when there are few recaptures, the estimator of Schnabel (1938); see da Silva (1999) for details. When $n_i^m / X_i \approx 0$,

$$\hat{\gamma} = \frac{\sum_{i=1}^t X_i^u}{\sum_{i=1}^t X_i^m} \quad (9)$$

closely approximates the maximum likelihood estimate of γ . In the case of the bowhead whales, this condition is satisfied since large numbers of photographs are taken and the number of marked whales in the sample is small compared to the number of photographs. The adequacy of the approximation was checked by comparing estimates of γ obtained using equation (9) to those obtained by maximising the likelihood function using the NAG library Fortran routine E04KDF (16 AUGUST 1993). Estimates differed only beyond the third decimal place.

The population size estimator obtained from the above equations is the same as that of Williams *et al.* (1993).

Parametric bootstrap standard error

Following Buckland (1980) and others, the parametric bootstrap is used to estimate standard error. Bootstrap methods depend on the notion of a bootstrap sample (Efron and Tibshirani, 1993). If the distribution from which the bootstrap samples are drawn provides a good approximation to the distribution from which the original data were drawn, then the standard deviation of the estimates of the parameter of interest (in this case, population size N) computed from the bootstrap samples will provide a good estimate of the standard error of the parameter estimate (in this case, \hat{N}) computed from the original data. When we obtain bootstrap samples by re-sampling the original data, giving each of the original n data points equal weight, we are using the empirical distribution function \hat{F}_n to approximate the true distribution F . Estimates of standard error obtained in this way are called non-parametric bootstrap estimates because \hat{F}_n is the non-parametric estimate of F . The parametric bootstrap uses a different estimate of F . In the parametric bootstrap setting we draw B samples of size n from the distribution \hat{F}_{par} , an estimate of F derived from a parametric model for the data. Where parameters are needed to specify the distribution, estimates of these parameters computed from the original data are used.

The choice between non-parametric and parametric bootstrap in capture-recapture is addressed by Buckland and Garthwaite (1991). They note that even though the non-parametric bootstrap is more widely used and more familiar than the parametric bootstrap, the latter allows a

choice of which underlying distribution model to assume for the data. Mark-recapture provides an example where the nonparametric bootstrap makes specific parametric assumptions that are not immediately apparent. That may lead a user to bootstrap on the wrong sampling unit, or to conclude erroneously that the results are more robust than those from a parametric approach. In fact, Bickel and Freedman (1981), in examining the theoretical basis for the bootstrap, developed a number of examples in which the nonparametric bootstrap fails to provide a consistent estimate of standard error while the parametric bootstrap succeeds. This occurs when \hat{F}_n provides a poor approximation to F and the probability model used in the parametric bootstrap is correct.

The model presented in expressions (3) and (5) was used in the parametric bootstrap approach used here, which involves the steps given below.

- (1) Obtain the 'original data' by running the data simulation program once or by using the real bowhead data.
- (2) Estimate the parameters $\hat{N}^m, \hat{p}_1, \dots, \hat{p}_4, \hat{\gamma}$ and \hat{N} , from the data obtained in step 1.
- (3) Using the estimated capture probabilities ($\hat{p}_1, \dots, \hat{p}_4$ and population size of the marked whales (\hat{N}^m), simulate the number of individuals with a given capture history w, u_w^* , by using Darroch's multinomial model (equation 3). This yields the sample sizes ($n_1^{m*}, \dots, n_4^{m*}$) and r^* to be used in calculating the estimate N^{m*} and p_i^* 's from the bootstrap sample.
- (4) Simulate truncated binomial distributions. The total number of photographs X_i obtained in the 'data' at each occasion i was kept fixed at its value in the original data and was divided among marked and unmarked whales as follows:
 - (i) A truncated binomial distribution with parameters

$$\left(X_i, \frac{1}{1 + \hat{\gamma}} \right)$$

- was simulated to obtain the number of good photographs of marked whales;
- (ii) The number of good photographs of unmarked whales was obtained by subtraction. This provides the data needed to calculate the estimate $\hat{\gamma}^*$.
- (5) Calculate the parameter estimates, including N^* , from the bootstrap sample.
- (6) Repeat steps 3-5 B times.

In the above steps, $*$ denotes data or an estimate from the bootstrap sample.

The standard deviation of N^* over the B bootstrap samples, *s.e.**, estimates the standard error of \hat{N} . The difference between the mean of the B values N^* and \hat{N} , *bias**, estimates the bias of \hat{N} . Confidence intervals may be found using the percentile method (Efron, 1981; Buckland and Garthwaite, 1991) as follows. Order the N^* from smallest to largest, and denote the ordered list by $\hat{N}_{(j)}$. Approximate 100(1-2 α)% confidence limits are then given by $\hat{N}_{(k)}$ and $\hat{N}_{(k')}$, where $k = (B + 1)\alpha$ and $k' = (B + 1)(1 - \alpha)$, both rounded to the nearest integer value.

The determination of the number B of bootstrap replications depends on the application. Efron (1981) suggests that bootstrap estimates of standard error usually have relatively little bias, and that seldom are more than $B =$

200 replications needed for estimating a standard error. Many more replications are needed to obtain a good estimate of bias or for construction of confidence intervals. The percentile method depends on the tail of the distribution where fewer samples occur. Buckland and Garthwaite (1991) advocate that for a 95% confidence interval $B = 1,000$ should be satisfactory whilst $B = 200$ will be inadequate.

The choice of B made here was based on the analysis of changes in coefficient of variation (CV) when 1,000, 2,000 and 3,000 bootstrap replications were drawn. Efron (1981) argued that the increased variability due to stopping after B bootstrap replications, rather than going on to infinity, was reflected in an increased CV. Working with simulations of data under closed and open population assumption, we observed that the CV based on 1,000 bootstrap samples compared to 2,000 and 3,000 presented much more dispersion than when the CV was calculated using 2,000 and 3,000 bootstrap replications. The last cases presented roughly close CVs, but to guarantee accurate results a value $B = 3,000$ was chosen. This value of B should achieve sufficient precision to estimate bias and obtain reliable confidence intervals.

Comparison of estimation methods using simulated data

Although our estimator \hat{N} is the same as that obtained by Williams *et al.* (1993), the method of estimating its standard error, bias and confidence interval differs. The two approaches are compared below using the simulated data described in Section 1. In addition to considering the symmetric confidence intervals of Williams *et al.* (1993), the delta method variance (equation 2) is also used to compute the confidence intervals suggested by Burnham *et al.* (1987).

According to Burnham *et al.* (1987), the symmetric 95% confidence interval for N

$$\hat{N} \pm 1.96\sqrt{V(\hat{N})}$$

can be improved by using transformations that better approximate normality. They recommend the log-transformation. Transformation makes little difference if the CV of the parameter estimator in question is small, say ≤ 0.1 (10% when expressed as a percentage). It makes a difference at moderate (near 20%) and large ($\geq 40\%$) CV. For an approximate $(1 - \alpha)100\%$ log-based confidence interval for a parameter, say N , Burnham *et al.* (1987) recommend the calculation of lower and upper bounds, \hat{N}_L and \hat{N}_U , as

$$(\hat{N}_L, \hat{N}_U) = (\hat{N} / C, \hat{N}C) \quad (10)$$

where

$$C = \exp\left(z_{\alpha/2} \sqrt{\log\left(1 + [\text{CV}(\hat{N})]^2\right)}\right) \quad (11)$$

and $\text{CV}(\hat{N})$ is the estimated standard error of \hat{N} from equation (2) divided by \hat{N} .

Some further definitions are needed. In the following expressions, N is the population size assumed in generating the simulated data, means are computed over the s simulated samples and bias^* is computed for each simulated sample as

$$\text{bias}^* = \frac{1}{B} \sum_{b=1}^B N^* - \hat{N} \quad (12)$$

where the N^* are the estimates of N from the B bootstrap samples and \hat{N} is the estimate of N from the simulated sample. With this notation,

- (1) true bias of $\hat{N} = \text{mean}(\hat{N}) - N$;
- (2) bias corrected $\hat{N} = \text{uncorrected } \hat{N} - \text{bias}^*$;
- (3) bias of corrected $\hat{N} = \text{mean}(\text{bias corrected } \hat{N}) - N$

$$(4) \text{RMSE} = \sqrt{\frac{1}{s} \sum_{i=1}^s (\hat{N} - N)^2}.$$

The summary statistics presented below are based on $s = 500$ simulated samples. For each of them, $B = 3,000$ parametric bootstrap replications were performed.

Results

In this section the multinomial model is analysed for five different cases in order to gain some insight into how the multinomial model works for varying values of total population size, capture probabilities and population size of unmarked individuals. For all of the cases studied, the number of marked individuals in the population was the same: 1,886 marked individuals. That has the advantage of keeping the number of cases in the study small, without leaving out the most interesting ones. In addition, the impact of departures from the closed population assumption on estimated population size for bowhead whales is investigated.

Firstly, the multinomial model is compared using simulations for closed and open populations. The rest of the population parameters needed in those simulations were kept fixed. Secondly capture probabilities and total population size were varied. A summary of the cases is presented in Table 1. For example, ‘case 0’ differs from ‘case 1’ because in the former it was assumed that the population was closed whereas in the latter it was open. The capture probabilities

Table 1

Description of the main parameters used in the simulation of five different cases for capture-recapture estimation of population size - 1,886 marked individuals for each case.

Case	Population Size		Number of individual photographs			
	1985	1986	Spring 1985	Summer 1985	Spring 1986	Summer 1986
0	6734	6734	641	1069	401	441
1	6649	6820	641	1069	401	441
2	6734	6734	2x641	2x1069	2x401	2x441
3	2x6734	2x6734	2x641	2x1069	2x401	2x441
4	2x6734	2x6734	641	1069	401	441

are almost the same for both cases since the same sizes were used in those simulations. 'Case 2' is an ideal case where the number of unmarked individuals in the population is not as bad as for cases 3 and 4, the population is closed and capture probabilities are twice as high as those for cases 0, 1 and 3. Case 4 is expected to give the worst results: large bias and standard deviation for the estimated value of N .

Table 2 contains uncorrected and bias corrected summary statistics for 500 estimated values of N under each case. The first column of Table 2 gives the average of \hat{N} for 500 datasets. The next two columns give true bias and RMSE as defined above. The fourth column gives the average bootstrap standard error over the 500 samples. The last three columns give the statistics on true bias and RMSE for bias corrected \hat{N} .

These results show that even when the percentage of unmarked individuals in the population is as high as 72% (cases 0-2) to 86% (cases 3-4), as is the case for the bowhead whale population, the proposed model works well as long as it is possible to draw large samples from the population. As expected, case 2 yields the smallest bias and variance. Cases 0 and 1 show when it is not possible to draw large samples, the estimator still works well, even when the population is not closed. Of course the time period considered here is just two years. Further investigation is required if longer time periods are to be considered. Cases 3 and 4 show that the availability of large samples leads to better estimates. Although 86% of the whales were unmarked in both cases, case 3, with a sample size twice as large as case 4, resulted in more accurate and precise estimates of N . Case 0 contrasted with case 3 reveals that the variance of \hat{N} increases with N and with the number of unmarked individuals in the population; the CV is small in both cases, being only slightly larger in case 3.

Bias is negligible in all cases but case 4. Otis *et al.* (1978) explain that the bias of the estimated value of a population size using Darroch's model is not significant when capture probabilities (p_i 's) are, on average, close to 0.1 or larger. However, if the p_i 's are smaller than 0.1, significant bias results. Otis *et al.* (1978) showed by simulation that positive bias is observed when capture probabilities are low. Seber (1982, p.72), showed that there is positive bias associated with the correction for unmarked whales when n and \hat{p}^* are small relative to N . Both these problems occur in case 4. Bias correction has a negligible effect in cases 0-3. For case 4, the correction substantially reduces bias and RMSE.

The parametric bootstrap estimates of the variance of \hat{N} are generally larger than the delta method estimates (equation 2). That may be because \hat{p}^* and \hat{N}^m were considered as being uncorrelated in the latter. Also of interest in evaluating the performance of the bootstrap is the study of coverage performance of confidence intervals for N . Percentile parametric bootstrap confidence intervals are compared below with intervals calculated from the delta

method variance estimates (equation 2), both the symmetric intervals used by Williams *et al.* (1993) and the log-normal intervals proposed by Burnham *et al.* (1987).

Table 3 shows the percentage of the times that the symmetric, log-normal and percentile confidence intervals (CI) missed the true value of N on the left or right side. For example, *miss left* means that the left endpoint was larger than N , i.e. the population size was overestimated. The desired coverage is 95%, so we expect *miss left* and *miss right* to be roughly 2.5%. Table 3 also gives mean CI widths. A total of 500 samples (500 CI realisations) with 3,000 bootstrap replications for each sample were considered.

Table 3

Percentage of 500 samples in which the confidence interval (CI) missed the true value N . Average CI widths are also given. Symmetric and log-normal intervals use the delta method variance estimate. Percentile parametric bootstrap intervals are based on 3,000 bootstrap replications.

Case	Type of CI	% Miss		Mean CI width
		Left	Right	
0	Symmetric	0.2	5.8	3,038
	Log-normal	1.2	3.8	2,988
	Percentile bootstrap	0.6	3.0	3,169
1	Symmetric	1.2	5.6	3,106
	Log-normal	2.4	3.8	3,102
	Percentile bootstrap	1.6	3.4	3,256
2	Symmetric	2.0	4.0	1,377
	Log-normal	2.6	3.2	1,351
	Percentile bootstrap	2.6	3.0	1,392
3	Symmetric	1.4	6.4	6,121
	Log-normal	1.8	4.6	5,863
	Percentile bootstrap	2.6	3.4	6,361
4	Symmetric	0.0	6.4	14,490
	Log-normal	2.2	3.4	13,740
	Percentile bootstrap	5.6	1.4	18,490

Overall Table 3 shows that the percentile intervals achieve better balance than the delta method based symmetric intervals on the left and right sides. The symmetric CI overcover on the left and undercover on the right in all cases, and their overall coverage is 94% or less in all cases. The parametric bootstrap comes closest, averaged over cases 0-4, to overall 95% coverage. However, the log-normal intervals deviate less from 95% coverage on average, and they have the shortest mean confidence interval widths in all cases. The percentile bootstrap intervals compare particularly badly with the log-normal intervals (poorer coverage and much larger mean CI width) in case 4, the sparse data case.

Case 4 in Table 2 suggests that bias correction can be important. Improved percentile bootstrap CI could no doubt be calculated, for example by using the bias corrected and

Table 2

Summary statistics for the estimated values of \hat{N} based on 500 samples.

Case	\hat{N} not bias corrected				Bias corrected		
	Mean	True bias	RMSE	s.e.*	Mean	Bias	RMSE
0	6,770	36	767	859	6,759	25	769
1	6,812	78	860	917	6,800	66	866
2	6,724	-10	360	355	6,730	-4	358
3	13,530	62	1,699	1,628	13,367	-101	1,652
4	14,410	942	4,689	5,072	13,311	-157	3,545

accelerated percentile method discussed by Efron and Tibshirani (1993). However, the delta method based log-normal CI do quite well overall, and they require much less computing effort than the parametric bootstrap percentile intervals. When the approximation (equation 9) can be shown to be adequate, so that our estimate of N and that of Williams *et al.* (1993) is the same, the delta method variance estimate (equation 2) might be judged to provide adequate CI, as long as log-normal rather than symmetric intervals are used.

3. HETEROGENEITY: HIGHLY VS. MODERATELY MARKED WHALES

Introduction

The capture-recapture model presented in the previous section, while taking account of unmarked whales, assumed that all marked whales had the same capture probability on a given sampling occasion. The goal of the quality scoring proposed by most researchers interested in using photographic data for capture-recapture (for example, Hammond, 1986; Hammond *et al.*, 1990; Friday *et al.*, 2000; Rugh *et al.*, 1998) has been to identify a quality level that is good enough to permit whales in photographs of that quality to be identified regardless of whether they are highly or moderately marked. It was hoped that by restricting capture-recapture analyses to photographs of this quality, heterogeneity in capture probabilities, with highly marked whales more likely to be captured than moderately marked whales, could be avoided. However, this goal has proved elusive. Positive correlations are generally found between quality and distinctiveness scores (Friday *et al.*, 1997), implying that photographs of highly marked whales are more likely to be scored as of good quality.

Consideration of the scoring system developed and tested by Rugh *et al.* (1998) indicates that this positive correlation is inevitable for bowhead whales. Only in photographs of excellent quality can one be certain that marks are not obscured. Thus a highly marked whale may well be scored as moderately marked in a photograph of only good quality. However, as shown below, if capture-recapture analyses are restricted to photographs of excellent quality, the dataset will be too small to provide a useful population estimate.

White *et al.* (1982) pointed out that numerous published studies demonstrate heterogeneity in capture probabilities for a wide range of species. In studies where the true population size was known (for example, Carothers, 1973), the commonly used estimators were biased severely by this heterogeneity. Computer simulation studies have also shown that heterogeneity can cause substantial negative bias in the commonly used estimators of population size (Carothers, 1973; Otis *et al.*, 1978).

Pollock (1991) reviewed efforts to develop models and estimation procedures that can handle heterogeneity without producing biased estimates of population size. A set of models that allow capture probabilities to vary due to heterogeneity (h), trap response (b), time variation (t) (i.e. capture probability for time i differs from that for time j) and all possible two- and three-way combinations of these factors is now available. The eight models ($M_o, M_h, M_b, M_{bh}, M_t, M_{th}, M_{tb}, M_{tbh}$) were first considered as a set by Pollock (1974) and were more fully developed by Otis *et al.* (1978), White *et al.* (1982), and Pollock and Otto (1983). According to Pollock (1991), models M_{th}, M_{tb} and M_{tbh} do not usually permit estimation of population size due to non-identifiability issues although they are often necessary

for real populations. In the case of bowhead whales, for example, time variation t is certain because of widely differing effort on the different sampling occasions.

Pollock *et al.* (1984) introduced a logistic regression technique to account for observable population heterogeneity in capture probabilities. In other words, the characteristics of the captured individuals were used to explain their probabilities of capture. They examined inferences based on the full likelihood, which necessitated the construction of categories of individuals according to the values of the covariates and estimation of the number of individuals in each category. This was necessary to overcome the problem that the covariates for uncaptured individuals were not known. Cormack (1989) also advocated the use of generalised linear models for capture-recapture but noted that, while his approach could diagnose heterogeneity, population size estimation was hampered by the lack of knowledge of the distribution of covariates in the unobserved part of the population.

Huggins (1989; 1991) and Alho (1990) independently suggested the use of a likelihood conditional on the captured individuals. The approach of Huggins is expanded below to develop a model that allows and accounts for heterogeneity in capture probabilities between moderately marked M and highly marked H whales. Although restricting photographs to those of highest quality might prevent heterogeneity, this would waste useful data and reduce precision. This is not necessary if models that allow for heterogeneity are used.

Heterogeneity in capture probability via logistic models

Initially a method to create the likelihood function for the marked individuals only is considered. This will then be combined with the unmarked whales to arrive at an estimate of total population size. The proposed model is based on Huggins (1989; 1991) who introduced a model that explains heterogeneous capture probabilities via observable characteristics of the individuals and time dependence via observable characteristics of the sampling occasions. Individual capture probabilities are expressed by linear logistic models with coefficients assumed to be the same for individuals in the same group as specified by the animals' covariates. That provides the homogeneity assumption needed to enable estimation of the parameters involved in the model. Population size is estimated by the method of moments as a function of the individual estimated values of the capture probabilities.

It is assumed here that the captures of a whale are independent from the previous occasions and that the individuals behave independently. That does not imply that all the whales have the same capture probabilities; this probability is allowed to be a function of the covariates included in the analysis. Under the assumptions, the full likelihood for the marked individuals is:

$$L^* = K \prod_{i=1}^{N^m} \prod_{j=1}^t p_{ij}^{\delta_{ij}} (1 - p_{ij})^{(1-\delta_{ij})} \quad (13)$$

where

N^m is the total number of marked individuals; and

p_{ij} is probability that animal i is captured at time j , where $i = 1, \dots, N^m$, and $j = 1, \dots, t$,

$$\delta_{ij} = \begin{cases} 1, & \text{if individual } i \text{ is captured at time } j, \\ 0, & \text{otherwise} \end{cases}$$

and K may depend on N^m but not on the parameters that define p_{ij} .

One complication with estimation of the parameters using the model above is that the covariates for the uncaptured marked individuals are not known. Huggins (1989) showed that inference can be based on the conditional likelihood,

$$L = \prod_{i=1}^r \prod_{j=1}^t \gamma_{ij}^{\delta_{ij}} (1 - \gamma_{ij})^{(1-\delta_{ij})}$$

where r is the number of captured individuals over the experiment and γ_{ij} is defined by Huggins (1989) as follows:

$$\gamma_{ij} = \frac{p_{ij}}{1 - (1 - z_{ij}) \prod_{l=j}^t (1 - p_{il}^*)} \quad (14)$$

where z_{ij} is the indicator of past capture history of individual i , i.e.

$$z_{ij} = \begin{cases} 1, & \text{if individual } i \text{ has been captured before } j, \\ 0, & \text{otherwise} \end{cases}$$

and p_{il}^* is p_{il} evaluated when $z_{il} = 0$. Notice that when $z_{ij} = 1$, $\gamma_{ij} = p_{ij}$.

Huggins (1989; 1991) modelled the p_{ij} using logistic regression. The same approach is followed here by considering a linear logistic model for the capture probabilities,

$$p_{ij} = \frac{\exp(\beta_0 + \beta_1 z_i + \beta_2 x_j + \beta_3 z_{ij})}{1 + \exp(\beta_0 + \beta_1 z_i + \beta_2 x_j + \beta_3 z_{ij})} \quad (15)$$

where z_i is an individual covariate and x_j is an occasion covariate.

Notice that when, for example, $z_{i2} = 1$ that means that up to time 2 either capture history 11 or 10 was observed, with 11 representing individual i was captured at times 1 and 2, and that $\gamma_{i2} = p_{i2}$. However, if $z_{i2} = 0$, then γ_{i2} is given by

$$\gamma_{ij} = \frac{p_{ij}}{1 - \prod_{l=j}^t (1 - p_{il}^*)} \quad (16)$$

with $j = 2$; γ_{ij} of equation (16) is denoted by γ_{ij}^* .

Huggins (1991), in his appendix 2, shows that the likelihood function defined in equation (13) can be re-expressed by

$$\prod_{i=1}^r \prod_{j=1}^t \frac{p_{ij}^{\delta_{ij}} (1 - p_{ij}^*)^{(1-\delta_{ij})}}{1 - \prod_{l=j}^t (1 - p_{il}^*)} \quad (17)$$

In the following sections, equation (17) is used in the likelihood.

In the logistic model of equation (15), the presence of z_{ij} allows capture probabilities to be modelled to vary according to an individual's capture history, i.e. allow for behavioural effect. In the case of the bowhead whales, the sampling procedure is not believed to produce any behavioural effect since systematic diving behaviour when the plane flies over

the animals when the photographs are taken has not been observed. Therefore, in the model used here, $\beta_3 = 0$ and $p_{il}^* = p_{il}$. In the model proposed below for the bowhead whale, capture probabilities will be considered to vary only according to *occasion* and according to a group specific covariate that describes the amount of marking: $z_i = 1$ for highly marked whales and $z_i = 0$ for moderately marked whales. The effort in hours expended to take pictures on occasion j is defined as x_j . Therefore, the capture probabilities as defined by the linear logistic model are,

$$p_{ij} = \frac{\exp(\beta_0 + \beta_1 z_i + \beta_2 x_j)}{1 + \exp(\beta_0 + \beta_1 z_i + \beta_2 x_j)} \quad (18)$$

The likelihood function

Estimating the total population size N requires the use of the available information on the marked individuals and some simplifying assumptions that also make sense in a biological context. Before describing the likelihood function which incorporates the unmarked whales, further notation must be introduced:

- p_{ij} is the capture probability of individual i at time j ;
- θ_j represents the encountering probability at time j ;
- λ_j^H is the average number of good photographs of highly marked whales;
- λ_j^M is the average number of good photographs of moderately marked whales;
- v is the probability of a marked whale being highly marked in the population;
- N^u is the population size of unmarked individuals;
- Z_i^H is an indicator, 1 if the marked whale is highly marked, and 0 if moderately marked;
- δ_{ij} is the indicator of capture of individual i at time j ;
- X_{ij}^m is the number of good photographs of marked individual i at time j ;
- X_j^u is the number of good photographs of unmarked whales at time j ;
- r^H is the number of different highly marked individuals captured over the experiment;
- r^M is the number of different moderately marked individuals captured over the experiment; and
- r is the total number of different marked individuals captured over the experiment, $r = r^H + r^M$.

The model developed here follows Hammond (1986). He noted that the process of 'capture' and marking can be divided into three component parts:

- (1) the whale must be sighted (encountered) by conducting a sample survey of some kind, usually from a boat or an aeroplane;
- (2) once a whale has been seen it must present itself in such a way that a photograph of its natural markings can be taken; and
- (3) once the best photograph of a particular whale has been selected, a decision must be made concerning how it should be treated.

Hammond (1986) argued that for all whales to have equal probability of capture they must all have the same probability of being sighted (encountered) and of presenting their markings (although strictly this need not be true in the unlikely event that the product of these probabilities were the same for all animals). Below it is assumed that all individuals have the same chance of being encountered (sighted) regardless of their amount of markings. The probability of an individual presenting its markings, that can be interpreted as the probability of a whale having at least one photograph that

is good enough to be used in capture-recapture analysis, may differ according to the amount of markings the individual possesses. There is some evidence that highly marked whales have a higher average number of photographs good enough to be used in capture-recapture studies than moderately marked ones. Such distinction gives rise to the following expressions for capture probabilities, with θ_j representing the encountering probability and $(1 - e^{-\lambda_j^H})$ the probability of a highly marked whale having at least one good photograph,

$$p_{ij} = \theta_j(1 - e^{-\lambda_j^H}) \quad i = 1, \dots, r^H; j = 1, \dots, t \quad (19)$$

and similarly for moderately marked whales

$$p_{ij} = \theta_j(1 - e^{-\lambda_j^M}) \quad i = r^H + 1, \dots, r; j = 1, \dots, t \quad (20)$$

Notice that actually only two different capture probabilities must be estimated at each sampling occasion: one for the highly marked and one for the moderately marked ones, since all the animals are assumed to be equally affected by the occasion variable.

The encountering probabilities at each time are estimated by summing up the capture probabilities above at each time. By using simple algebraic calculation, the encounter probabilities θ_j are described as

$$\theta_j = \frac{r^H p_{1j} + r^M p_{rj}}{r^H(1 - e^{-\lambda_j^H}) + r^M(1 - e^{-\lambda_j^M})} \quad (21)$$

The encounter probabilities above are needed in the formulation of the modelling for the number of good photographs of unmarked whales as expressed by a random sum. Another assumption in our model is that the average number of good photographs of unmarked individuals is the same as for the moderately marked whales. That assumption, even though not ideal, is appropriate if the degree of marking affects the selection of photographs. It is not an unreasonable assumption, and it translates our belief that the average number of good photographs of unmarked whales is more likely to be closer to the moderately marked than to the highly marked ones.

The likelihood function is given by

$$\begin{aligned} L &= P(\{\delta_{ij}, X_{ij}^m, Z_i^H\}, \{X_j^u\}) \\ &= P(\{X_{ij}^m | \delta_{ij}, Z_i^H\}) P(\{\delta_{ij} | Z_i^H\}) P(\{Z_i^H\}) P(\{X_j^u\}) \\ &= \prod_{i=1}^r \prod_{j=1}^t P(X_{ij}^m | \delta_{ij}, Z_i^H) P(\delta_{ij} | Z_i^H) \\ &\quad \times \prod_{j=1}^t P(\{X_j^u\}) \prod_{i=1}^r P(Z_i^H) \\ &= \prod_{i=1}^{r_h} \prod_{j=1}^t P(X_{ij}^m | \delta_{ij}, Z_i^H = 1) P(\delta_{ij} | Z_i^H = 1) \\ &\quad \times \prod_{i=r^H+1}^r \prod_{j=1}^t P(X_{ij}^m | \delta_{ij}, Z_i^H = 0) P(\delta_{ij} | Z_i^H = 0) \end{aligned}$$

$$\begin{aligned} &\times \prod_{j=1}^t P(X_j^u) \prod_{i=1}^r P(Z_i^H) \\ &= \prod_{i=1}^{r_h} \prod_{j=1}^t \frac{e^{-\lambda_j^H \delta_{ij}} (\lambda_j^H)^{x_{ij}^H \delta_{ij}}}{(x_{ij}^H \delta_{ij})!} \frac{1}{[(2 - \delta_{ij}) - e^{-\lambda_j^H \delta_{ij}}]} \\ &\quad \times \prod_{i=r^H+1}^r \prod_{j=1}^t \frac{e^{-\lambda_j^M \delta_{ij}} (\lambda_j^M)^{x_{ij}^M \delta_{ij}}}{(x_{ij}^M \delta_{ij})!} \frac{1}{[(2 - \delta_{ij}) - e^{-\lambda_j^M \delta_{ij}}]} \\ &\quad \times \prod_{i=1}^r \frac{P_{ij}^{\delta_{ij}} (1 - p_{ij})^{(1-\delta_{ij})}}{1 - \prod_{l=1}^t (1 - p_{il})} \\ &\quad \times \prod_{j=1}^t \left[\sum_{k=1}^{N^u} \frac{e^{-k\lambda_j^M} (k\lambda_j^M)^{x_j^u}}{x_j^u!} \binom{N^u}{k} \theta_j^k (1 - \theta_j)^{(N^u-k)} \right] \\ &\quad \times \prod_{i=1}^r v^{Z_i^H} (1 - v)^{(1-Z_i^H)} \quad (22) \end{aligned}$$

Note that $\{Z_i^H\}$ has been included in the likelihood to make it possible to allow highly marked whales to have a different average number of good photographs than moderately marked ones. That is essential in the characterisation of the model since capture probabilities are related to the number of good photographs, as can be seen from equation (19) and (20). The presence or not of the parameter v in the likelihood does not affect the estimation of the other parameters in the model, but it is necessary for some calculations involved in the unconditional parametric bootstrap procedure for this model since the total number of distinct individuals observed over the sampling experiment is random and so are the respective numbers of highly and moderately marked individuals.

The log of the likelihood function (equation 22) is maximised using an iterative procedure that consisted of maximising the function with respect to its continuous parameters when N^u was given a fixed initial value. Using the continuous parameter estimates, the function was then maximised with respect to N^u . This process was repeated until convergence. The stopping rule was based on the comparison of successive values of the log-likelihood function. The maximisation with respect to N^u was performed by finding the value of N^u which solved the difference equation

$$\log L(N^u) = \log L(N^u - 1) \quad (23)$$

This is the value of N^u that solves

$$\sum_{j=1}^t \log \left(\frac{\sum_{k=1}^{N^u} \frac{e^{-k\lambda_j^M} (k\lambda_j^M)^{x_j^u}}{x_j^u!} \binom{N^u}{k} \theta_j^k (1 - \theta_j)^{(N^u-k)}}{\sum_{k=1}^{N^u-1} \frac{e^{-k\lambda_j^M} (k\lambda_j^M)^{x_j^u}}{x_j^u!} \binom{N^u-1}{k} \theta_j^k (1 - \theta_j)^{(N^u-1-k)}} \right) = 0 \quad (24)$$

The estimated value of N^u obtained by fitting the multinomial model described in Section 2 was used as an initial value. Initial values for parameters β_0 , β_1 , and β_2 ,

were estimated from a logistic regression that was fitted using *Splus* function *glm*. The dependent variable consisted of counts of the number of highly and moderately marked whales at each sampling occasion out of their respective estimated population sizes. Independent variables were Z_i^H and hours of sampling effort.

Estimation of N

Having estimated the population size of unmarked individuals, N^u , the next stage is to estimate the total population size, N , where $N = N^m + N^u$. The population size of the marked individuals, N^m , is composed of highly (H) and moderately (M) marked individuals, and it is described by the relationship $N^m = N^H + N^M$.

Following Huggins (1989), the method of moments is used to estimate N^H and N^M . Suppose that the full parameter vector denoted by θ is known. Let the probability that an individual is captured at least once during the course of the sampling experiment be denoted by

$$p_i(\theta) = 1 - \prod_{j=1}^t (1 - p_{ij}) \quad (25)$$

Thus,

$$\hat{N}^m(\theta) = \sum_{i=1}^r p_i^{-1}(\theta) \quad (26)$$

while N^H and N^M may be estimated separately by adding over the appropriate indices in the summation in equation (26) according to the probabilities expressed by equation (19) and (20).

Simulations

A set of 100 simulated datasets was generated. They comprise capture histories of the individuals and their respective number of good photographs, and a variable describing if a photographed individual was marked or unmarked and whether or not a naturally marked individual was highly or moderately marked. The average number of good photographs for the highly marked individuals was set to be slightly higher than for the moderately marked ones to mimic the true situation for bowhead whales. It is also assumed that unmarked individuals had the same average number of good photographs as moderately marked individuals.

The model described by equation (22) was fitted for the 100 generated datasets, and the multinomial model (equation 6) was also fitted for comparison (Table 4). The population size for the simulations was 6,734. Table 4 shows that both models seem, on average, to estimate the population size reasonably. The results do not strongly suggest that the model allowing for heterogeneity in capture probabilities is better than the simple multinomial model, although the standard deviation for the 100 \hat{N} for the former model is smaller. The similarity in performance may be related to the fact that large differences in capture probabilities of highly and moderately marked individuals were not allowed for.

Table 4
Multinomial versus heterogeneity model.

Model	Mean	Bias	s.d.	c.v.
Multinomial	6,643	-91	774	0.12
Heterogeneity	6,841	107	701	0.10

In practice, the analyst has one dataset and, after estimating the population size, wishes to obtain a standard error for the estimate and a confidence interval. Huggins (1989) suggested a conditional parametric bootstrap, and da Silva (1999) also developed an unconditional parametric bootstrap. However, since each bootstrap sample requires a time-consuming iterative analysis, it is not feasible to compute many bootstrap replicates \hat{N} . The best approach for obtaining standard errors and confidence intervals for the heterogeneity model is the subject of ongoing work.

4. NONRANDOM SAMPLES: AGE SEGREGATION

Introduction

Capture-recapture theory is primarily based on the assumption that samples are drawn randomly. If this assumption is to hold, all animals in the population must be present in the survey area during each sampling occasion. For bowhead whales, that is unlikely given limitations in the time and area covered by the photographic surveys and age segregation in the population, both during the spring migration and on the summering grounds.

Hammond (1986) noted that if a group of animals is consistently less available to be sampled, heterogeneity in capture probabilities is present because this group will have a lower probability of being photographed than the rest of the population. Because age segregation is likely to define such a group in the bowhead case, here we develop methods of accounting for non-random sampling based on categorising the photographed whales as either immature (≤ 13.0 m long) or mature (> 13.0 m long). This is possible because a major goal of most of the photographic surveys was to determine the distribution of lengths, and ultimately ages, in the population. To achieve this, most of the photographed whales were measured using photogrammetric techniques and their lengths included in the data base.

The photographic surveys have provided good information about the proportions of mature and immature whales in the population, summarised by Angliss *et al.* (1995). While it is certainly possible that a sample with the expected proportion of mature and immature whales could nevertheless be non-random, samples with a greatly disproportionate number of mature or immature whales are certainly non-random. For example, the sample taken in summer 1985 had far too many immature animals to be a random sample of the whole population. The one taken in spring 1986 had too many mature animals, while the sample taken in summer 1986 had again too many immature animals.

Reasons why some samples were not random are known, and are related to severe weather conditions or logistical problems that prevented conducting surveys throughout the season. Withrow and Angliss (1992) noted that the spring 1986 study began two weeks late and missed the beginning of the migration. Angliss *et al.* (1995) demonstrated temporal age segregation during the spring migration. The earliest whales to migrate tend to be small. The later migrants are mostly adults (mature whales). Therefore, since the spring 1986 survey missed the first portion of the migration, which is composed primarily of immatures, this segment is underrepresented in the spring 1986 sample.

In summer 1985, a major photographic effort was conducted with the goal of estimating bowhead gross annual reproductive rate. Virtually all of the known summer range of the bowhead whales was searched, but, for unknown reasons, very few adults were found. Davis *et al.* (1986) speculated that

The unusually heavy ice conditions in the Beaufort Sea in 1985 apparently caused major shifts from the normal patterns of summer whale distribution. Results from aerial photography suggest that the actively breeding segment (adults with calves) of the population was essentially absent from the study area in 1985. In late August, only an estimated 229 of the 2251 bowhead whales accounted for were adults.

Koski *et al.* (1988) summarised the evidence for age segregation on the summering grounds.

Table 5, compiled from the above sources, summarises the percent mature/immature whales by sampling occasion and reveals wide differences in percent mature. An attempt to estimate population size with the methods developed so far would be suspect. Methods for estimating population size in the presence of non-random samples are highly desirable because this occurs frequently in capture-recapture studies involving cetaceans. To accommodate non-random sampling, the model in Section 3 is adapted by defining a new covariate that accounts for departures from random sampling. The additional covariate will help correct the magnitude of the capture probabilities to reflect the effect of the non-random samples. The idea is to treat non-randomness as a form of heterogeneity in capture probabilities as Hammond (1986) suggested.

Table 5
Percent mature whales by sampling occasion.

Sample	% Mature
Spring 1985	42.5
Summer 1985	13.6
Spring 1986	61.7
Summer 1986	23.3

Notation

- p_{ij} is the capture probability of individual i at time j .
 v_j represents the encountering probability at time j .
 λ_j is the average number of good photographs of an encountered whale.
 ϕ_{1j} is the conditional probability of encountering an individual at time j given that it is mature.
 ϕ_{2j} is the conditional probability of encountering an individual at time j given that it is immature.
 θ is the probability of an individual being mature.
 N^u is the population size of unmarked individuals.
 δ_{ij} is the indicator of capture of individual i at time j .
 X_{ij}^m is the number of good photographs of marked individual i at time j .
 X_j^u is the number of good photographs of unmarked whales at time j .
 I_j is a vector describing whether a good photograph is from a mature (1) or immature (0) whale at time j .
 ef_j^{mat} is the sampling effort expended to catch mature whales at time j .
 ef_j^{imm} is the sampling effort expended to catch immature whales at time j .
 mat_i is an indicator variable that assumes value 1 if marked whale i is mature and 0 elsewhere.

Let us now define some events that will be needed in the description of some probabilities that are used in the formulation of the model.

- C_j is the event a whale is captured at time j .
 E_j is the event a whale is encountered at time j .

- M is the event a whale is mature.
 I is the event a whale is immature.
 1_j^+ is the event an encountered whale has at least one good photograph at time j .

The model idealised to allow for non-randomness is based on the estimation of the population size of the marked individuals when non-random samples were taken, but at least one random sample is available. A covariate describing departures from that random sample was defined and it accounts for differences in effort per maturity class. Once population size of the marked whales is estimated, the unmarked part of the population is accounted for via the random sum model for the number of good photographs of the unmarked individuals. The encountering probabilities needed in the random sum model are a function of capture probabilities and probability of a whale being mature. This assumes that encounter probabilities are related to maturity but not amount of markings since marked and unmarked mature individuals tend to migrate together. The same occurs with marked and unmarked immature individuals. Therefore ϕ_{1j} and ϕ_{2j} , $j = 1, \dots, t$ are assumed to be the same for marked and unmarked individuals.

The conditional probability of capturing a whale at time j , given that it is mature, is expressed by the product of the probability of a whale having at least one good photograph taken given that it was encountered, times the conditional probability of encountering that whale at time j given that it is mature,

$$P(C_j|M) = P(E_j \cap 1_j^+ | M) = P(1_j^+ | E_j) P(E_j | M) = (1 - e^{-\lambda_j}) \phi_{1j}$$

so the conditional probability of encountering a whale at time j given that it is mature is

$$\phi_{1j} = P(C_j | M) / (1 - e^{-\lambda_j}) \quad (27)$$

The probability of encountering a whale at time j is defined as a function of the probabilities above,

$$\begin{aligned} P(E_j) &= P(E_j | M) P(M) + P(E_j | I) P(I) \\ &= \phi_{1j} \theta + \phi_{2j} (1 - \theta) \\ &= v_j \end{aligned} \quad (28)$$

Only the data from the random sampling occasions are used in the estimation of the probability of a whale being mature. The best data available for the estimation of a whale being mature in the population are from the spring 1985 survey. The probability of a whale being mature must not change in the small time window being considered here (two years). All good photographs of whales from the spring 1985 survey are used in the estimation of the probability of a whale being mature (θ). These whales are categorised as being mature or immature based on their length. In the simulated data, it is assumed that lengths are available for all whales. Although an immature whale could reach maturity between the 1985 and 1986 samples, this possibility is ignored because the slow growth of bowhead whales and the small sample size make it unlikely that such a whale would be sampled.

The ‘outcome’ of a photograph being from a mature whale is being modelled as a Bernoulli trial, although such modelling has limitations since some of its assumptions are violated, because multiple photographs of some whales are

not independent. However, the violation is mild because few photographs are taken of each whale (1.5 photographs/whale).

The likelihood function

$$\begin{aligned}
 L &= P(\{I_1\}, \{X_j^u\}, \{X_{ij}^m\}, \{\delta_{ij}\}) \\
 &= P(\{I_1\} | \{X_{i1}^m\}, \{X_1^u\}) \times P(\{X_{ij}^m\} | \{\delta_{ij}\}) P(\{\delta_{ij}\}) P(\{X_j^u\}) \\
 &= \prod_{g=1}^{x_1^u + x_1^m} \theta^{I_{1g}} (1 - \theta)^{(1 - I_{1g})} \\
 &\times \prod_{j=1}^t \prod_{i=1}^r \frac{e^{-\lambda_j \delta_{ij}} (\lambda_j)^{x_{ij}^m \delta_{ij}}}{(x_{ij}^m \delta_{ij})!} \frac{1}{[(2 - \delta_{ij}) - e^{-\lambda_j \delta_{ij}}]} \\
 &\times \prod_{j=1}^t \prod_{i=1}^r \frac{p_{ij}^{\delta_{ij}} (1 - p_{ij})^{(1 - \delta_{ij})}}{1 - \prod_{l=1}^t (1 - p_{il})} \\
 &\times \prod_{j=1}^t \left[\sum_{k=1}^{N^u} \frac{e^{-k \lambda_j} (k \lambda_j)^{x_j^u}}{x_j^u!} \binom{N^u}{k} v_j^k (1 - v_j)^{(N^u - k)} \right] \quad (29)
 \end{aligned}$$

where v_j is the conditional probability of encountering a whale at time j given that it is unmarked, and it is given by

$$v_j = \varphi_{1j} \theta + \varphi_{2j} (1 - \theta) \quad (30)$$

Capture probabilities are described by:

$$p_{ij} = \frac{\exp(\beta_0 + \beta_1 (mat_i \times ef_j^{mat} + (1 - mat_i) \times ef_j^{imm}))}{1 + \exp(\beta_0 + \beta_1 (mat_i \times ef_j^{mat} + (1 - mat_i) \times ef_j^{imm}))} \quad (31)$$

As earlier, the log of the likelihood (equation 29) is maximised using an iterative procedure that consisted of maximising that function with respect to its continuous parameters when N^u was given a fixed initial value. Using the resulting estimates of the continuous parameters, equation 29 was then maximised with respect to N^u . Once the likelihood was maximised, N^m is estimated as in Section 3.

Simulations

A set of 100 datasets was generated. The composition of the drawn samples at each sampling occasion in terms of proportion mature was simulated to reflect the values displayed in Table 5. It is assumed that 58% of the whales in the population were immature. Among the unmarked whales, 70% were assumed to be immature. The simulated population size was 6,734.

The data consisted of capture histories of the individuals and their respective number of good photographs, a variable describing if a photographed individual was marked or unmarked, one describing whether the individual was mature or immature, and the effort data for mature and immature whales on each sampling occasion. The average number of good photographs was constant for all the whales.

The model described by equation (29) was fitted for the 100 generated datasets. A comparison of the results with the multinomial model (equation 6) is given in Table 6.

Table 6
Multinomial versus non-random sample model.

Model	Mean	Bias	s.d.	c.v.
Multinomial	8254	1520	1211	0.15
Non-random	6815	81	984	0.14

As expected, the non-random sample model performed better than the multinomial model for estimating the total population size N . While the bias of the estimated value of N obtained by the multinomial model is 1,520, that value is only 81 for the non-random sample model. There is also a considerable gain in precision. As in Section 3, a parametric bootstrap was developed to estimate standard errors (da Silva, 1999), but only a few bootstrap replicates for a few samples could be computed because of time constraints.

5. RESULTS FROM THE ACTUAL DATA

Datasets used

Rescoring of the 1985 and 1986 photographs using the scoring system of Rugh *et al.* (1998) was completed by two of us (LB and GM) and a data base containing all the data from these years prepared by WK. Preliminary analyses by JZ confirmed that the mid-back region (Rugh *et al.*, 1998) provided the most good photographs (quality at least 2) and the most recaptures, compared to the rostrum, lower back and fluke. Four sampling occasions (spring 1985, summer 1985, spring 1986, and summer 1986) were considered. The variables in the data base were used to create a dataset containing records with the following information:

- (1) WHALE: whale's number. Each marked whale has a unique number, but the same unmarked whale could occur in the dataset more than once with different numbers.
- (2) H: a categorical variable indicating whether the photographed whale in a good photograph was unmarked (-1), moderately marked (0), or highly marked (1).
- (3) MAT: a categorical variable indicating whether the photographed whale in a good photograph was immature (0), or mature (1).
- (4) Four columns indicating the capture histories of the bowhead whales, with 1 indicating that the whale was, and 0 that it was not, captured in the sample represented by the column.
- (5) Four columns indicating the number of good photographs obtained for each of the captured individuals by sampling occasion.

There were 1,190 records in the dataset, of which only 175 belonged to marked individuals. The subset of 175 marked whales was used for capture-recapture estimation. Only 12 of the 175 were captured more than once over the four sampling occasions.

It is important to recognise that there are many more than 175 identified bowhead whales in the photographic collection, and many more re-identifications than 12, even when attention is restricted to the years considered here. The capture-recapture dataset does not contain them all because

many did not provide good photographs of the mid-back, or the marks by which they are identified occur on different parts of the body.

The requirement for length data so that the whale could be categorised as mature or immature also reduced the dataset. To mitigate this problem, a larger dataset was created that could be used in all of the estimation procedures discussed here with the exception of that which allows for non-random samples. The larger dataset contained 1,677 records, 229 belonging to marked individuals, with 16 of 229 captured on more than one occasion.

Table 7 compares the real to simulated data with respect to the frequencies of recaptured individuals with a given capture history w . For the simulated data, the average number of individuals (rounded to the nearest integer) with a given capture history was taken, based on 100 simulated datasets where the samples were not random. The simulations were used under the non-random sampling model for the comparisons of this section because they are expected to more closely match the actual data than the other simulations.

Notation w_{12} , for example, means that an individual was captured on sampling occasions 1 and 2. Although the number of captured individuals in the simulated data is much larger than in the real data (see Table 8), the scarcity of recaptures between the spring and summer 1985 samples (w_{12}) causes some concern. The 1985 sampling occasions had the largest sampling effort. In the simulated data the average number of recaptures for that category was 11, the largest in the table. This issue requires further investigation.

Table 8 shows the number of marked individuals captured by sampling occasion and the percentage of the marked population (estimated by \hat{N}^m from the model of Section 2) for the real datasets. Averages over the simulated datasets are also given, and for these, the average numbers of marked individuals captured are small, representing at most 8.2% of the total number in the marked population. For the real data the situation is worse. The largest estimated capture probability, even in the large dataset, is 6.7% in the spring 1985 sample. On the fourth sampling occasion, only 18 individuals were captured in the smaller and 26 in the larger dataset. This cannot be expected to yield very reliable estimated values for N .

There were also fewer highly marked whales than expected in the real datasets. Table 9 compares the numbers in the real datasets with the numbers in the simulated data. In the actual data, only 18% to 19% of the marked whales captured were highly marked, compared to 27% in the simulated data.

Table 10 compares the numbers of marked mature individuals captured at each sampling occasion in the actual data with the average numbers obtained in the simulated data. There is good agreement between the percent values for real and simulated data. Note these numbers differ from the

Table 8
Real versus simulated data - number of marked individuals captured by sampling occasion.

	Sp85	Su85	Sp86	Su86
Real data, 175 individuals	Sp85	Su85	Sp86	Su86
Number captured	59.0	52.0	58.0	18.0
% of marked population	5.8	5.1	5.7	1.8
Real data, 229 individuals	Sp85	Su85	Sp86	Su86
Number captured	87.0	56.0	76.0	26.0
% of marked population	6.7	4.3	5.8	2.0
Average of simulated data	Sp85	Su85	Sp86	Su86
Average number captured	147.0	153.0	115.0	77.0
% of marked population	7.9	8.2	6.2	4.2

Table 9
Real versus simulated data - number of highly marked captured individuals.

Data set	Sp85	Su85	Sp86	Su86
Real data, 175 individuals	13	9	9	3
Real data, 229 individuals	22	9	10	6
Average of simulated data	46	25	43	18

Table 10
Real versus simulated data - mature individuals in samples.

	Sp85	Su85	Sp86	Su86
Real data, 175 individuals	Sp85	Su85	Sp86	Su86
# of mature whales	44	20	49	7
% of sampled marked whales	75	38	84	39
Average of simulated data	Sp85	Su85	Sp86	Su86
# of mature whales	109	59	97	42
% of sampled marked whales	74	39	87	55

percentage of mature whales in the population, estimated at around 50% of the 1+ population in our capture-recapture analyses and around 43% by Angliss *et al.* (1995) from a larger dataset. This is because many more immature than mature whales are unmarked.

Precise information about effort is not available and it was necessary to use an *ad hoc* procedure to obtain a crude estimate of hours of effort expended to catch individuals in a given maturity class. This was done by counting up hours in which any whale of that maturity class (whether marked or unmarked) was photographed. The effort data by maturity class used in the analyses are summarised in Table 11. This table also gives the overall effort expended to capture whales of either maturity class. This overall effort is used in estimation of capture probabilities under the heterogeneity model. It is less than the sum of the separate efforts because both mature and immature whales were captured during some hours.

Table 7
Real versus simulated data - number of recaptured individuals with capture history w .

Case	w_{12}	w_{13}	w_{14}	w_{23}	w_{24}	w_{34}	w_{123}	w_{124}	w_{134}	w_{234}	w_{1234}
Real data											
175 ind.	0	5	0	1	6	0	0	0	0	0	0
Real data											
229 ind.	1	7	0	1	7	0	0	0	0	0	0
Sim. data											
446 ind. avg.	11	8	5	6	7	3	0	1	0	0	0

Table 11
Effort data (hours).

Maturity	Sp85	Su85	Sp86	Su86
Mature	55	56	52	32
Immature	57	108	27	42
Either	80	132	68	58

Results

Using the multinomial model described in Section 2, the total population size N is estimated using the datasets containing 175 and 229 marked individuals. The results are summarised in Table 12. The dataset containing 229 whales led to a higher estimated value of N . The standard error, estimated from 3,000 bootstrap replications, was also somewhat higher but the CV lower. The bootstrap bias estimate was around 400 in both cases.

Table 12
Real bowhead data – summary of the results.

Model	Marked captured	\hat{N}	<i>s.e.</i> *	C.I.	<i>bias</i> *
Multinomial	175	5,071	1,871	(3,195,10,002)	410
Heterogeneity	175	5,116	–	–	–
Non-random	175	4,719	1,696	(2,382,9,343)	–
Multinomial	229	7,022	2,017	(4,701,12,561)	413
Heterogeneity	229	7,331	–	–	–

It is encouraging that both the population estimates and their standard errors are comparable to the estimates obtained from the combined visual and acoustic census efforts conducted near Point Barrow in 1985 and 1986. Raftery and Zeh (1998) applied the generalised removal method to the combined visual and acoustic data collected during those years and obtained estimates of the size of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (including calves) of 6,039 (SE = 1,915) and 7,734 (SE = 1,450) for 1985 and 1986 respectively. Both these years were ones in which environmental conditions for conducting a census were not ideal. Estimates with smaller standard errors are obtained from the census when conditions are better, but years with ideal conditions are relatively rare.

Recall that the estimates in Table 12 exclude calves, unlike the estimates of Raftery and Zeh (1998). The estimates of Table 12 also compare well with the 1985 and 1986 estimates of 6,649 and 6,820 (excluding calves) from the Bayesian synthesis analysis of Givens (pers. comm.). The estimates of Givens incorporate the estimates of Raftery and Zeh (1998) and additional data on bowhead whale population dynamics.

Table 12 also shows population estimates from the heterogeneity model of Section 3. They are slightly higher than the multinomial model estimates, suggesting that there may be some negative bias in the multinomial model values because highly marked whales are more likely to be captured than moderately marked. However, convergence to the estimates given was slow. Consideration of the number of parameters in this model and the limitations of the actual data, as compared to simulated data (Table 9), leads to the conclusion that the heterogeneity model has too many parameters for the data to support. There were too few highly marked whales in the actual data.

Bootstrap standard errors for the heterogeneity model were not estimated since the slow convergence would have made computing time prohibitive.

Only the smaller dataset could be used in the model of Section 4 that accounts for non-random sampling because length data are required to assess maturity. Using the model for non-random sampling described in Section 4, we obtained the population estimate given in Table 12 for that model. As expected, it is smaller than the multinomial model estimate since it was designed to avoid the positive bias exhibited by the multinomial model estimate (Table 6) when applied to simulated bowhead data with non-random sampling. Some 100 bootstrap replications were carried out for the non-random sampling model to obtain the standard error given in Table 12, too few to provide an estimate of bias or permit use of a percentile confidence interval. The confidence interval given in Table 12 is the log-normal confidence interval (equation 10) using the parametric bootstrap standard error estimate. It covers the values of 1985 and 1986 population size obtained from the ice-based census and population dynamics modelling.

Discussion

The estimated values of N in Table 12 agree with the results from the simulations discussed in the previous chapters. When applied to the data, the heterogeneity model corrects for negative biases resulting from highly marked whales being more likely to be recaptured than moderately marked ones. The non-random sample model corrects for positive biases caused by the reduced number of recaptures that can occur when samples are non-random. Both \hat{N} and its standard error are somewhat smaller than the values from the multinomial model. Those results are in agreement with the simulations. The estimates in Table 12 are not precise enough to provide a clue as to whether the two kinds of bias partially cancel each other in the multinomial model estimates.

The differences between the models are small compared to the differences that result from increasing the number of marked whales by 31%, and the number of photographs of both marked and unmarked whales correspondingly, by relaxing the requirement for length data. While da Silva (1999) has outlined a model that accounts for both heterogeneity and non-random sampling, it is clear that model will have too many parameters for the data to support. Even if the heterogeneity side of the model is refined to reduce the number of parameters, it is unlikely that the 1985 and 1986 bowhead data can support its use. We hope, however, that the approaches developed in this paper prove useful for other photographic studies.

Regardless of the possible sources of bias mentioned, the confidence intervals of Table 12 all cover the 1985 and 1986 estimates of 6,649 and 6,820 (excluding calves) from the Bayesian synthesis analysis of Givens (pers. comm.), which reflect the best information available on the size of the Bering-Chukchi-Beaufort Seas stock of bowhead whales in those years. Since the population size data and estimation methods on which the Givens estimates are based are completely different from the data and methods used here, our results provide independent confirmation for the population estimates currently accepted by the IWC Scientific Committee.

The real dataset available so far is too small to provide a precise estimate of population size for the bowhead whale. In addition, refinements in both data and methods are needed. Work that needs to be undertaken includes the following:

- (1) more thorough review of the data to ensure that all matches have been located and other data errors have been corrected;
- (2) more refined estimation of sampling effort;
- (3) measurement or estimation of length data for as many whales as possible and development of an estimator that allows for missing length data;
- (4) development of models that permit use of rostrum, lower back and/or fluke data in addition to mid-back data, so the sample size of marked whales can be increased – this may require developing models that allow for matching error, i.e. the failure to recognise that two photographs are of the same whale;
- (5) implementation of a model that accounts for both heterogeneity and non-random sampling but is as parsimonious as possible, and testing of that model on simulated data;
- (6) extension of the methods developed here to open population models so data collected over the last two decades can be included to improve precision;
- (7) the extended models need to allow for changes in markings and maturity status over the years;
- (8) completion of scoring and matching work and incorporation of all years of data, not just 1985 and 1986, into the data base so that the extended methods can be used;
- (9) examination of the relative cost and difficulty of the census effort, compared to the collection and analysis of several large photographic samples, since we have shown that comparable population estimates can be obtained using the two methods.

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REFERENCES

- Alho, J.M. 1990. Logistic regression in capture-recapture models. *Biometrics* 46:623-35.
- Angliss, R.P., Rugh, D.J., Withrow, D.E. and Hobbs, R.C. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*). *Rep. int. Whal. Commn* 45:313-24.
- Bickel, P. and Freedman, D.A. 1981. Some asymptotic theory for the bootstrap. *Ann. Stat.* 9:1196-217.
- Buckland, S.T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. *Biometrics* 36:419-35.
- Buckland, S.T. and Garthwaite, P.H. 1991. Quantifying precision of mark-recapture estimates using the bootstrap and related methods. *Biometrics* 47:255-68.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. and Pollock, K.H. 1987. *American Fisheries Society Monographs*. No. 5. *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society, Bethesda, Maryland. x+437pp.
- Carothers, A.D. 1973. Capture-recapture methods applied to a population with known parameters. *J. Anim. Ecol.* 42:125-46.
- Chapman, D.G. 1952. Inverse, multiple and sequential sample censuses. *Biometrics* 8:286-306.
- Cormack, R.M. 1989. Log-linear models for capture-recapture. *Biometrics* 45:395-413.
- Cormack, R.M. 1992. Interval estimation for mark-recapture studies of closed populations. *Biometrics* 48:567-76.
- Darroch, J.N. 1958. The multiple-recapture census. I: Estimation of a closed population. *Biometrika* 45:343-59.
- da Silva, C.Q. 1999. Capture-recapture estimation of bowhead whale population size using photo-identification data. Doctoral Thesis, University of Washington, Seattle, WA. i-x + 190pp.
- Davis, R.A., Koski, W.R., Miller, G.W., McLaren, P.L. and Evans, C.R. 1986. Reproduction in the bowhead whale, summer 1985. Paper SC/38/PS2 presented to the IWC Scientific Committee, May 1986 (unpublished). 127pp. [Available from the Office of this Journal].
- Efron, B. 1981. Nonparametric standards errors and confidence intervals (with discussion). *Can. J. Stat.* 9:139-72.
- Efron, B. and Tibshirani, R.J. 1993. *An Introduction to the Bootstrap*. Chapman & Hall, New York. 436pp.
- Friday, N., Smith, T.D., Stevick, P. and Allen, J. 2000. Measurement of photographic quality and whale distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. *Mar. Mamm. Sci.* 16: 355-74.
- Garthwaite, P.H. and Buckland, S.T. 1990. Analysis of a multiple-recapture census by computing conditional probabilities. *Biometrics* 46:231-8.
- George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* 77:571-80.
- Givens, G.H. 1993. A Bayesian framework and importance sampling methods for synthesising multiple sources of evidence and uncertainty linked by a complex mechanistic model. Doctoral Dissertation Thesis, University of Washington, Seattle, WA 98195. i-xii + 157pp.
- Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn* (special issue 8):253-82.
- Hammond, P.S., Mizroch, S.A. and Donovan, G.P. (eds.). 1990. *Rep. int. Whal. Commn.* (special issue 12). *Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters*. International Whaling Commission, Cambridge, UK. [vi]+440pp.
- Huggins, R.M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76:133-40.
- Huggins, R.M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725-32.
- International Whaling Commission. 2000. Report of the Scientific Committee. Annex E. Report of the Standing Working Group on the Development of an Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 2:125-54.
- Johnson, K. 1986. The bizarre diet of the walrus. A look at the history and natural history of the most unusual animal on two teeth. *Discovery* 19(1):2-7.
- Koski, W.R., Miller, G.W. and Davis, R.A. 1988. The potential effects of tanker traffic on the bowhead whale in the Beaufort Sea. Report from LGL Limited, King City, Ontario, to Department of Indian Affairs and Northern Development, Hull, Quebec, K1A 0H4, Canada. 150pp.
- Miller, G.W., Davis, R.A., Koski, W.R., Crone, M.J., Rugh, D.J., Withrow, D.E. and Fraker, M.A. 1992. Calving intervals of bowhead whales - an analysis of photographic data. *Rep. int. Whal. Commn* 42:501-6.
- Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62:1-135.
- Pollock, K.H. 1974. The assumption of equal catchability of animals in tag-recapture experiments. Doctoral Thesis, Cornell University, Ithaca, New York.
- Pollock, K.H. 1991. Modelling capture, recapture and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present and future. *J. Am. Stat. Assoc.* 86:225-38.
- Pollock, K.H. and Otto, M.C. 1983. Robust estimation of population size in closed animal populations from capture-recapture experiments. *Biometrics* 39:1035-49.
- Pollock, K.H., Hines, J.E. and Nichols, J.D. 1984. The use of auxiliary variables in capture-recapture and removal experiments. *Biometrics* 40:329-40.
- Raftery, A.E. and Zeh, J.E. 1998. Estimating bowhead whale population size and rate of increase from the 1993 census. *J. Am. Stat. Assoc.* 93:451-63.

- Raftery, A., Givens, G.H. and Zeh, J.E. 1995. Inference from a deterministic population dynamics model for bowhead whales. *J. Am. Stat. Assoc.* 90:402-30.
- Richardson, W.J., Koski, W.R., Miller, G.W. and Würsig, B. 1995. Bowhead whale results: movements, behavior and basic biology. pp. 138-246. In: W.J. Richardson, W.R. Koski, G.W. Miller and B. Würsig (eds.) *Acoustic effects of oil production activities on bowhead and white whales visible during spring migration near Pt. Barrow, Alaska-1991 and 1994 phases*. Unpublished report number MMS 95-0051 by LGL Ltd., King City, Ont., and Greeneridge Sciences Inc., Santa Barbara, CA, for Minerals Management Service. xxxii+539pp. [Available from U.S. Minerals Management Service, Procurement Operations, 381 Elden St./MS 2500, Herndon, VA 22070-4817].
- Robson, D.S. and Rieger, H.A. 1968. Estimation of population and mortality rates. pp. 124-58. In: W.E. Ricker (ed.) *IBP Handbook No. 3. Methods for Assessment of Fish Production in Fresh Waters*. Blackwell Scientific Publications, Oxford. xv+365pp.
- Rugh, D.J. 1990. Bowhead whales reidentified through aerial photography near Point Barrow, Alaska. *Rep. int. Whal. Commn* (special issue) 12:289-94.
- Rugh, D.J., Braham, H.W. and Miller, G.W. 1992. Methods for photographic identification of bowhead whales, *Balaena mysticetus*. *Can. J. Zool.* 70:617-24.
- Rugh, D.J., Zeh, J.E., Koski, W.R., Baraff, L.S., Miller, G.W. and Shelden, K.E.W. 1998. An improved system for scoring photo quality and whale identifiability in aerial photographs of bowhead whales. *Rep. int. Whal. Commn* 48:501-12.
- Schnabel, Z.E. 1938. The estimation of the total fish population of a lake. *Amer. Math. Month.* 45:348-52.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd Edn. Charles Griffin and Company Ltd., London. i-xvii+654pp.
- Whitcher, B.J., Zeh, J.E., Rugh, D.J., Koski, W.R. and Miller, G.W. 1996. Estimation of adult bowhead whale survival rates. Paper SC/48/AS12 presented to the IWC Scientific Committee, June 1996 (unpublished). 22pp. [Available from the Office of this Journal].
- White, G.C., Anderson, D.R., Burnham, K.P. and Otis, D.L. 1982. *Capture-Recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, Los Alamos, NM, USA. xvi+235pp. [Available from NTIS, 5285 Port Royal Road, Springfield, VA 22161].
- Williams, J.A., Dawson, S.M. and Slooten, E. 1993. Abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool.* 71:2080-8.
- Withrow, D. and Angliss, R. 1992. Length frequency of bowhead whales from spring aerial photogrammetric surveys in 1985, 1986, 1989 and 1990. *Rep. int. Whal. Commn* 42:463-7.

Humpback whale activity near Cap Lopez, Gabon

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ABSTRACT

Two days of aerial transects were flown in mid-August 1998, just below the equator near Cap Lopez, Gabon. Two groups of humpback whales (*Meagaptera novaeangliae*) were sighted to the north of Cap Lopez and eighteen groups were sighted to the south. A large proportion of whales in the southern sector engaged in display behaviour. Similar observations were made during brief boat surveys on 14 August 1998 and 6–12 September 1999. Three surface-active groups were also observed, suggesting that humpback whales mate in the waters surrounding Cap Lopez. Three calves were observed during surveys. Historical whaling records and recent reports of whale sightings imply that humpback whale breeding grounds lie further north and west, in the Gulf of Guinea. Observations also suggest that humpback whales may feed at Cap Lopez and possibly at other points along the Gabonese coast. Common dolphins (*Delphinus delphis*) were abundant in the area and one other, unconfirmed, dolphin species was observed. Further research is needed to better establish the status of humpback whales and other cetaceans in the Gulf of Guinea.

KEYWORDS: BREEDING GROUNDS; SURVEY–AERIAL; CONSERVATION; ATLANTIC OCEAN; AFRICA; BEHAVIOUR – DISPLAY; POLLUTANTS; HUMPBAC WHALE; COMMON DOLPHIN

INTRODUCTION

The Gulf of Guinea (Fig. 1) may be the equatorial terminus for many humpback whales migrating from Antarctic Areas II and/or III¹ (Budker, 1952). A large number of humpback whales once utilised the Gulf, however, intense commercial exploitation during the 20th century radically depleted humpback whale numbers. Published records (Committee for Whaling Statistics, 1933; Budker, 1953; Budker and Roux, 1968) show that at least 15,000 humpbacks were taken in the Gulf during the 1900s. These published records undoubtedly underestimate the impact of whaling in the Gulf because much of the catch, particularly from factory ships, went undocumented (Budker, 1954; Tonnessen and Johnsen, 1982; Aguilar, 1985). In addition, many of the tens of thousands of whales captured off Angola and the western coast of South Africa (Committee for Whaling Statistics, 1933; Tønnessen and Johnsen, 1982) were probably migrating members of the same population that visited the Gulf of Guinea.

Several times during the century, overexploitation at the major whaling port in the Gulf (Cap Lopez, Gabon) caused the humpback catch to plummet. In 1937, whaling was abandoned for eleven years after the catch dropped to 298 whales (from 1,241 whales in 1935). Whaling was again abandoned in 1952 when the catch dropped to 264 after catches of over 1,000 in the three previous years. An attempt at a resumption of whaling in 1959 failed when only 160 whales were captured during a 59 day season (Budker and Roux, 1968). Similar patterns were observed at other whaling grounds in the Gulf, including the islands of São Tome (Budker, 1954) and Pagalu (Aguilar, 1985). An attempt to restart whaling at São Tome in 1951 was abandoned after the initial season yielded only 323 whales (Budker, 1954).

Little published information exists on the distribution and abundance of humpbacks in the Gulf since the cessation of whaling there in 1959, making this a priority area for

assessment and evaluation (e.g. see IWC, 1994). The purpose of this study was to begin the process of updating the status of humpback whales in the Gulf of Guinea. More specifically, it was to: (1) evaluate whether the area adjacent to Cap Lopez, Gabon is a humpback whale mating and/or calving area; and (2) derive a sense of the number of whales using the area.

STUDY SITE

Cap Lopez (0°37.5'S, 8°40'E) lies at the tip of the peninsula that creates la Baie du Cap Lopez, a large, shallow bay at the northern mouth of the Ogoue, the second largest river in Central Africa (Fig. 1a). Port Gentil, 8km to the south of Cap Lopez, is now Gabon's petroleum capital and second largest city. Onshore there is a refinery and facilities for storage of petroleum. In the Baie there are loading facilities for tankers and several active oil rigs. Offshore to the south and west of Cap Lopez there are a large number of active oil rigs.

METHODS

The primary method of investigation was aerial survey. Given inexperienced observers and rough sea surface conditions in the Cap Lopez area during the humpback season, a relatively low altitude (1,000ft, 304.8m) and a tight (2km) transect spacing were chosen to enhance the probability of detecting whales. Parallel transects were flown in a Cessna 182 at a speed of approximately 200km/h. Four observers (including the pilot) searched for whales. Each time a whale was sighted, latitude and longitude were noted using a global positioning system. Any whale detected within 100m of another whale was considered to be part of a 'group'. An attempt was made to count the number of individuals in each group sighted. Unfortunately, even when groups were circled repeatedly, obtaining an accurate count from the plane proved difficult. Therefore, the number of animals that could be unambiguously counted was taken as the recorded group size. This probably tended to underestimate true group size, particularly for larger groups.

¹ Area II: 60°W–0°W and Area III: 0°–70°E – see Donovan, 1991.

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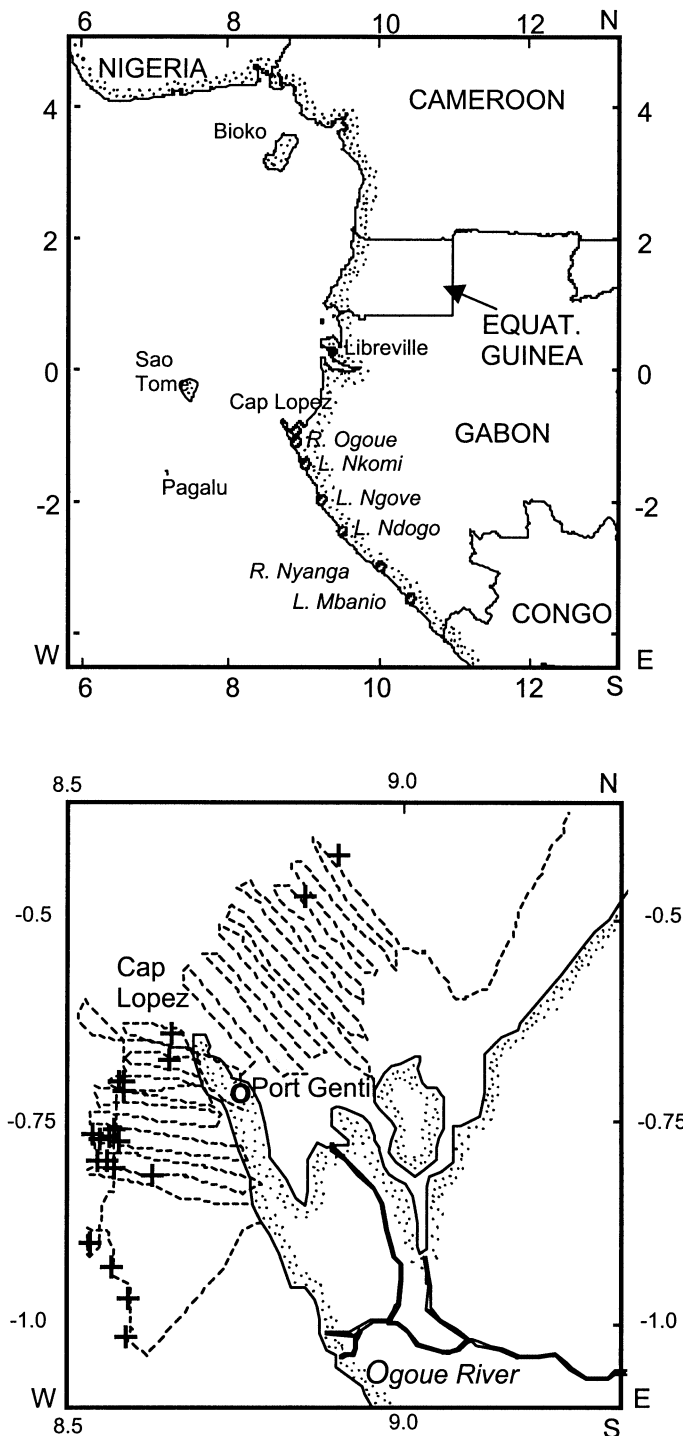


Fig. 1. Above, a map of the Gulf of Guinea. Mouths of major rivers ('R.') and lagoon systems ('L.') between Cap Lopez and the Congo border are shown. Below, a map of the study area. Crosses represent locations where groups of whales were sighted. The dotted line indicates the route taken by the survey aircraft.

Furthermore, some proportion of groups that were either below the surface or on the surface but inconspicuous, were undoubtedly not detected. Because the sampling effort necessary to estimate either the true mean group size or the proportion of groups detected was not available, the whale counts given here represent minima.

Interviews conducted with local fishermen and boat pilots in 1997 suggested that whale activity reached an annual peak during the months of July and August. Therefore, transects were flown on two consecutive days in early August 1998.

On 11 August transects were flown to the north of Port Gentil, including most of the Baie du Cap Lopez and shallow waters that extend to the north. On 12 August transects were flown over the open ocean to the west and southwest of Cap Lopez. Ad hoc observations were also made on the trip from Libreville to the start of transects on 11 August, from the end of transects to Port Gentil on August 11 and from Port Gentil to Libreville on 12 August.

Observations were made from a small motorboat in 1997, 1998 and 1999. In 1997 and 1998 two different fibreglass boats were used, each approx. 8m in length. In 1999, a 13m aluminium boat was used. No systematic sampling plan was followed so thus these sightings data are not analysed in this paper. Whales were videotaped in 1998 and 1999. Recordings of singing whales were made in 1999, although the quality was poor due to ambient noise caused by the strong currents and winds. In 1999, biopsy samples were taken using a crossbow.

RESULTS

Distribution

Approximately 670km of aerial transects were flown (Fig. 1). The northern transect zone extended about 36km northeast of Cap Lopez and covered an area of approx. 890km². The southern transect zone extended 25km south of Cap Lopez and covered an area of about 570km².

Only two groups of whales were sighted during transects in the northern zone, both near its northern extreme. Both groups had two whales, one consisting of a cow and [a young] calf. Fourteen groups of humpback whales were sighted on transects in the southern zone. Summing the minimum group size estimates gives a minimum of 27 whales in the southern transect zone. During an excursion 25km to the south of the transect zone, an additional four groups of whales (six individuals) were sighted. No whales were seen on 11 August during the flight from Libreville to the northern transect zone, or on August 12 during the flight from Port Gentil to Libreville.

A total of eight days of boat survey were performed. In 1997, surveying took place on 20-21 September, almost entirely inside the Baie and no whales were seen. In 1998, a survey was carried out on 14 August to the west and south of Cap Lopez. Five groups of whales were observed, including one group comprising a mother and calf with three other whales, approximately 15km southwest of Cap Lopez. In 1999, surveys were carried out on 5, 6, 8, 10 and 12 September, both in the Baie and to the south and west of Cap Lopez. At least two groups of whales were seen on each day. A mother with a [young] calf was seen on 10 September, approx. 10km southwest of Cap Lopez.

Behaviour

Many common humpback whale behaviours were seen at high frequency in the southern sampling zone, including breaching, lob-tailing and flipper slapping. These have often been associated with mating (e.g. Tyack and Whitehead, 1983) but not exclusively. The high speed of the plane made it difficult to establish exactly how many individuals were engaged in each activity. However, their incidence was not confined to a single group or sub-region. Roughly ten different individuals were observed breaching at locations spread fairly evenly between Cap Lopez and the terminus of sampling 45km to the south. Likewise, two different individuals separated by 15km were observed in the midst of intense lob-tailing sessions. Flipper slapping was also widespread. One individual escorting the mother-calf pair

observed from the boat in 1998 alternated between flipper slapping and breaching for over an hour. Two 'surface-active' groups (one with at least four individuals and the other with at least five individuals) were observed from the aeroplane in 1998 during the formal transects. Another surface-active group of at least six individuals was observed from the boat in 1999, despite the relatively late date (8 September).

Group size

Humpback minimum (see 'Methods') group size on formal aerial transects showed a maximum of five, with a mean of 2.13. Excluding the large concentration of individuals described below, mean group size for both survey methods during 1998 was 2.17. Group size distributions are given in Fig. 2.

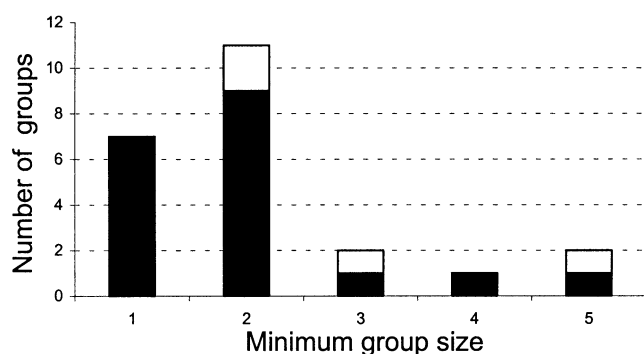


Fig. 2. Frequency histogram of minimum group sizes from 1998: black bars = aerial survey, white bars = boat survey. Not included is a large concentration of whales observed returning through transect zone after sampling.

Biopsy sampling

In 1999, eight biopsy samples were obtained and these will be analysed in due course.

Video identification

A preliminary inspection of videotapes taken in 1999 suggests that images of the tails of at least three whales are of sufficient quality for individual identification. A larger number of whales (perhaps ten) may prove to be identifiable from video images of dorsal fins.

Other species

Dolphins were seen on most days of survey during the three years. They were observed swimming with humpback whales twice during aerial survey on 12 August 1998. Dolphins in photographs taken during the 1997 boat survey have been identified (W. Perrin, pers. comm.) as common dolphins (*Delphinus delphis*). One of several groups of common dolphins observed in 1997 contained approximately 100 individuals. Similar dolphins were again sighted during boat survey in 1998, intermingled with a group of humpback whales. Groups of what again appeared to be common dolphins numbering in the twenties or thirties were seen repeatedly in 1999, with some groups much larger (i.e. 50-100). Many of the sightings were concentrated at the mouth of the Baie between Cap Lopez and the Buoy du Prince (Fig. 1b).

DISCUSSION

Humpback whales appear to be common around Cap Lopez. During the aerial surveys, 14 groups of whales were seen in the southern transect zone, which covered an area of 570km². The true concentration may have been higher as

almost all whales were detected along a single line running south-southwest from Cap Lopez (Fig. 1b), which lay just inside the margin of the continental shelf, which approaches to within about 2km of Cap Lopez.

The fact that a single flight through the area to the south of the transect zone produced an additional four groups of whales suggests that the zone of high whale activity extends substantially further south than the southern transect zone. These groups were distributed fairly evenly from north to south along the same line as the whales in the formal transect zone, and exhibited similar display behaviour (one breaching, one lobtailing) as the whales in the transect zone.

The true southern range may in fact be substantially further south. Our southern excursion reached a point about 45km south of Cap Lopez, offshore from the mouth of the Ogoe River. This is only about half way to the mouth of the Nkomi Lagoon at Fernan Vaz. Maps presented in Budker and Roux (1968) show that in August, the peak month of the 1959 whaling season, more than half of the catch was taken south of Fernan Vaz. Seven whales (4.3% of the catch) were caught some 200km south of Cap Lopez, near the mouth of the Ndogo Lagoon. In earlier years, whales were captured just offshore of Pointe St. Catherine, at the mouth of the Ngove Lagoon and near Mayumba, at the mouth of the Mbanio Lagoon (Budker, 1953). These observations suggest the possibility that the densities observed near Cap Lopez may be typical of the entire Gabonese coastal shelf south of Cap Lopez, or at least the areas near the six major river and lagoon systems that discharge their waters at fairly regular intervals on the coast (Fig. 1b).

The apparent association of whales with the outlets of major river and lagoon systems may be related to an observation made during the 1999 boat survey. On several occasions, solitary whales or pairs were seen diving on 2-4 minute dive cycles. They moved up and back through the same stretch of water repeatedly. On one occasion this occurred in shallow water (< 10m) on the southwest coast of the Baie du Cap Lopez. During the incident, large schools of small fish broke the surface within 50m of the boat (apparently chased by some predatory fish) while a lone humpback engaged in repetitive diving behaviour nearby (within 100m). This is suggestive of feeding behaviour. Several other observations of apparent feeding occurred along the distinct coastal-pelagic interface between the plume of warm water flowing from the Ogoe River and cold oceanic waters to the west. The position of this interface changes with the tides and the seasons, but is usually pushed inside the margin of the continental shelf by the strong Antarctic current that passes Cap Lopez. The observation of feeding was surprising because previous reports suggested that humpback feeding was rare in the area (e.g. Budker, 1953; Budker and Roux, 1968), although feeding has been reported in other tropical waters (e.g. Herman and Antinaja, 1977).

These observations of possible feeding are potentially relevant to the overall distribution of whales because the southern Gulf of Guinea provides a unique habitat. It both experiences an annual upwelling of cold, nutrient rich waters offshore (Budker and Roux, 1968) and contains vast expanses of mangroves onshore. In practice this is an ideal habitat for humpback prey species. For most of the year the mangroves provide a safe haven for small fish and crustacea which once each year leave the mangrove system and aggregate in large schools along the coastal-pelagic interface to feed on the annual pulse of superabundant phytoplankton produced by the upwelling (Budker and Roux, 1968). Larger

fish, local fishermen (particularly the growing commercial shrimp fishery) and, apparently, humpback whales and dolphins, exploit this fact by themselves concentrating along the interface.

It remains to be seen whether feeding by humpback whales in this region is merely rare and facultative or represents a fundamental aspect of humpback whale use of the waters around Cap Lopez. The latter alternative gains some support from the spatio-temporal pattern of humpback activity. R. Puerta (pers. comm.) reports that during the peak of the season (mid July-late August), large groups of whales are often observed to the west of the coastal-pelagic water interface, with acrobatic behaviour common as was observed on the 12 August aerial survey. However, Puerta reports that in September and early October large groups become much less common and acrobatic behaviour is rare. At this time, humpback whales are still present but tend to be found in ones or twos along the coastal-pelagic interface or in the Baie. One might also predict segregation based on age, sex and reproductive status, with individuals not involved in sexual competition or calf rearing (e.g. non-lactating females and immatures of both sexes) more likely to be engaged in feeding behaviour. Oil company pilots report that late in the season whales become much more clumped around each of the lagoon entrances on the southern coast (particularly Mayumba) and appear to be feeding.

Breeding activity

The behavioural observations made in this study suggest that the waters around Cap Lopez may be the site of humpback whale mating. The incidence of display behaviours such as breaching and lob-tailing appears high for a transient migratory zone (although there is no *a priori* reason why mating cannot occur along the migration route as has been observed in gray whales, for example – see Swartz, 1986). The observation of surface-active behaviour also points to mating activity. For example, on 12 August in the course of flying back through the southern transect zone, a concentration of at least 18 whales was in an area of less than 1 km². These appeared to be whales that had been earlier observed in separate groups, but had subsequently converged. A large, core group of approximately ten individuals was engaged in surface-active behaviour, while individuals in several satellite groups breached as they converged on the core group. Large surface-active groups such as this are thought to be associated with mating (Tyack and Whitehead, 1983).

A further indication that this area may not be simply a migratory corridor is the fact that the Cap Lopez region appears to show a unimodal pattern of visitation (Budker and Collignon, 1952; Calzada and Aguilar, 1996) typical of humpback breeding areas (Dawbin, 1966; Findlay *et al.*, 1994). That is, the abundance of whales in the Gulf does not show separate peaks corresponding to the passing of whales on their northward migration to breeding grounds and southward migration back to the Antarctic. Rather, abundance shows one strong peak, which catch records (Budker and Roux, 1968) and conversations with local fisherman and pilots suggest starts in mid-July and extends throughout August. It might also be considered that, 'pretty often a pair of humpbacks (male and female) were caught at the same place and at the same time' (Budker and Roux, 1968).

The coastal shelf of Gabon extending to the south into the Republic of Congo provides the warm, shallow waters that are typical of humpback whale calving and calf rearing areas worldwide (e.g. Hawaii, Herman and Antinaja, 1977; Silver

Bank, Whitehead and Moore, 1982; Virgin Bank, Mattila and Clapham, 1989; Mozambique, Findlay *et al.*, 1994; Baie de Antongil, Rosenbaum *et al.*, 1997). The waters in the lee of Cap Lopez seem particularly suited for calf rearing. However, whether or not Cap Lopez is a calving and/or nursery area remains unclear. Three calves were seen in the area (one during the aerial survey and two from the boat), but survey effort was insufficient to draw any firm conclusions.

What is clear is that Cap Lopez is certainly not the terminus of all humpback migration in the Gulf of Guinea. Whalers operated at several points to the north and west including on the coast 67 km north of Cap Lopez (Tonnessen and Johnsen, 1982), near Libreville and off of Cameroon (Budker, 1953) and on the islands of São Tome (Budker and Roux, 1968), Bioko (referred to by Tonnessen and Johnsen, 1982 as Fernando Poo) and Pagalu (Aguilar, 1985). Humpback whales have been seen 35 km north of Port Gentil and some are occasionally observed from shore at Point Denis, near Libreville (C. Mbina, pers. comm.; R. Os里斯, pers. comm.). They are also observed regularly from shore in Equatorial Guinea (R. Ensono, pers. comm.), with frequent observations of calves (F. Stennmans, pers. comm.). In addition, local fisherman report that large groups are common south and west of the island of Corisco. These are all potential humpback breeding areas and it seems likely that most, if not all, of the whales bound for these other sites would be funnelled through Cap Lopez. It also seems plausible that humpback whales (particularly males) might move between areas. Given a recorded rate of 4–6 n.miles per hour (Dawbin, 1966), Pagalu, São Tome and Equatorial Guinea are within two days swim of Cap Lopez. More effort needs to be invested in establishing: (1) where Gulf of Guinea calving grounds are; (2) how large the population using each area is; and (3) what the relationships between the animals seen in the Gulf of Guinea populations and those seen in the Antarctic are. Photo-identification studies would be particularly valuable in this regard (e.g. Hammond *et al.*, 1990).

Conservation concerns

The Gulf of Guinea, particularly the region around Cap Lopez, supports a rich cetacean fauna. In addition to humpback whales and the dolphin species already noted, historic records suggest that (in decreasing frequency) sei and Bryde's (*Balaenoptera borealis* and *B. edeni*), sperm (*Physeter macrocephalus*), fin (*Balaenoptera physalus*) and southern right whales (*Eubalaena australis*) were captured by whalers based at Cap Lopez (Budker, 1952; Budker and Collignon, 1952). Pilot whales (*Globicephala macrohynchus*?) are also reported to frequent the area (J. Rouzaud, pers. comm.).

In the short term, several factors may threaten these whales. A growing commercial shrimp fishery operates in and around the Baie du Cap Lopez which may pose an entanglement risk to whales and dolphins. Commercial fishing is effectively unregulated and overfishing may directly or indirectly deplete cetacean food species. The large amount of boat traffic associated with the petroleum industry and the industry itself may also pose problems via collision, noise pollution and chemical pollution. Lack of data limits our ability to evaluate how much of a threat, if any, these factors represent to cetaceans in the area. Obtaining the data necessary to identify and monitor threats will require a concerted effort and considerable resources. Neither the Gabonese Government nor local non-governmental organisations have the means or the

expertise to monitor threats to cetaceans. Their support is vital should management responses be required. Cetacean conservation must be seen in the context of the coastal marine ecosystem and potential coastal development in the area.

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REFERENCES

- Aguilar, A. 1985. Aboriginal whaling off Pagalu (Equatorial Guinea). *Rep. int. Whal. Commn* 35:385-6.
- Budker, P. 1952. Quelques considérations sur la campagne baleinière 1951 au Cap Lopez (Gabon). *Mammalia* 14(4):154-8. [In French].
- Budker, P. 1953. Les campagnes baleinières 1949-1952 au Gabon. (Note préliminaire). *Mammalia* 17(3):129-48. [In French with English summary].
- Budker, P. 1954. Whaling in French oversea territories. *Norsk Hvalfangsttid.* 43(6):320-6. [In Norwegian and English].
- Budker, P. and Collignon, J. 1952. Trois campagnes baleinières au Gabon (1949-1950-1951). *Bull. Inst. Etud. Centrafr.* 3:75-100. [In French].
- Budker, P. and Roux, C. 1968. The 1959 summer whaling season at Cape Lopez (Gabon). *Norsk Hvalfangsttid.* 6:141-5. N.
- Calzada, N. and Aguilar, A. 1996. Flipper development in the Mediterranean striped dolphin (*Stenella coeruleoalba*). *Anat. Rec.* 245:708-14.
- Committee for Whaling Statistics. 1933. *International Whaling Statistics* Vol. IV, Oslo.
- Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp. 145-70. In: K.S. Norris (ed.) *Whales, Dolphins, and Porpoises*. University of California Press, Berkeley and Los Angeles. xv+789pp.
- Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn* (special issue) 13:39-68.
- Findlay, K.P., Best, P.B., Peddemors, V.M. and Gove, D. 1994. The distribution and abundance of humpback whales on their southern and central Mozambique winter grounds. *Rep. int. Whal. Commn* 44:311-20.
- Hammond, P.S., Mizroch, S.A. and Donovan, G.P. (eds.). 1990. *Rep. int. Whal. Commn.* (special issue 12). *Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters*. International Whaling Commission, Cambridge, UK. [vi]+440pp.
- Herman, L.M. and Antinaja, R.C. 1977. Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst., Tokyo* 29:59-85.
- International Whaling Commission. 1994. Report of the Scientific Committee, Annex E. Report of the Sub-Committee on Southern Hemisphere Baleen Whales, Appendix 3. Report of the Working Group on Humpback Whale Stock Identification. *Rep. int. Whal. Commn* 44:105-6.
- Mattila, D.K. and Clapham, P.J. 1989. Humpback whales, *Megaptera novaeangliae*, and other cetaceans on Virgin Bank and in the northern Leeward Islands, 1985 and 1986. *Can. J. Zool.* 67(9):2201-11.
- Rosenbaum, H.C., Walsh, P.D., Razafindrakoto, Y., Vely, M. and DeSalle, R. 1997. First description of a humpback whale breeding ground in Baie d'Antongil, Madagascar. *Conserv. Biol.* 11:312-4.
- Swartz, S.L. 1986. Gray whale migratory, social and breeding behavior. *Rep. int. Whal. Commn* (special issue) 8:207-29.
- Tønnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling*. C. Hurst & Co., London. i-xx+798pp.
- Tyack, P. and Whitehead, H. 1983. Male competition in large groups of wintering humpback whales. *Behaviour* 83:132-54.
- Whitehead, H. and Moore, M.J. 1982. Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool.* 60:2203-11.

A note on food consumption and growth of common dolphins (*Delphinus delphis*)

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ABSTRACT

Food consumption, body weight and body length were recorded in four female common dolphins (*Delphinus delphis*) at Marineland of New Zealand between 1974 and 1996. The study is based on historical data that were recorded for short-term husbandry purposes. The composition and caloric value of the diet sometimes varied from day to day. The food intake quantities should therefore be viewed as rough weight estimates of what wild conspecifics might eat (depending on their diet). Annual food intake of two dolphins increased to 3,300kg at around 12 years of age, after which it decreased, stabilising at around 2,200kg between the ages of 16 and 25 years. Annual food intake of the other two animals increased to 2,700kg at six/seven years of age, then declined and stabilised at around 2,100kg between the ages of seven/eight and 12 years. The weights of two of the animals were first recorded at the ages of seven and eight years. During the following 19 years, their body weight gradually increased by about 15kg. The other two animals grew from around 57kg at the age of two/three years to about 100kg at around 12 years of age. The two animals grew much in length when they were between two and eight years old. The other two animals appeared to have reached asymptotic length by 18 and 19 years of age when their length was measured for the first time. As body weight increased, daily food consumption as a percentage of body weight decreased. At a body weight of around 60kg, the dolphins consumed the equivalent of around 12% of their body weight per day. When body weight had reached around 100kg, daily consumption had fallen to around 6% of body weight.

KEYWORDS: ENERGETICS; FEEDING; NUTRITION; MORPHOMETRICS; COMMON DOLPHIN; CAPTIVITY

INTRODUCTION

The common dolphin (*Delphinus delphis*) is found worldwide in temperate, tropical and sub-tropical seas. In those areas, it is present along most coasts over the continental shelf, roughly along the 200–300m isobath, or over prominent underwater topography such as the mid-Atlantic Ridge and sea mounts (Evans, 1994). Common dolphins feed on a wide variety of squid and fish species, particularly schooling fish such as sardines, anchovies, herring, mackerel and pilchards (Fitch and Brownell, 1968; Ross, 1984; Major, 1986; Overholtz and Waring, 1991; Gaskin, 1992; Evans, 1994; Kuiken *et al.*, 1994; Osnes-Erie, 1995). The diet varies seasonally and geographically (Evans, 1994). Herds frequently cooperate in prey capture; for example, they may dive below a school of fish to drive it to the surface. Common dolphins have also been reported to catch fish in mid-air. Off southern California, they feed mostly nocturnally, on organisms associated with the deep scattering layer, which rises at night (Gallo, 1991; Evans, 1994). Dives of up to 260m and eight minutes have been recorded (Evans, 1971).

Although this is one of the most widely distributed cetacean species (Gaskin, 1992) and much is known about its foraging habits, no information exists on its energetic requirements. Such information can, to some extent, be derived from studies of captive animals. However, the common dolphin is a species that has seldom been maintained in captivity (Evans, 1994), and no quantitative information is available in the literature on its food intake requirements. Marineland of New Zealand has kept four female common dolphins over a long period of time, and collected data on their food consumption, body weight and

body length. However, it should be stressed that these data were not collected as part of a long-term experiment to estimate the energetic requirements of common dolphins.

Records of food consumption, body weight and length in toothed whales kept in captivity may be of interest to other zoological institutions that keep the same species, providing a reference for veterinary and husbandry purposes; the records may also be used to estimate the relationship between wild individuals and their prey populations.

Given the lack of data available on the common dolphin, this paper summarises the available data for the four Marineland specimens.

MATERIALS AND METHODS

Study animals and measurements

The four female common dolphins used in this study were caught in Hawke Bay, North Island, New Zealand. The birth date of each animal was estimated from body length (based on the age-body length relationship of seven male and one female common dolphin caught in the eastern tropical Pacific as reported by André *et al.* (1990); it should be noted that the study animals came from a different population), weight, condition of the teeth and general body condition (Table 1). These estimates are believed to be fairly accurate for animals 003 and 004, as the animals were young and were measured on arrival. However, the age estimates for animals 001 and 002 are less accurate since the animals were not measured on arrival. Their ages may be overestimated by one to two years. Age one represents the first calendar year after the estimated year of birth. The number of body weight measurements per year increased during the study period from one per year in the beginning of the study to about five

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Table 1
The body length, body weight and estimated ages on arrival of the four female common dolphins at Marineland of New Zealand.

Animal	Body length (cm)	Body weight (kg)	Estimated age (year)	Estimated year of birth	Arrival date at Marineland
DdMNZ001	*	*	3	1971	13 Dec. 1974
DdMNZ002	*	*	4	1970	13 Dec. 1974
DdMNZ003	170	56	3	1984	27 Jan. 1987
DdMNZ004	162	57	2	1985	26 Jan. 1987

* not measured on arrival

times per year towards the end. The data are insufficient to examine seasonal trends. The standard body length (straight line from tip of rostrum to notch of tail fluke) of each animal was measured three to four times between 1987 and 1997. None of the study animals reproduced during the study period as no males were present; hormone analyses were not conducted.

Study area

The animals were maintained primarily in an outdoor pool system consisting of a main pool (30 × 15m, 4.1m deep) and an adjacent holding pool (9.2 × 9.2m, 2.3m deep). The animals had free access to both pools. The main pool was the location of the 2-3 daily shows. A second pool system, consisting of a round pool (15m diameter, 2.3m deep) and an adjacent holding pool (9.1 × 4.5m, 2m deep), was used during maintenance work on the main system. The dolphins had free access to both pools and shows were presented as usual. Maintenance work on the main pool was carried out in 1977, 1978, 1983, 1984, 1989, 1990, 1991, 1992, 1993 and 1995, generally in November. The water was pumped from the sea via feeder pipes laid under the seabed and wells on the beach front. The salinity was recorded from 1992 to 1996 and remained stable at around 35 parts per thousand. The average monthly water temperature from 1981 onwards varied from 11.1°C in June to 22.2°C in January. The average monthly air temperature at Marineland (1981-1996) ranged from 8.9°C in July to 28.4°C in February. Napier, the site of Marineland, lies on the east coast of the North Island, New Zealand (39°20'S and 176°56'E).

Food

The study animals were fed primarily on a vitamin-enriched diet of defrosted fish. Until 1981, the enrichment consisted of a mixture of multi-vitamin tablets, vitamins A, B1 (Thiamine), C, E, K, kelp and cod liver oil. From 1981 this mixture was replaced by Sea Tabs (Pacific Research Laboratories, California, USA; these were later called 'Mazuri' Vita-zu). The diet consisted of a variety of fish species: jack mackerel (*Trachurus declivis*), barracouta (*Thyrstites atun*), Dutch herring (*Clupea harengus harengus*), king salmon (*Oncorhynchus tshawytscha*), yellow eyed mullet (*Aldrichetta forsteri*), tuna/albacore (*Thunnus alalunga*), sprat (*Sprattus antpodum*), gemfish (*Rexia solandri*), alfonso (*Beryx splendens*), pelagic cardinalfish (*Howella brodiei*), blue mackerel (*Scomber australasicus*), red gurnard (*Chelidonichthys kumu*), red cod (*Pseudophycis bachus/Phyculus bachus*), trevally (*Pseudocaranx dentex*), kahawai (*Arripis trutta*), hake (*Merluccius australis*), hoki (*Macruronus novaezelandiae*) and arrow squid (*Nototodarus sloanii*). Proportions varied, but jack mackerel and barracouta dominated the diet. When available (quite frequently in summer but infrequently in winter), the same species of fish were given fresh. The type

and amount of food eaten per feed was recorded for each dolphin; these historical daily food records, originally collected for short-term husbandry purposes, form the basis of the present study. The composition and caloric content of the fish and squid species were not measured, but probably varied per year class of fish, seasonally and depending on the location where the fish were caught. Given this variation, the total amounts per month and per year were used rather than attempting unreliable extrapolations based on unverifiable assumptions.

The animals were fed a fixed base ration each day, normally in three feeds. The base ration for each animal was monitored and, if necessary, adjusted weekly, on the basis of a number of factors including progress in training, speed at which the fish were swallowed and the animal's body weight.

RESULTS

Annual food consumption and growth

All ages reported in this study are estimated ages. Dolphin 001 showed an increase in annual food consumption from 1,800kg at four years of age to 3,300kg at 12 years of age. Thereafter, annual food intake gradually decreased, to stabilise at around 2,300kg at the age of 17 years (Fig. 1). Average annual body weight was stable between the ages of seven and eight years, after which it increased until the age of 11 years, then stabilised (Fig. 2). Between the ages of 18 and 26 years, standard body length showed little change (Fig. 3).

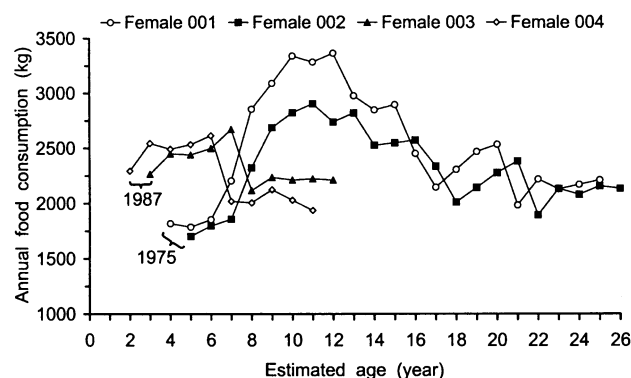


Fig. 1. The annual food consumption of four female common dolphins at Marineland.

Between the ages of five and 11 years, the annual food consumption of dolphin 002 increased rapidly from 1,700kg to 2,900kg, then gradually decreased, stabilising at around 2,100kg at the age of 18 years (Fig. 1). Average annual body weight increased gradually from eight to 26 years of age (Fig. 2). Between the ages of 19 and 27 years, there was little change in standard body length (Fig. 3).

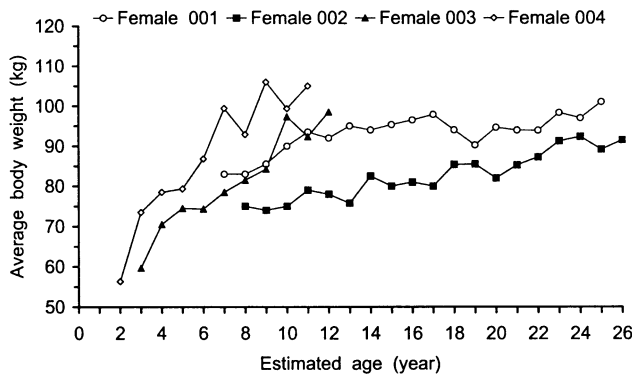


Fig. 2. Average annual body weight of four female common dolphins at Marineland ($n = 1-5$ measurements per year).

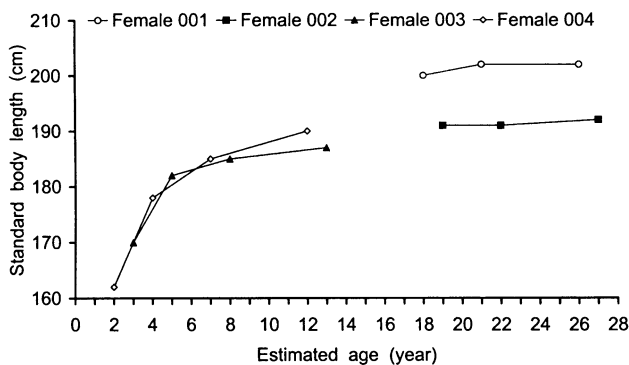


Fig. 3. Estimated age versus standard body length (single measurements per year) of the four study animals.

Dolphin 003 showed an increase in annual food consumption from 2,250kg to 2,700kg between the ages of three and seven years. Thereafter, annual food intake decreased rapidly and stabilised at around 2,200kg (Fig. 1). Between the ages of three and 12 years, her annual average body weight showed a gradual increase (Fig. 2). Standard body length increased greatly between the ages of three and five years, after which the growth rate decreased (Fig. 3).

Between the ages of two and six years, dolphin 004 showed an increase in annual food consumption from 2,300kg to 2,600kg. Thereafter, intake fell and stabilised at around 2,000kg (Fig. 1). Between two and 11 years of age, her average body weight increased gradually (Fig. 2). Standard body length increased much between the ages of two and four years, after which the growth rate decreased (Fig. 3).

During the course of a year, body weights fluctuated in all animals, but in years in which four or more weight measurements were made, these fluctuations were not seasonal.

Body length-body weight relationship

Based on the four study animals, the relationship (Fig. 4) between standard body length (L in cm) and body weight (W in kg) can be expressed as:

$$W = 7.5814 (L-140)^{0.5345}$$

Food consumption as a percentage of body weight

There is a negative relationship between body weight and average daily food consumption in the month in which the weight measurement was recorded as a percentage of body weight (Fig. 5). At around 60kg, the dolphins consumed, on average, the equivalent of around 12% of their body weight

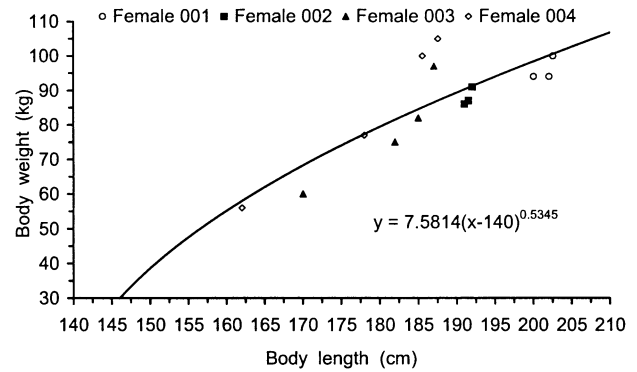


Fig. 4. The relationship between standard body length and body weight of the four study animals.

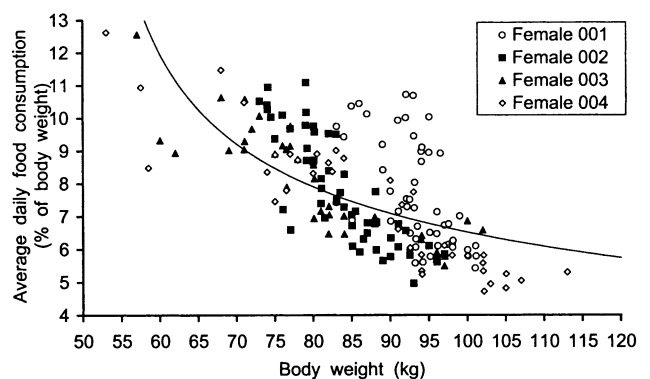


Fig. 5. The relationship between body weight and average daily food intake as a percentage of body weight for the four female common dolphins. Each point is the average daily food intake of the month in which the body weight was measured.

per day; this fell to an average of around 6% at a body weight of around 100kg. Dolphin 001 showed wide fluctuations around this pattern.

DISCUSSION AND CONCLUSIONS

Annual food consumption

As explained earlier, it was not possible to estimate food consumption in terms of actual caloric values. Weight of food per year is considered the most appropriate unit to use under these circumstances, given seasonal variation in the energy content of individual prey species and variation in the species composition of the diet.

Patterns in food intake and growth of the dolphins that arrived simultaneously were comparable. However, the intake of the first pair between the ages of four and seven years was lower than that of the second pair. While this could be due to natural variation, it may reflect a slow habituation to captivity by animals 001 and 002. During the first 2-3 years after arrival, these animals ate relatively little and their body weights showed little change. Animals 003 and 004 may have habituated faster to captivity in the presence of habituated animals 001 and 002 and due to the increased husbandry experience of the staff.

All four animals showed an initial increase in annual food intake, followed by a decrease and stabilisation. The maximum food intake in animals 001 and 002 was reached at 11-12 years of age, while the intake of animals 003 and 004 peaked at the ages of six and seven years. The high food intake of dolphin 001 between the ages of six and 12 years coincided with a period of strong weight increase,

suggesting extra food intake to fuel growth. Dolphin 002's food intake increased between the ages of seven and 11 years. However, her body weight did not increase greatly during that period and the extra food intake can therefore not be explained. The high food intake of dolphins 003 and 004 between the ages of two and seven years coincided with high growth rates (both in weight and length), suggesting that, as in dolphin 001, the high food intake fuelled growth.

The decline in food intake and reduction in growth rate in the present study occurred when the dolphins were between seven and 12 years old. This is around the age that growth curves of common dolphins in the wild reach an asymptote in most areas (André *et al.*, 1990; Ferrero and Walker, 1995) and the energetic requirements for growth are expected to decrease. The geographical distribution of the common dolphin is wide and regional variations in body size are large (Gühr and Pilleri, 1969; Evans, 1994; Ferrero and Walker, 1995). In the North Pacific, females are sexually mature at the age of approximately eight years, with an average length of 171cm and with a predicted asymptotic length of 179cm (Ferrero and Walker, 1995). Off southern California females mature at around seven to 12 years of age, at a length of between 165 and 182cm (Hui, 1979).

There are few available data on the relationship between age and body weight in common dolphins. The majority of studies of body weight used stranded animals, which are unlikely to be representative of healthy animals. A number of studies, however, relied on animals accidentally caught in fisheries and are thought to be more representative of healthy animals in a population. Although based on a sample size of only eight animals (seven of which were male), common dolphins in the eastern tropical Pacific generally appear to weigh slightly less than the animals in the present study (André *et al.*, 1990) (Table 2). Only a 93kg 14-year-old male was within the weight range of the females in the present study, possibly due to pronounced sexual dimorphism at an older age. Whether the weight difference between studies is due to sexual dimorphism, differences between stocks, or obesity of the study animals is not clear.

Body length-body weight relationship

Gühr and Pilleri (1969) report on the body length-weight relationship of five female common dolphins captured in the Mediterranean. Those animals weighed approximately 10kg less at similar body length than the animals in the present study. André *et al.* (1990) report on the body length-weight relationship of one female common dolphin caught in the eastern tropical Pacific which was 145cm long and weighed 28kg. The measurements were close to the regression line based on the animals in the present study (Fig. 4). A captive adult female from waters around New Zealand (the area from which the animals in the present study originate) had a body length (201cm) to weight (94kg) relationship similar to that

Table 2
Body measurements and estimated ages of common dolphins caught in the eastern tropical Pacific (from André *et al.*, 1990).

Sex	Body length (cm)	Body weight (kg)	Age (year)
M	128	27	0.6
F	145	28	0.8
M	165	49	2
M	179	60	3
M	195	73	12
M	205	80	10
M	206	78	14
M	210	93	14

of the animals in the present study (Logan and Robson, 1971). Ross (1984) reports on the length-weight relationship of eight common dolphins (sex unspecified) which were caught in shark nets on the southeast coast of southern Africa. The relationship is similar to that found in the present study. Ross noticed that the animals from southeast southern Africa were heavier per unit length than the animals reported by Gühr and Pilleri (1969) from the Mediterranean, and similar to those of the northeast Atlantic (Aloncle, 1964; 1968).

Food consumption as a percentage of body weight

Four common dolphins accidentally bycaught off the northeastern United States were shown, on the basis of stomach contents, to have been feeding exclusively on Atlantic mackerel, *Scomber scombrus* (Overholtz and Waring, 1991). Their daily ration (Table 3) was estimated from a theoretical model of energetic needs and an assumed energy content of 1.43 kcal/g for Atlantic mackerel. The estimates generally agree with the food intake data from the present study (Fig. 5), although the daily food requirement of the 62kg animal was underestimated by Overholtz and Waring. They probably did not consider that common dolphins of that weight are young and undergoing rapid growth, and therefore require a relatively large amount of food. Adult animals require less energy per kg body weight than growing animals as was shown in the present study for common dolphins and for bottlenose dolphins (*Tursiops truncatus*) by Reddy *et al.* (1994).

Ecological significance

The present study provides only a rough estimate of the food intake of wild common dolphin populations, as it is based on only four females and uses mass of a mix of fish species per year as the energy 'unit'. Common dolphins show distinct sexual dimorphism, the asymptotic length of adult males being on average 10cm greater than females from the same stock (Hui, 1979; Ferrero and Walker, 1995). After maturation, therefore, the food intake of males may differ

Table 3

The stomach contents weight of four common dolphins, caught incidentally off the northeastern United States, which had been feeding exclusively on Atlantic mackerel (*Scomber scombrus*). Also shown are the estimate of Overholtz and Waring (1991)* for the daily required ration and the estimated daily ration based on the body weight-food intake relationship of the present study.

Body length (cm)	Body weight (kg)	Sex	Weight of stomach contents (kg)	Estimated % of ration	Estimated daily ration (kg) *	Estimated daily ration based on data of present study (kg)
170	62	M	0.7	20	3.5	5.5
200	94	M	1.2	23	5.2	4.9, 5.0, 5.6, 5.8, 5.9, 7.2, 8.5
207	104	F	2.4	44	5.5	5.1
213	110	M	0.3	6	5.0	5.0

from that of non-lactating females of similar age. Information on food intake of males is necessary to provide a more accurate estimate of the food intake of a common dolphin population. The females in the present study did not reproduce, as no males were present. Lactating bottlenose dolphins and Commerson's dolphins (*Cephalorhynchus commersonii*) require much more food than non-lactating females (Kastelein *et al.*, 1993; In press-a; b; Reddy *et al.*, 1994), suggesting that the average consumption of lactating female common dolphins is higher than that of the study animals.

Water temperature may influence food intake in cetaceans by affecting thermoregulation. While the common dolphin has been found in waters between 1-24°C, most sightings occur in waters between 7-23°C (Gaskin, 1968; Winn, 1982; Selzer and Payne, 1988). The water temperature at Marineland of New Zealand falls within this range, suggesting that the animals were maintained within the thermoneutral range for the species, assuming wild animals are well adapted to their environment. Therefore, when considering temperature, the food intake data from the present study may be considered representative of wild populations.

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REFERENCES

- Aloncle, H. 1964. Premières observations sur les petits cétacés des côtes Marocaines. *Bull. Inst. Pêches Marit. Maroc* 12:21-42. [In French].
- Aloncle, H. 1968. Deuxième note sur les petits cétacés de la baie Ibéro-Marocaine. *Bull. Inst. Pêches Marit. Maroc* 16:33-44. [In French].
- André, J.M., Ribeyre, F. and Boudou, A. 1990. Relations between age, total length, total weight and weight of the organs in three species of dolphins from the Eastern tropical zone of the Pacific Ocean. *Mammalia* 54(3):479-88. [In French with English summary].
- Evans, W.E. 1971. Orientation behaviour of delphinids: radio telemetric studies. *Ann. NY Acad. Sci.* 188:142-60.
- Evans, W.E. 1994. Common dolphin, white-bellied porpoise - *Delphinus delphis* Linnaeus, 1758. pp. 191-224. In: S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 5. *The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.
- Ferrero, R.C. and Walker, W.A. 1995. Growth and reproduction of the common dolphin, *Delphinus delphis* Linnaeus, in the offshore waters of the north Pacific Ocean. *Fish. Bull.* 93(3):483-94.
- Fitch, J.E. and Brownell, R.L. 1968. Fish otoliths in cetaceans stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Bd Can.* 25(12):2561-74.
- Gallo, J.P. 1991. Group behaviour of common dolphins (*Delphinus delphis*) during prey capture. *An. Inst. Biol. Univ. Nac. Autón. México* 62(2):253-62.
- Gaskin, D.E. 1968. Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. *NZ J. Mar. Freshwater Res.* 2(3):527-34.
- Gaskin, D.E. 1992. Status of the common dolphin (*Delphinus delphis*) in Canada. *Can. Field-Nat.* 106(1):55-63.
- Gihl, M. and Pilleri, G. 1969. On the anatomy and biometry of *Stenella styx* Gray and *Delphinus delphis* L. (Cetacea, Delphinidae) of the western Mediterranean. p. 219. In: G. Pilleri (ed.) Vol. 1. *Investigations on Cetacea*. Brain Anatomy Institute, Berne, Switzerland.
- Hui, C.A. 1979. Correlates of maturity in the common dolphin, *Delphinus delphis*. *Fish. Bull.* 77:295-300.
- Kastelein, R.A., McBain, J., Neurohr, B., Mohri, M., Saijo, S., Wakabayashi, I. and Wiepkema, P.R. 1993. Food consumption of Commerson's dolphins (*Cephalorhynchus commersonii*). *Aquat. Mamm.* 19(2):99-121.
- Kastelein, R.A., Nieuwstraten, S.H., Walton, S. and Wiepkema, P.R. In press-a. Food intake and growth of Atlantic bottlenose dolphins (*Tursiops truncatus*). *Mar. Environ. Res.*
- Kastelein, R.A., Staal, C. and Wiepkema, P.R. In press-b. Food consumption and growth of Atlantic bottlenose dolphins (*Tursiops truncatus*). *Mar. Mammal Sci.*
- Kuiken, T., Simpson, V.R., Allchin, C.R., Bennett, P.M., Codd, G.A., Harris, E.A., Howes, G.J., Kennedy, S., Kirkwood, J.K., Law, R.J., Merrett, N.R. and Phillips, S. 1994. Mass mortality of common dolphins (*Delphinus delphis*) in south west England due to incidental capture in fishing gear. *Vet. Rec.* 134(4):81-9.
- Logan, F.D. and Robson, F.D. 1971. On the birth of a Common dolphin (*Delphinus delphis* L.) in captivity. *Zool. Garten.* 40(3):115. -24.
- Major, P.F. 1986. Notes on a predator-prey interaction between common dolphins (*Delphinus delphis*) and short-finned squid (*Illex illecebrosus*) in Lydonia Submarine Canyon, Western North Atlantic Ocean. *J. Mammal.* 67(4):769-0.
- Osnes-Erie, L.D. 1995. Food habits of short-beaked (*Delphinus delphis*) and long-beaked (*Delphinus capensis*) common dolphins off California. Abstract of the Marine Mammal Society Conference, Orlando.
- Overholtz, W.J. and Waring, G.T. 1991. Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. *Fish. Bull.* 89(4):723-8.
- Reddy, M., Kamolnick, T., Curry, C., Skaar, D. and Ridgway, S. 1994. Energy requirement of bottlenose dolphins in relation to sex, age and reproductive status. *Marine Mammals: Public Display and Research* 1(1):26-31.
- Ross, G.J.B. 1984. The smaller cetaceans of the southeast coast of southern Africa. *Ann. Cape Prov. Mus. (nat. Hist.)* 15(2):173-410.
- Selzer, L.A. and Payne, P.M. 1988. The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. *Mar. Mammal Sci.* 4(2):141-53.
- Winn, H.E. 1982. A characterization of marine mammals and turtles in the Mid- and North Atlantic areas of the US outer continental shelf, Final Report. Nat. Tech. Inf. Serv. PB83-215855. 586pp.

Strike Limit Algorithm optimisation: a realistic example

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ABSTRACT

This paper illustrates a process for finding an improved variant of an aboriginal whaling management procedure *Strike Limit Algorithm* (SLA), applying the merging and optimisation approach of Givens (1997; 1999b). A modified version of the SLA developed by Punt and Butterworth (1997) was chosen as the procedure to be optimised for management of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. The optimisation considers functions of the catch limit and other outputs from the nominal SLA, along with outputs from two other SLAs and estimates of certain population dynamics parameters. The result reduced the Bayes risk by over 90%, compared to the nominal procedure, and improved simulated SLA performance by usually allowing more strikes at less depletion risk. Such results suggest that this approach may be attractive in the general development of wildlife management procedures.

KEYWORDS: MANAGEMENT PROCEDURE; MODELLING; WHALING – ABORIGINAL; ARCTIC; BOWHEAD WHALE

INTRODUCTION

International Whaling Commission (IWC) management of aboriginal subsistence whaling will eventually rely on an aboriginal whaling management procedure (AWMP) chosen from a collection of candidate procedures after extensive simulation testing (e.g. see Donovan, 1999; IWC, 2000). An AWMP is a fully automatic algorithm designed to operate on the results of an assessment (i.e. a statistical estimation problem relying on sparse series of whale abundance data), and to produce a catch limit in each year of real (or simulated) management. The only inputs to an AWMP which vary over time are: (i) stock abundance estimates and corresponding coefficients of variation; (ii) point and variance estimates for the proportion of the stock that belongs to certain age or size classes; (iii) a number of whales 'needed' to be caught for each year up to the present; and (iv) numbers of whales actually caught during past years. As time progresses, new data on these quantities become available.

'Need' is usually expressed as a number of whales and is set periodically, often in 4–5 year blocks, by the IWC on the basis of 'need statements' submitted by individual IWC member nations. Evaluation of such need statements is a political rather than a scientific process. Nations requesting aboriginal hunting catch limits provide information about the operation and history of the aboriginal whaling fishery and their estimation of present-day nutritional and cultural needs to justify their requests. Thus, the setting of 'need' is the function of the political body of the IWC. However, that body instructs its Scientific Committee to assess whether a whale stock can safely sustain the established 'need' level. Since future 'need' is unknown, the IWC has asked the Scientific Committee to ensure that candidate AWMPs perform adequately within a range of potential future need trajectories. By explicitly providing this range, the IWC has enabled AWMP developers to avoid a complex and probably futile scientific debate over predicting future need and to instead focus on ensuring need satisfaction (IWC, 1999).

Although potential AWMPs may employ sophisticated modelling and estimation strategies, an AWMP can also be a completely arbitrary procedure (i.e. a 'black box'); ultimately, an AWMP will be judged primarily on how it performs in simulation. An AWMP should, as far as

possible, meet the potentially conflicting IWC objectives of low chance of population extinction or severe depletion, high satisfaction of needed catch and high rate of population recovery (IWC, 1999). The key component of an AWMP is the *Strike Limit Algorithm* (SLA) that calculates catch limits from available data.

AWMPs are tested through extensive computer simulation. A population dynamics model is used to project a whale stock from a specific date in history (usually associated with pre-exploitation) to 100 years in the future. All available past data about the stock are available to the AWMP, as are simulated future abundance survey and other data, and future need. Simulations are repeated for a vast collection of scenarios that vary assumptions about whale biology and dynamics, hunting and the environment. Each scenario is replicated 100 times (this is termed a 'trial') so that different random future data sequences are encountered by the AWMP for each scenario.

An analogous management procedure (the 'Revised Management Procedure' – RMP) for commercial whaling has already been developed (e.g. IWC, 1994). One strength of the RMP development process was the concentrated effort on whale population dynamics and assessment models. This resulted in rigorous simulation comparison of five competing commercial whaling management procedures, many of which employed such models (e.g. see IWC, 1992).

A major difference in the development of the AWMP from the RMP is that the focus is on a case-specific rather than a generic approach, partially in recognition of the accomplishments of the RMP development process, but largely because aboriginal subsistence whaling is limited to a few stocks and areas with recognised 'need' but with quite different levels of biological knowledge (IWC, 1999). It is not enough for an AWMP to have the best average performance across implementations. Rather, performance must be optimised individually for each stock so that in each case aboriginal need is met to the greatest extent possible subject to risk and recovery limitations.

One idea proposed to address this stock-specific approach was a framework for embedding the development and selection of one of a small number of candidate SLAs in a larger statistical estimation problem. From this idea has grown a number of techniques (Givens, 1997; 1998; 1999a; b; c; Givens and Bernstein, 1998; Givens *et al.*, 1999):

- (1) *H-optimisation*: a method for enhancing a nominal *SLA* to improve its performance.
- (2) *H-tuning for equivalence*: a method for equivalencing several competing *SLAs* so that their performance may be fairly compared.
- (3) *Merging*: a method for the optimal mathematical combination of several competing *SLAs* to produce strike limits that better meet management goals.

These terms are used by the IWC Scientific Committee Standing Working Group on the Development of an AWMP (IWC, 1999). In statistical terminology, all three methods amount to choosing a Bayes rule estimator within some class.

Much of the work with these methods has used relatively simple *SLAs*, limited trials, abbreviated result summaries, or abstracted examples to investigate the methods and illustrate their features. In this paper, a realistic application is presented: the development of an optimised *SLA* for the set of scenarios designed by the Scientific Committee (IWC, 1999) to resemble management of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. The scope of this application is similar to the approach that the IWC Scientific Committee might take if it were to attempt a final optimisation or merging of candidate *SLAs* for this stock. The analysis that follows is the first comprehensive and realistic test of the optimisation and merging approach.

Terminology and labels

The AWMP development process has resulted in a long list of esoteric terms and labels; these are defined in appendix 2 of IWC (1999).

The term *Initial Exploration Trial* is relevant here, referring to a case-specific set of simulation assumptions used to test an AWMP *SLA*. In this paper, the 'fishery type 2' *Initial Exploration Trials* will be used. 'Fishery type 2' refers to a case where there is a relatively large amount of available information and the existing IWC guidelines for the management of aboriginal whaling have largely been met, such as the Bering-Chukchi-Beaufort Seas stock of bowhead whales. There are six type-2 trials; the assumptions of each are given in appendix 3 of IWC (1999). In this paper, only the trials denoted B3 and B7 will be used. Trial B7 is one of the most pessimistic trials, assuming very low productivity, a low recent stock abundance and high increasing 'need'. Trial B3 is one of the most optimistic, assuming a high productivity rate and high recent abundance.

The IWC Scientific Committee will ultimately judge the *SLAs* by assessing how they accomplish depletion avoidance, need satisfaction and stock recovery for the management of a simulated stock across 100 replicate trial simulations of 100 years length, over a wide variety of trials. No formulaic combination of these criteria is intended. Two very important statistics used by the Scientific Committee and later in this paper are final depletion (denoted $D1_{1+}$) and total need satisfaction (denoted $N1$). Final depletion is the ratio of final abundance of whales aged 1 or older after 100 years of simulated management to the number of whales aged 1 or older in an unexploited, equilibrium population. Total need satisfaction is the total number of permitted harpoon strikes divided by the total 'needed' strikes over 100 years of simulated management. Across replications, these statistics have probability distributions; percentiles such as the 5% and 50% points are usually reported. The precise

definitions of all performance evaluation statistics used by the Scientific Committee are given in appendix 3 of IWC (1999).

Many *SLAs* rely on terms in common use by the Scientific Committee to refer to notions related to density-dependent population dynamics including maximum sustainable yield (MSY), MSY level (MSYL), MSY productivity rate (MSYR), and replacement yield (RY). Hereafter, these terms should be interpreted as referring to the population component aged 1 year or older, unless otherwise specified.

Brief review of *H-optimisation* and *merging*

The optimisation and merging approach empirically adjusts an *SLA* by estimating a parameterised function of the nominal *SLA* outputs. The parameter estimation is set up in a manner for which the solution is an admissible Bayes rule, and hence has certain statistically desirable properties. The resulting optimal catch limits are functions of the output from one or more nominal *SLAs*. An informal review of this approach follows; a more formal presentation of the approach is given by Givens (1997; 1999b).

Let θ denote the values of unknown parameters such as MSYR and carrying capacity (K) which constitute the assumptions of a particular *Initial Exploration Trial*. At a particular point in time, in the ideal situation where θ is known, let an idealised strike limit be denoted $H(\theta)$ and let N represent aboriginal need at this time, both expressed as a number of whales.

H is an artificial construct used to shape or improve *SLA* simulation performance that may be discarded after use so that the IWC Scientific Committee may evaluate *SLAs* on whatever basis it desires. The Scientific Committee's current suggestion for H is given by IWC (1999) as the minimum of aboriginal need and the quantity $H^*(\theta)$ defined at time t as:

$$H^*(\theta) = \begin{cases} 0.9\text{MSY} & \text{if } P_t/K \geq \text{MSYL} \\ 0.8\text{RY} & \text{if } 2000/K \leq P_t/K < \text{MSYL} \\ 0 & \text{if } P_t < \text{MSYL} \end{cases} \quad (1)$$

In application, the idealised strike limits, $H(\theta)$, are never known because θ is unknown. However, the Scientific Committee would be thrilled to obtain an *SLA* with the performance characteristics of $H(\theta)$. Therefore, $H(\theta)$ can be used to obtain a simple performance goal that circumvents individual consideration of dozens of univariate performance statistics.

Given data X available at this time point and arising from likelihood function $\ell(X|\theta)$, the strike limit calculated by a candidate *SLA* at this time is denoted Q . Usually X would include a series of past abundance estimates and a catch history. Although one hopes to improve strike limits by using *H-optimisation* or *merging*, this *SLA* could be used as is; it is therefore called a *nominal SLA*. This *SLA* may rely upon some tuning parameters whose values are chosen by the developer, or for which several alternative values are used by the person doing the optimisation, as shown later in this paper.

Note that subscripts for time, trial scenario and trial replication number have been omitted from $H(\theta)$, N , X and Q here. The suppression of nuisance subscripts is continued hereafter where possible.

If a developer wished to improve the performance of one or more nominal *SLAs* on a variety of trials to which s/he assigned weights $p(\theta)$, the H-optimisation or merging approach would be to estimate ideal strike limits using a set of predictor variables derived from the nominal *SLA*(s). This estimation proceeds as follows:

- (1) Identify the ideal strike limits, $H(\theta)$. For a collection of possible values of θ , calculate $H(\theta)$ over a sample of replicate datasets (X) and time points. Recall that *SLAs* are tested via computer simulation. Thus, this step consists of simulating a replicated collection of trial scenarios and recording the ideal catch limits as each simulation progresses. The values of $H(\theta)$ are actually known here because specification of a trial scenario entails specification of θ .
- (2) Identify and observe potentially useful predictor variables, Y_0 . To predict $H(\theta)$, the obvious predictor variables to employ would be strike limits from nominal *SLA*(s). If more than one nominal *SLA* were used, these *SLAs* might be different tunings of the same procedure or one or more tunings of different procedures. With more than one nominal *SLA*, the H-optimisation process has been called merging because it extracts and combines the best information from several candidate *SLAs*. Other predictor variables might include intermediate calculations of nominal *SLAs*, particularly estimates of interesting biological parameters that are internal to the *SLAs*.

Denote the values of the complete collection of potential predictors at a particular time point as $Y_0 = \{Y_1, \dots, Y_p\}$.

In practice, the Y_0 and $H(\theta)$ can be collected simultaneously during the simulation of a replicated collection of trial scenarios.

- (3) Select predictors and a model class for optimisation. Of the p potential predictors (which may include interactions, polynomial terms, etc.) a subset may be selected for use in a model to predict $H(\theta)$. Suppose the selected predictors, Y are a subset of the potential predictors. The choice of Y is a statistical model selection problem: which predictors are believed to be most useful for predicting $H(\theta)$? This step is analogous to selecting the predictors in a linear regression model before solving for the optimal estimated regression coefficients.

Let $g(Y, \alpha)$ represent a way to combine the selected Y_i to form a strike limit – an example for three predictors might be:

$$g(Y, \alpha) = \min\left(N, \max\left(0, \alpha_0 + \alpha_1 Y_1 + \alpha_2 Y_2 + \alpha_3 Y_1^2 + \alpha_4 Y_3\right)\right) \quad (2)$$

where $\alpha = \{\alpha_0, \dots, \alpha_3\}$ and, for example, $Y_3 = Y_1 Y_2$. The α_i are parameters to be chosen through the optimisation process.

- (4) Define a Bayesian estimation context. In order to establish an optimality criterion for fitting models like equation (2), we must pose the solution of α as an estimation problem. This requires choosing a weighting, $p(\theta)$, of the trials. Also define a loss function to characterise the penalty accrued if $g(Y, \alpha)$ does not equal the ideal strike limit. Denote the loss $L(g(Y, \alpha), H(\theta))$. A typical choice would be squared error loss, namely $L(g(Y, \alpha), H(\theta)) = (g(Y, \alpha) - H(\theta))^2$.
- (5) Optimise. Optimisation amounts to minimising the average posterior expected loss, called the Bayes risk. In other words, the α_i are chosen to minimise:

$$\int_{\theta} \int_X \sum_{\text{time}} L(g(Y, \alpha), H(\theta)) p(\theta|X) dX d\theta \quad (3)$$

where $p(\theta|X) \propto p(\theta) \ell(X|\theta)$. If $\hat{\alpha}$ minimises the Bayes risk, then $g(Y, \hat{\alpha})$ is the optimal *SLA* within the class of *SLAs* characterised by a model class $g()$ and the inferential context established by $p(\theta)$, the likelihood and the loss function. By ‘optimal’ we mean that it is the estimated Bayes rule. Givens (1999b) also notes that it is an admissible estimate.

In practice, an estimated $\hat{\alpha}$ can be obtained by replacing the integrals in (3) with summations over the simulated trials and replicated data. The objective function is still a smooth function in α that depends only on a fixed set of constants (instances of X and θ).

Full technical details about H-optimisation and merging are provided by Givens (1997; 1999b).

Of course, an *SLA* with reduced mean Bayes risk does not necessarily have superior performance with respect to univariate evaluation statistics such as final depletion or total need satisfaction. However in the examples to date examined (Givens, 1997; 1998; 1999b), reduced risk did translate to enhanced performance. The application discussed next is no exception: a 90% reduction in Bayes risk resulted in an *SLA* that generally allowed more strikes at less depletion risk to the stock. This improvement in performance was possible because the optimised *SLA* made more efficient use of the available data.

OPTIMISATION OF THE PUNT-BUTTERWORTH *SLA*

The analysis that follows is organised into sections corresponding to the steps outlined above.

Identification of the ideal strike limits, $H(\theta)$

The choice of $H(\theta)$ given in equation (1) was used because it reflects IWC Scientific Committee performance preferences.

Identification of potentially useful predictors, Y_0

The Punt-Butterworth *SLA*

The goal of this paper is to improve the *SLA* described by Punt and Butterworth (1997). A slight variation on their procedure will hereafter be called the ‘nominal’ *SLA*. For setting a strike limit Q^{pb} in year t , their procedure is roughly as follows.

The *SLA* is based on a modified version of the estimator underlying the *Catch Limit Algorithm* (*CLA*) of the RMP for commercial whaling (IWC, 1994). Define Z_1 to be the q_1^{pb} posterior percentile of P_{t+20}/K , where P_t is the total stock size in year t , K is the corresponding carrying capacity, and the posterior distribution is the one calculated by their version of the estimator component of the *CLA*. Define Z_2 to be the q_2^{pb} percentile of P_{t+20}/P_t with respect to the same posterior. Projections made at time t about future P_{t+n} assume that future hunting mortality will remain constant for n years at the level it was in year t .

Punt and Butterworth (1997) made some alterations to the estimator at the core of the *CLA*; since these are superseded below, they are not mentioned further here.

The *SLA* estimates the highest level of catch which leads to at least one of $Z_1 \geq \text{MSYL}$ and $Z_2 \geq 1$ being satisfied. If this catch level is less than aboriginal need, then let Q^{pb} equal this catch level. Otherwise, let Q^{pb} equal aboriginal need. Since the estimator underlying the *CLA* does not employ an age-stratified dynamics model, *MSYL*, P_t , and K should be

interpreted here as referring to the total population component rather than the component aged 1 year or older.

The estimation relies on a variety of tuning parameters whose values were provided by Punt.

Modifications to the Punt-Butterworth SLA and predictors derived from it

To find an optimal variant of the Punt-Butterworth SLA, some small modifications were introduced to the original procedure. This modified version was used in the merging and optimisation framework.

For convenience, the full computation of Q^{pb} was done only each time a new abundance estimate was obtained. If aboriginal need changed in the interim, Q^{pb} was changed to equal the minimum of the most recent catch bound and the new need level. Otherwise, Q^{pb} remained constant until the new abundance estimate was available. There was no phase-out rule. All of these convenient omissions would be remedied in an implementable SLA.

The estimator used in the modified Punt-Butterworth SLA was revised from that proposed by Punt and Butterworth. Their estimator was based on that used in the CLA (IWC, 1994). In that original algorithm, the log-likelihood of the data was downweighted relative to the log prior by a multiplicative factor of

$$k = \frac{1}{16}.$$

The modification introduced here is that the downweighting factor was taken to be a time series starting at value k in the first year and ending at $k/(\beta^{pb})^2$ in the final year of the 100-year simulated management period. The change in this factor was not linear with time; rather β^{pb} changed linearly with time. Positive values of β^{pb} were allowed.

The variables Z_1 , Z_2 and Q^{pb} from this SLA (at various tunings) were used as potential predictors.

Predictors from other SLAs

The next step is to exploit the merging idea (Givens, 1997; 1999b). Merging is the empirical combination of strike limits from several independent SLAs to produce a final strike limit which minimises posterior expected loss. The merged SLA never has worse Bayes risk than the best of the individual SLAs. In some early examples, modest improvements were achieved through merging (Givens, 1997; 1999b; Givens *et al.*, 1999).

For this paper, two additional SLAs were used to generate predictors. These SLAs were based on the catch control laws denoted Q_0 and Q_1 by Wade and Givens (1997). Q_0 was originally designed by Givens *et al.* (1996) to mimic the existing aboriginal whaling management protocol as defined in Sub-paragraph 13(a) of the International Convention for the Regulation of Whaling (IWC, 1995a) and reiterated by IWC Resolution 1994-4 (1995b) calling for AWMP development. Specifically, the catch control laws used here were:

$$Q_0 = \begin{cases} \beta_3 \text{MSY} & \text{if } P_t / K \geq \text{MSYL} \\ \min(\beta_1(\text{RY} - 1), \beta_2 \text{MSY}) & \text{if } 2000 / K \leq P_t / K < \text{MSYL} \\ 0 & \text{if } P_t < 2000 \end{cases} \quad (4)$$

and

$$Q_1 = \begin{cases} \beta_3 \text{MSY} & \text{if } P_t / K \geq \text{MSYL} \\ \min(\beta_1 P_t \text{MSYR}, \beta_2 \text{MSY}) & \text{if } 2000 / K \leq P_t / K < \text{MSYL} \\ 0 & \text{if } P_t < 2000 \end{cases} \quad (5)$$

where the β_i are tuning parameters chosen to reflect performance goals.

The q^{wg} posterior quantiles of Q_0 and Q_1 (at various SLA tunings) were used as potential predictors. The posterior used to derive quantiles is the one calculated by the estimator component of the modified Punt-Butterworth SLA.

Again, for convenience, the full computation was done only each time a new abundance estimate was obtained. If aboriginal need changed in the interim, the strike limit was changed to the minimum of the calculated limit and the new need level. Otherwise, the strike limit remained constant until the new abundance estimate was available. There was no phase-out rule. All of these convenient omissions would be remedied in an implementable SLA.

Predictors based on estimated population dynamics parameters

Another source of potentially useful predictors is intermediate calculations in SLA assessment models. The q^{bio} posterior quantiles of four biological quantities were used as potential predictors: MSYR, MSYL, MSY and RY. Quantiles were calculated with respect to the posterior derived from the estimator component of the modified Punt-Butterworth SLA (at various tunings). K was not used because it is linearly related to MSYL for the dynamics model used. However, the MSYL predictor was expressed as a number of whales rather than a fraction of K .

For convenience, these quantiles were calculated only when an abundance estimate was obtained.

The complete set of potential predictors, Y_0

The eventual goal was to find the optimal α_i for models of the form:

$$Q = \min(N, \max(0, \alpha_0 + \alpha_1 Y_1 + \dots + \alpha_n Y_n)) \quad (6)$$

where the Y_i were individual quantiles from or two-way multiplicative interactions between quantiles from the following list of variables: Z_1 , Z_2 , Q^{pb} , MSYR, MSYL, MSY, RY, Q_0 , and Q_1 .¹ The immediate problem, however, was to determine which predictors to use. Unlike some previous applications of the method, no polynomial predictors were considered and time was not allowed as a predictor. Superior results could be obtained if these restrictions were relaxed.

Many different versions of these potential predictors were considered by varying the values of k , β^{pb} , q_1^{pb} , q_2^{pb} , q^{bio} , q^{wg} , β_1 , β_2 and β_3 . Table 1 lists the values of these parameters used to generate each potential predictor. Within each block of this table, a full factorial crossing of relevant parameters (i.e. all possible combinations), and all possible multiplicative two-way interactions except those involving italicised entries, were used to generate potential predictors. Thus, for example, the first block of Table 1 describes

$$3 \times 4 \times 2 + \binom{24}{2} = 300 \text{ possible predictors } Y_i.$$

Table 1 therefore lists 28,436 potential predictors overall.

To consider all possible multiplicative two-way interactions between blocks would raise the total number of potential predictor variables to 11,103,828. If one calculated the predictors only every 5 simulation years, on 100 replicates of two simulation trial scenarios, this would amount to a dataset of over 44 billion numbers to be used for

¹ For Q^{pb} , both Z_1 and Z_2 were calculated using $q_1^{pb} = q_2^{pb}$ and the same values for K and β^{pb} . This reduces the number of possible predictors.

prediction of $H(\theta)$. Such effort is far beyond the scope of this paper, so some shortcuts are described in the section on predictor selection.

Software used

Data used in this paper (including values of predictors and $H(\theta)$) were generated using the August 1998 version of the IWC's AWMP simulation software, which implemented the simulation model, type-2 trials and summary statistics specified at the September 1997 Scientific Committee meeting. Since September 1997 the model, trials and statistics have been substantially modified. IWC software to implement these changes was not available at the time this paper was written. The most current version of the IWC AWMP simulation software can be found at www.colostate.edu/~geof/iwcawmp.html.

Selecting predictors and a model class

This section describes the process by which a subset of predictors, Y , and a model class, $g(Y, \alpha)$, were selected. Table 1 lists 28,436 potential predictors, and ideally all 11 million potential predictors arising from two-way multiplicative interactions should be added to that list. Without computing all of these, it is instructive to examine the available 28,436 predictors listed in Table 1 to look for hints about which ones might be involved in useful

interactions. To limit computational effort, only a single investigative measure was used: the sample correlation of each of the 28,436 predictors with the ideal strike limits², pooled across the B3 and B7 trials. Based on these correlations, some of the predictors with the highest positive correlations with ideal strike limits were chosen, along with some which had strong negative correlations with ideal. Among both sets, the selection also focussed on maintaining a diverse list of potential predictors.

By examining the results in this manner, a list of 128 potential predictors was identified for closer examination of interactions; these are listed in Table 2. The new predictors consisting of all two-way multiplicative interactions between those listed in Table 2 were examined. Excluding those interactions already considered as part of Table 1, that amounts to another 8,128 potential predictors, for a total of 36,564 predictors that one might use to find an optimal SLA . This amounts to less than 0.33% of the potential predictors originally mentioned, and even a smaller percent of all possible useful predictors since predictors generated from other biological quantities, other $SLAs$, or various non-linear functions any predictor were never considered.

Despite having pared the problem down so much, a formidable search remained: which subset of the 36,564 remaining potential predictors was the best to use for estimating ideal strike limits? For the model $Q = \min(N, \max(0, \alpha_0 + \alpha_1 Y_1 + \dots + \alpha_p Y_p))$, with $p \leq 36,564$, there would be $2^{36,564}$ different possible models – far too many to apply any standard statistical model selection technique. Again, the correlations between predictors and ideal strike limits were used to simplify the problem. Using the same reasoning as previously, the 28 candidate predictors shown in Table 3 were chosen for further study. These included $SLAs$ based on Q_0 , Q_1 and Q^{pb} .

The required optimisation is non-linear and it would still be computationally demanding to fit all 2^{28} possible models. However, H-optimisation models closely resemble linear regression models, and there are a variety of fast, efficient statistical model selection procedures that can be employed to identify the best and most parsimonious regression models. The 'leaps and bounds' approach of Furnival and Wilson (1974) was used to compare the Mallows (1973; Neter *et al.*, 1990) for all possible regression models. Mallows C_p is a popular measure of how poorly a model fits, with an additional penalty term for model complexity. Fig. 1 shows a plot of $\log(C_p)$ versus p , with several interesting models labelled. The best³ regression model according to this criterion used the constant term plus 18 predictors: all those in Table 3 except c, d, g, h, j, k, n, q, za and zb. One model which fit much more poorly but stood out among all such simpler models was the model using only predictors e, f, m and z. The model using only these four predictors was adopted as $g(\theta, \alpha)$.

Defining the Bayesian estimation context

To reduce computing demands, only two trials are considered: the optimistic B3 and pessimistic B7 scenarios. Thus, $p(\theta)$ assigns non-zero weight to these two scenarios. Equal weight was given to each. Two reasons why this crude approximation to a full integration over θ may be adequate are as follows. First, the goal is to find a model class and estimation framework which allow the identification of good $SLAs$. Despite examining only two scenarios, the chosen

Table 1

Summary of predictor variables examined during correlation search strategy. Within each block, the results from all possible combinations of parameter values were correlated with ideal strike limits, as were the results from all two-way multiplicative interactions except for those involving the italicised parameter value entries. Table 2 shows which between-block interactions were examined.

Predictor Variables	Parameters	Parameter Values
Z_1	q_1^{pb}	0.3, 0.4, 0.5
	k	$1, \frac{1}{4}, \frac{1}{16}, \frac{1}{36}$
	β^{pb}	$\sqrt{k}, 1$
Z_2	q_2^{pb}	0.3, 0.4, 0.5
	k	$1, \frac{1}{4}, \frac{1}{16}, \frac{1}{36}$
	β^{pb}	$\sqrt{k}, 1$
Q^{pb}	$q_1^{pb} = q_2^{pb}$	0.3, 0.4, 0.5
	k	$1, \frac{1}{4}, \frac{1}{16}, \frac{1}{36}$
	β^{pb}	$\sqrt{k}, 1$
Biological quantities	Name	MSYR, MSYL, MSY, RY
	q^{bio}	0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50
	k	$1, \frac{1}{4}, \frac{1}{16}, \frac{1}{36}$
	β^{pb}	$\sqrt{k}, 1$
Wade-Givens strike limits	Catch control law	Q_0, Q_1
	β_1	1.0, 0.9, .075
	β_2	1.0, 0.9, 0.75
	β_3	1.0, 0.9, 0.75
	q^{wg}	0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50
	k	$1, \frac{1}{4}, \frac{1}{16}, \frac{1}{36}$
	β^{pb}	$\sqrt{k}, 1$

² The ideal strike limits, $H(\theta)$, are described later in the next subsection.

³ This model was the simplest model for which C_p achieved a minimal value less than or equal to p .

Table 2

For the k and β^{pb} choices indicated in the side margin, the interactions between certain variants of each predictor listed in the top margin were investigated in a complete two-way factorial search. Thus, the two-way multiplicative interactions between all possible pairs of entries in this table were correlated with ideal strike limits. For ‘biological quantities’, all four of MSYR, MSYL, MSY and RY were used.

(k, β^{pb})	Predictor Variables			
	Z_1 when $q_1^{pb} = \dots$	Z_2 when $q_2^{pb} = \dots$	Biological quantities when $q^{bio} = \dots$	Q_0 and Q_1 when $(\beta_1, \beta_2, \beta_3, q^{wg}) = \dots$
$(\frac{1}{4}, \sqrt{k})$	0.3	0.3	0.05	(0.9, 0.75, 0.75, 0.15)
			0.10	(0.9, 0.75, 0.75, 0.05)
			0.15	(0.9, 0.75, 1.0, 0.15)
$(\frac{1}{4}, 1)$	0.3 0.5	0.3	0.05	(0.9, 0.75, 0.75, 0.05)
			0.10	
			0.15	
$(\frac{1}{16}, \sqrt{k})$	0.3 0.4	0.3 0.4	0.05	(0.9, 0.75, 0.75, 0.15)
			0.15	(0.9, 1.0, 0.75, 0.15)
			0.25	(1.0, 0.75, 0.75, 0.15)
$(\frac{1}{16}, 1)$	0.5	0.3 0.4	0.05	(0.9, 1.0, 1.0, 0.05)
			0.10	(0.75, 1.0, 1.0, 0.05)
			0.15	(0.75, 0.75, 1.0, 0.05)
			0.25	(0.75, 1.0, 0.75, 0.05)
				(0.9, 0.75, 0.75, 0.05)
$(\frac{1}{36}, \sqrt{k})$	0.3 0.4 0.5	0.3 0.4 0.5	0.25	(0.75, 0.75, 0.75, 0.05)
			0.50	(1.0, 1.0, 0.75, 0.05)
$(\frac{1}{36}, 1)$	0.5	0.3 0.4 0.5	0.10	(1.0, 0.9, 0.75, 0.10)
			0.15	
			0.25	

approach provides ample information about *SLA* performance and a flexible class of models. Therefore, it is likely that the optimum within this space will represent a significant improvement in terms of management performance, even if a broader exploration of trials might have found an even better *SLA*. Second, the apparent high-dimensionality of the scenario space indexed by θ is somewhat misleading. For whales like the bowhead, population dynamics and management essentially boil down to a simple catch/productivity trade-off. The B3 and B7 trials effectively stake out the ends of this continuum, and all other trials lie between these. It is not critical to evaluate all corners of a high-dimensional θ space if this space essentially maps onto a 1-dimensional catch/productivity continuum. Averaging performance at the endpoints of this continuum can capture most relevant performance features of an *SLA*.

The likelihood, $\ell(X|\theta)$, is determined by the IWC’s simulation framework (IWC, 1999) which generates simulated abundance estimates using a mechanism that includes lognormal errors with contamination from a complex process error model. A full discussion of this likelihood is beyond the scope of this paper; however $\ell(X|\theta)$ need not be explicitly calculated to carry out the optimisation. Integration of equation (3) with respect to X is done via Monte Carlo by summing over the results from replicate simulated data series without requiring knowledge of the stochastic mechanism that generated these data.

The other aspect of Bayesian estimation is the loss function. Three different loss functions were used for *SLA* optimisation:

$$L_1(Q, H) = (H - Q)^2 / \sum_{\text{time}} \sum_X H^2 \quad (7)$$

$$L_2(Q, H) = |H - Q| / \sum_{\text{time}} \sum_X |H| \quad (8)$$

$$L_3(Q, H) = (H - Q)^2 \quad (9)$$

Equation (7) matches the prescriptions of IWC (1999) except in one detail: H and Q are both calculated in year t assuming that past catches have been taken according to a nominal *SLA*. This differs from the IWC (1999) prescription that past catches should be taken according to H for calculation of an ideal strike limit and according to the *SLA* itself for calculation of Q . The reasons for this deviation are that: (i) the current version of the simulation control program does not implement what is prescribed; and (ii) huge computational demands are already imposed in this analysis without this added complexity. For the B3 trial used in this example, the deviation is irrelevant since both versions of H always equal need levels. In the remaining cases, the difference in the two versions of H or Q amounted to only a few whales. Therefore, the effect of this deviation from IWC (1999) should be quite small.

The optimisation: estimating $\hat{\alpha}$ to minimise Bayes risk
Based on the results of the variable selection, the model:

$$Q = \min(N, \max(0, \alpha_0 + \alpha_1 Y_e + \alpha_2 Y_f + \alpha_3 Y_m + \alpha_4 Y_z)) \quad (10)$$

Table 3

The 28 predictors used at the final stage of model selection. Note that nominal $SLAs$ Q^{pb} , Q_0 and Q_1 are listed as predictors w, zb and za respectively.

Label	Predictor		
a	$MSYR_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q^{bio}=0.15\}} \times Z_2_{\{k=\frac{1}{36}, \beta^{pb}=1, q_2^{pb}=0.5\}}$		
b	$MSYL_{\{k=\frac{1}{4}, \beta^{pb}=1, q^{bio}=0.15\}} \times Z_2_{\{k=\frac{1}{16}, \beta^{pb}=1, q_2^{pb}=0.4\}}$		
c	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=0.9, \beta_2=1.0, \beta_3=1.0, q^{bio}=0.05\}} \times MSYL_{\{k=\frac{1}{4}, \beta^{pb}=1, q^{bio}=0.05\}}$		
d	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=0.9, \beta_2=1.0, \beta_3=1.0, q^{bio}=0.05\}} \times Z_2_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_2^{pb}=0.3\}}$		
e	$RY_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q^{bio}=0.05\}} \times MSY_{\{k=\frac{1}{4}, \beta^{pb}=\sqrt{k}, q^{bio}=0.05\}}$		
f	$RY_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q^{bio}=0.05\}} \times MSYL_{\{k=\frac{1}{36}, \beta^{pb}=1, q^{bio}=0.25\}}$		
g	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=0.9, \beta_2=1.0, \beta_3=1.0, q^{bio}=0.05\}} \times Q_0_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, \beta_1=0.9, \beta_2=0.75, \beta_3=0.75, q^{bio}=0.15\}}$		
h	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=0.75, \beta_2=1.0, \beta_3=1.0, q^{bio}=0.05\}} \times Q_0_{\{k=\frac{1}{4}, \beta^{pb}=\sqrt{k}, \beta_1=0.9, \beta_2=0.75, \beta_3=0.75, q^{bio}=0.05\}}$		
Label	Predictor	Label	Predictor
i	$Z_1_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q_1^{pb}=0.4\}} \times Z_1_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_1^{pb}=0.4\}}$	s	$RY_{\{k=\frac{1}{16}, \beta^{pb}=1, q^{bio}=0.05\}}$
j	$Z_1_{\{k=\frac{1}{16}, \beta^{pb}=1, q_1^{pb}=0.5\}} \times Z_1_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_1^{pb}=0.3\}}$	t	$MSYR_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q^{bio}=0.20\}}$
k	$Z_2_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q_2^{pb}=0.3\}} \times Z_2_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_2^{pb}=0.3\}}$	u	$RY_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q^{bio}=0.20\}}$
l	$Z_2_{\{k=\frac{1}{16}, \beta^{pb}=1, q_2^{pb}=0.3\}} \times Z_2_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_2^{pb}=0.3\}}$	v	$Q^{pb}_{\{k=\frac{1}{4}, \beta^{pb}=\sqrt{k}, q_1^{pb}=q_2^{pb}=0.3\}}$
m	$Z_1_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q_1^{pb}=0.3\}}$	w	$Q^{pb}_{\{k=\frac{1}{16}, \beta^{pb}=1, q_1^{pb}=q_2^{pb}=0.4\}}$
n	$Z_1_{\{k=\frac{1}{36}, \beta^{pb}=1, q_1^{pb}=0.4\}}$	x	$Q_1_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, \beta_1=1.0, \beta_2=0.75, \beta_3=0.75, q^{bio}=0.15\}}$
o	$Z_1_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_1^{pb}=0.4\}}$	y	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, \beta_1=1.0, \beta_2=1.0, \beta_3=1.0, q^{bio}=0.15\}}$
p	$Z_2_{\{k=\frac{1}{16}, \beta^{pb}=1, q_2^{pb}=0.3\}}$	z	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=1.0, \beta_2=1.0, \beta_3=0.75, q^{bio}=0.05\}}$
q	$Z_2_{\{k=\frac{1}{16}, \beta^{pb}=\sqrt{k}, q_2^{pb}=0.3\}}$	za	$Q_1_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=0.9, \beta_2=0.9, \beta_3=0.9, q^{bio}=0.05\}}$
r	$Z_2_{\{k=\frac{1}{36}, \beta^{pb}=\sqrt{k}, q_2^{pb}=0.3\}}$	zb	$Q_0_{\{k=\frac{1}{16}, \beta^{pb}=1, \beta_1=0.9, \beta_2=0.9, \beta_3=0.9, q^{bio}=0.05\}}$

was fit, where the Y variables are subscripted to refer to the labels in Table 3.

Optimisation relied on a quasi-Newton method with multiple starting values using the double dogleg step with the BFGS secant update to the Hessian (Dennis and Mei, 1979; Dennis *et al.*, 1981).

RESULTS

Table 4 shows summary results for the original Punt-Butterworth SLA , the modified version of it and the optimisations described above. The $SLAs$ in this table were

not intentionally equivalenced in any way. However, each of these $SLAs$ has a median $D1_{1+}$ result on the B7 trial within 0.02 of the result achieved by H (namely 51.3). Therefore, it is fair to compare these $SLAs$ since they are balanced with respect to depletion risk.

The results in Table 4 describe the final depletion ($D1_{1+}$) and total need satisfaction (N1) achieved in two type-2 trials: the pessimistic B7 trial and the optimistic B3 trial. High N1 values are desired (perfect = 100), as are $D1_{1+}$ values in the range 60–100. As $D1_{1+}$ increases above 60, higher values become less important than increasing N1. Considering a hypothetical bowhead stock of 9,000 whales and need ranging from 68–204, a ten-unit change in the depletion

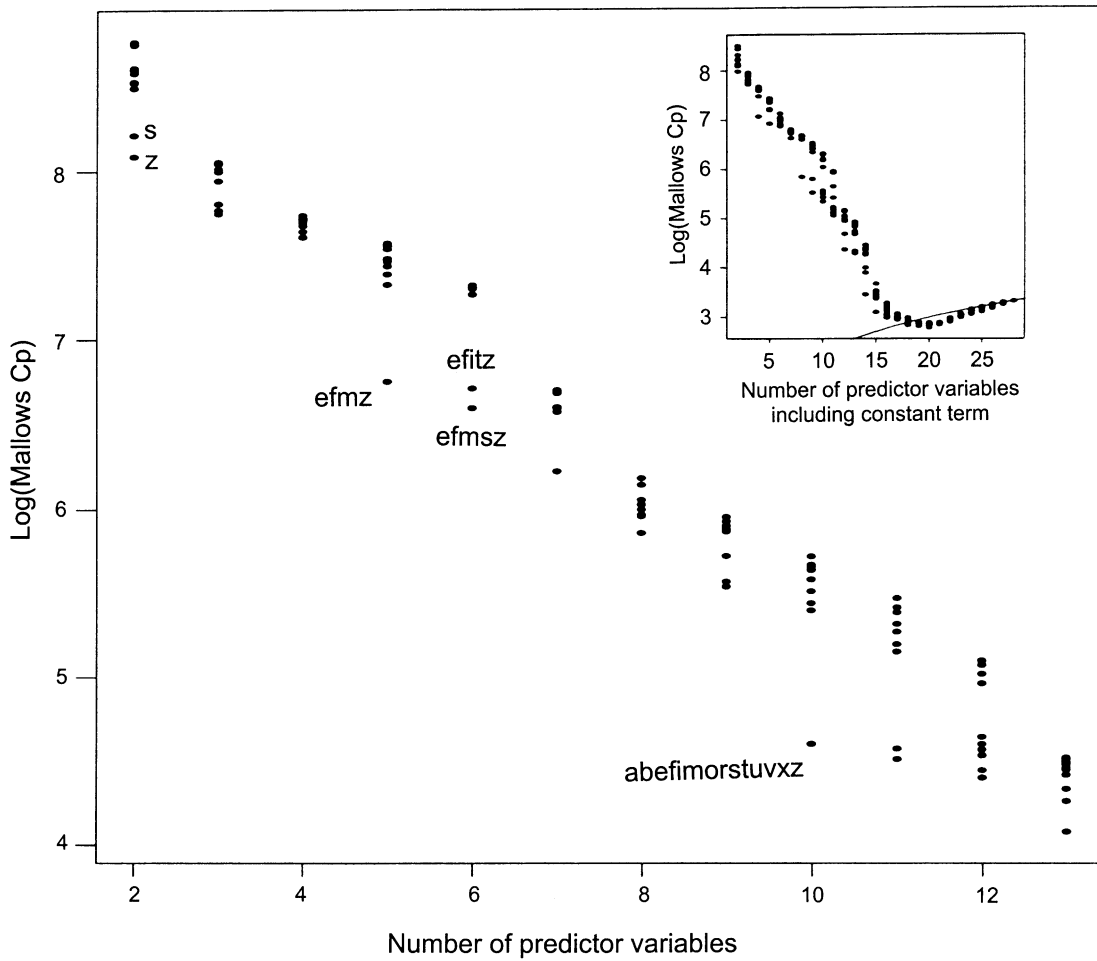


Fig. 1. A portion of the plot of Mallows C_p versus the number of predictors (including the constant term) for selecting a model for optimisation. This plot was made after omitting the 10 candidate predictors listed in the text. Several interesting models are labelled according to the annotation in Table 3. The inset shows the full C_p plot using all 28 candidate predictors; the reference 45° line is superimposed.

scores in Table 4 corresponds to 900 bowhead whales, and a ten-unit change in the need satisfaction scores corresponds to between about 7 and 20 strikes per year.

Table 4

Percentiles of the $D1_{1+}$ (final depletion) and N1 (total need satisfaction) summary statistics for the nominal SLA and several optimised variants. B7 and B3 are pessimistic and optimistic type-2 trial scenarios, as given by IWC (1999). Results are multiplied by 100. High N1 values are desired (perfect=100), as are $D1_{1+}$ values in the range 60-100.

Trial	Stat.	Perc.	P-B	Strike Limit Algorithm				
				Mod. P-B	Opt. L_1	Opt. L_2	Opt. L_3	Opt. other
B7	$D1_{1+}$	5%	35	48	41	41	40	41
		50%	50	51	51	50	50	50
		N1	5%	39	55	53	52	53
B3	$D1_{1+}$	5%	87	95	85	85	85	85
		50%	91	97	88	87	86	86
		N1	5%	86	64	76	80	78
		50%	93	68	92	95	96	95

The optimal SLA based on L_3 using the tuning in Table 4 was:

$$Q = \min(N, \max(0, 74.74 + 0.02137Y_e - 0.0002635Y_f + 37.50Y_m + 1.649Y_z)) \quad (11)$$

The optimised SLAs using L_2 and L_1 had similar coefficients. The optimisations reduced Bayes risk by 95%, 94% and 93%, respectively, when using L_1 , L_2 and L_3 , compared to the modified Punt-Butterworth SLA.

The column labelled 'Opt., other' in Table 4 shows results for an SLA not yet mentioned. For this variant, the Punt-Butterworth SLA was further modified so that a linear trend in hunting mortality, estimated from the last 20 years, was projected forward from current hunting mortality when making projections of P_{t+n} . The nominal method had been to assume constant future mortality. This change alters the quantities Z_1 , Z_2 and Q^{pb} . The model search and optimisation was repeated starting with a subset of the predictors in Table 3: a, b, e, f, i, l, m, o, p, r, z. These were chosen because: (i) they involved e, m, f, z, Z_1 , or Z_2 ; (ii) they did not involve Q^{pb} which was previously much less useful than Z_1 and Z_2 ; and (iii) they were not among the 10 variables eliminated from Fig. 1 for their irrelevance given the remaining predictors. This search identified the model using b, e, f, l, m and p as one with an attractive Mallows C_p . This 6-predictor model was then optimised and tuned in the same manner as the rest. The results show that the change to linear projection of future hunting mortality does not appear to have improved SLA performance.

Clearly the modifications to the Punt-Butterworth SLA did not unequivocally improve its performance; therefore any superior performance for the optimised variants relative to this SLA should be attributed to the optimisation process rather than to the modifications themselves.

Table 4 shows that the optimised *SLAs* offered some improvements relative to the nominal *SLA*; in the risky scenario the optimised variants allowed more catch and simultaneously more protection for the stock, while in the safe scenario, they usually satisfied more need (although not at the 5th percentile). The optimised variants provided this superior performance despite having been built upon the apparently inferior, modified *SLA* rather than Punt and Butterworth's original procedure. The extra protection provided by the optimised variants usually did not incur a significant decrease in catch – in fact the extra protection was usually achieved while simultaneously allowing more catch. Such performance is possible because the optimised variants extracted more or better information from the available data than did the nominal *SLA*. Although the optimisation and merging strategy employed here is complex and computationally intensive, its ability to provide higher catch limits at less risk to the stock – achieved through a more efficient extraction of information from the available data and a reduction in estimation uncertainty – is highly desirable. Its success in this realistic example suggests that the approach may also be rewarding for the development of procedures for environmental and wildlife management in other settings.

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REFERENCES

- Dennis, J.E. and Mei, H.H.W. 1979. Two new unconstrained optimization algorithms which use function and gradient values. *J. Opt. Theory and Appl.* 28:453-83.
- Dennis, J.E., Gay, D.M. and Welsch, R.E. 1981. An adaptive nonlinear least-squares algorithm. *ACM Transactions on Mathematical Software* 7:348-83.
- Donovan, G.P. 1999. Editorial. *J. Cetacean Res. Manage.* 1(1):ii-v.
- Furnival, G.M. and Wilson, R.W. 1974. Regressions by leaps and bounds. *Technometrics* 16:499-511.
- Givens, G.H. 1997. Separable multicriterion design and performance optimization of AWMPs. Paper SC/49/AS4 presented to the IWC Scientific Committee, September 1997 (unpublished). 21pp. [Paper available from the Office of this Journal].
- Givens, G.H. 1998. AWMP development and diverse prototypes. *Rep. int. Whal. Commn* 48:483-95.
- Givens, G.H. 1999a. Comparing methods for optimising *Strike Limit Algorithms*. Paper SC/51/AWMP5 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 18pp. [Paper available from the Office of this Journal].
- Givens, G.H. 1999b. Multicriterion decision merging: competitive development of an aboriginal whaling management procedure. *J. Am. Stat. Assoc.* 94:1003-4.
- Givens, G.H. 1999c. On statistical methods that permit and improve the use of simpler model-based *Strike Limit Algorithms*. Paper SC/51/AWMP4 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 12pp. [Paper available from the Office of this Journal].
- Givens, G.H. and Bernstein, T.A.O. 1998. Further investigations of AWMP *Strike Limit Algorithms* and their optimisation. Paper SC/50/AWMP5 presented to the IWC Scientific Committee, April 1998 (unpublished). [Paper available from the Office of this Journal].
- Givens, G.H., Zeh, J.E. and Raftery, A.E. 1996. Implementing the current management regime for aboriginal subsistence whaling to establish a catch limit for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. *Rep. int. Whal. Commn* 46:493-9.
- Givens, G.H., Punt, A.E. and Bernstein, T.A.O. 1999. Equivalence tuning of *SLAs*. *J. Cetacean Res. Manage.* 1(3):289-95.
- International Whaling Commission. 1992. Report of the sub-committee on management procedures, Appendix 2. Technical descriptions of revised management procedures. *Rep. int. Whal. Commn* 42:93-103.
- International Whaling Commission. 1994. Report of the Scientific Committee, Annex H. The Revised Management Procedure (RMP) for Baleen Whales. *Rep. int. Whal. Commn* 44:145-52.
- International Whaling Commission. 1995a. Chairman's Report of the Forty-Sixth Annual Meeting, Appendix 21. Amendments to the Schedule. *Rep. int. Whal. Commn* 45:52.
- International Whaling Commission. 1995b. Chairman's Report of the Forty-Sixth Annual Meeting, Appendix 4. IWC Resolution 1994-4. Resolution on a Review of Aboriginal Subsistence Management Procedures. *Rep. int. Whal. Commn* 45:42-3.
- International Whaling Commission. 1999. Report of the Scientific Committee. Annex F. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP). *J. Cetacean Res. Manage. (Suppl.)* 1:157-78.
- International Whaling Commission. 2000. Report of the Scientific Committee. Annex E. Report of the Standing Working Group on the Development of an Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 2:125-54.
- Mallows, C.L. 1973. Some comments on Cp. *Technometrics* 15:661-75.
- Neter, J., Wasserman, W. and Kutner, M.H. 1990. *Applied Linear Statistical Models*. Irwin, Boston. i-xi+1,181pp.
- Punt, A.E. and Butterworth, D.S. 1997. Preliminary evaluation of a (generic) strike limit algorithm for aboriginal subsistence whaling with comments on performance statistics and simulation trials. Paper SC/49/AS7 presented to the IWC Scientific Committee, September 1997, Bournemouth (unpublished) 22pp. [Paper available from the Office of this Journal].
- Wade, P.R. and Givens, G.H. 1997. Designing catch control laws that reflect the intent of aboriginal subsistence management principles. *Rep. int. Whal. Commn* 47:871-4.

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