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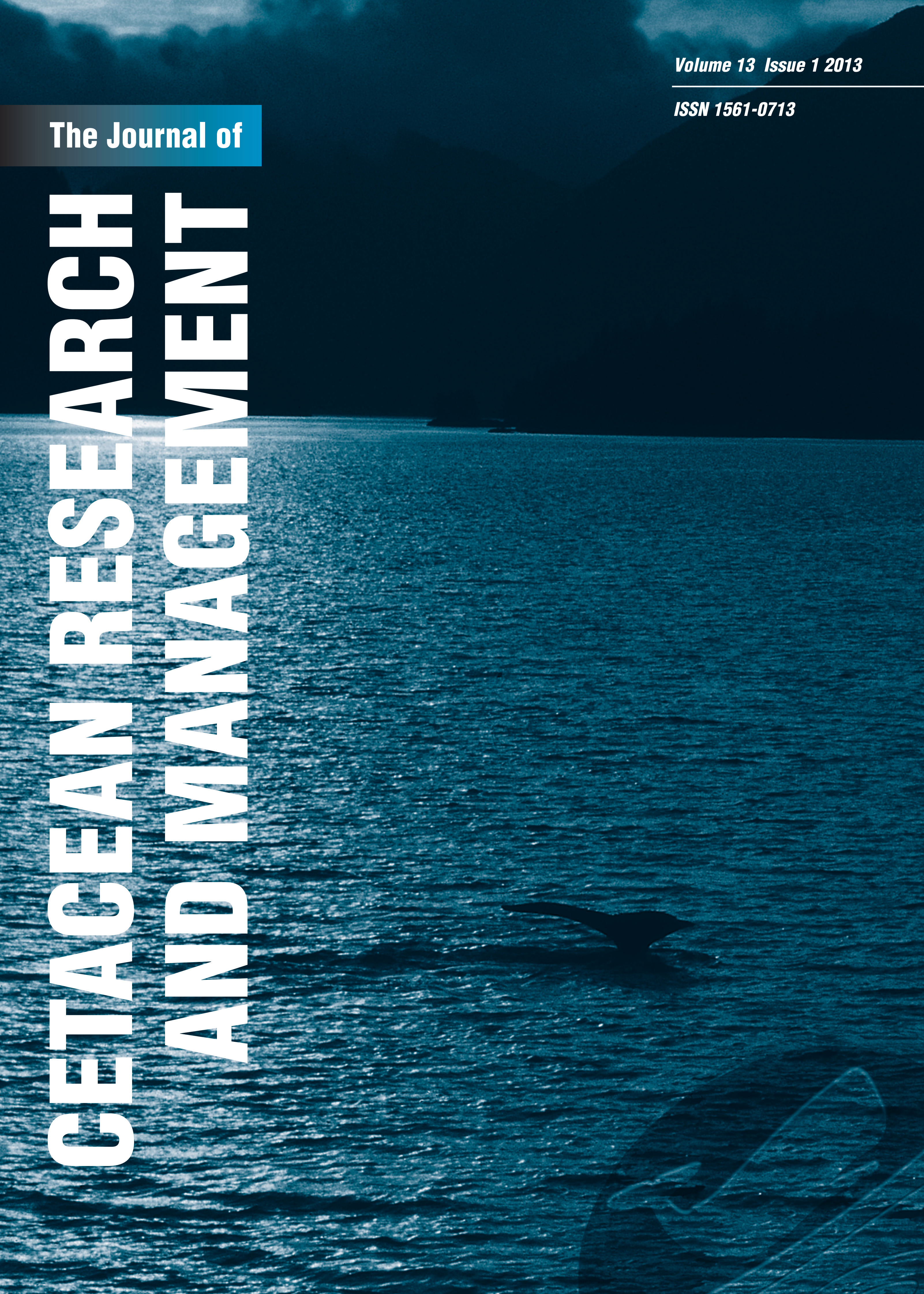

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Editorial

Welcome to this the first issue of the thirteenth volume of the *Journal of Cetacean Research and Management*. This volume contains nine papers covering a wide range of conservation and management issues.

To submit a manuscript to the Journal, please contact in the first instance Jessica Peers (*jessica.peers@iwc.int*).

A *Guide for Authors* is published at the end of this volume.

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G.P. DONOVAN
Editor

Growth and maturity of belugas (*Delphinapterus leucas*) in Cumberland Sound, Canada, and in captivity: evidence for two growth layer groups (GLGs) per year in teeth

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ABSTRACT

The beluga (*Delphinapterus leucas*) is one of the few cetaceans to adapt, year-round, to an Arctic environment, one of the most challenging marine habitats, incorporating shallow estuaries, high turbidity, shifting pack-ice and extreme tidal ranges. Adaptation is attributed in part, to year-round herd integrity and synchrony, occupying a sequence of restricted seasonal habitats and calving sites, which are reflected in tooth laminae. Field research, 1966–1969, led to the conclusion that females are sexually mature at 5.75 years and males at 8.75 years, gestation is 15–16 months, reproductive cycle 3 years, with a lifespan of 30–35 years. Newborn and the first four year-classes are recognisable by length, body colour and morphology. The two-year nursing period results in rapid growth, coincident with a training period to acquire social, feeding, and crucial under-ice navigational skills. Belugas in Cumberland Sound had been reduced through exploitation, thus it is unlikely that present numbers are food limited, reflecting maximum rate of increase. We examine growth indices for captive belugas, either captured as calves, or first and second generations born in captivity, to compare known-age animals. Onset of sexual maturity in males and females is similar to findings for Cumberland Sound, which was based on two growth layer groups per year in the teeth, or GLG/2. We analyse studies where previous oral doses of tetracycline, as well as bomb radiocarbon ^{14}C from 1958 were used to argue for single annual GLGs or GLG/1. Dedicated field studies, using appropriate dosage of intramuscular tetracycline, provide evidence for GLG/2. The ^{14}C study appears to have been compromised by preparation technique and burdens sampled in the 1990s may have been of maternal origin, transferred during foetal growth and nursing, or from recent fallout to 1980. Fundamental to the issue of growth-at-age: arguments for GLG/1 are based on back-calculation from adults of unknown age, while GLG/2 is based on projection from newborn to known-age young and adults. Direct observations and cross-referenced parameters do not substantiate GLG/1, which requires halving the growth rate, thus doubling the age of sexual and physical maturity as well as lifespan, resulting in a 40% reduction of the intrinsic rate of natural increase, substantially lower than the present rate of recovery observed.

KEYWORDS: AGE DETERMINATION; BELUGA; BOMB RADIOCARBON ^{14}C; CAPTIVE; DENTINAL GLGS; GROWTH; MANAGEMENT; NARWHAL; REPRODUCTION; AGE AT SEXUAL MATURITY; TETRACYCLINE

INTRODUCTION

This paper re-examines the issue as to whether one or two growth layer groups (GLGs) are deposited annually in the teeth of Arctic belugas (Brodie, 1969b; 1971; 1982; Brodie *et al.*, 1990; Goren *et al.*, 1987; Heide-Jørgensen *et al.*, 1994; Hohn and Lockyer, 1999; Lockyer *et al.*, 2007; Overstrom, 1991; Sergeant, 1959; 1973; Stewart *et al.*, 2006). The beluga has adapted to one of the most challenging marine habitats. It faces combinations of shallow estuaries, high turbidity, shifting pack-ice, extreme ranges in tides and water temperature. It tolerates many weeks without feeding and long periods of near total darkness. It demonstrates body and neck flexibility, such that it can poke its head between pack-ice to breathe, nose into small streams and back out of tight situations. It survives the extremes of an Arctic environment by shifting habitats while escorting 1–2 month old calves under the fields of pack-ice, affording protection and assistance by swimming in echelon formation (Brodie, 1985). During the calving period, the herd moves into shallow estuaries on the nearby coast which few other cetaceans can negotiate, and which provide sites for sloughing of epidermis as well as protection. Herd integrity, continuous communication, massive energy reserves and insulation, intensive parental investment and rapid growth, may combine to offset the higher natural mortality of young which might be presumed in such a challenging habitat.

Ice extent and duration increases northward, constraining movements and feeding opportunities for Arctic populations (Brodie, 1969b). By contrast, the isolated, post-glacial, southern beluga population of the St. Lawrence River (Sergeant, 1986; Sergeant and Brodie, 1969a; 1975) is exposed to pack-ice for 2–3 months *vs* 9–10 months in the Arctic, a reverse ratio which allows newborns to achieve substantial growth before ice formation. This population occupies a unique habitat (47°N) having adapted to tidal and flow effects of the St. Lawrence River which widens from 25km to 60km, and to 100km entering the Gulf of St. Lawrence. It may have been affected by lowered water temperatures and seasonal changes in flow of adjoining tributary estuaries, a consequence of hydro-electric development in the 1960s, which altered qualities of traditional calving sites (Sergeant and Brodie, 1975). Feeding during winter continues in open areas within the pack-ice to the exclusion of other cetaceans (Sergeant, 1986). Unique amongst beluga habitats however, during the following 9–10 months of open water, the diversity of prey attracts numbers of an additional 12 species of mysticetes and odontocetes representative of the northwest Atlantic,

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creating a site recognised globally for whalewatching. Extralimital sightings of belugas from this population occur regularly, moving further south along the Nova Scotia coast, Bay of Fundy, to New England (Sergeant, 1986; Brodie, recent obs.; Sergeant and Brodie, 1975). Adaptions for survival by this southern population are intriguing, considering the diminishing ice cover now observed in Arctic beluga habitat. Exploitation of the St. Lawrence River population had ceased by the 1970s, so examination of carcasses is now limited to those from incidental and natural mortality. Sampling of Arctic belugas relies on landings by hunters, usually adult animals. Predictable migratory behaviour and manageable size of calves has resulted in live-capture of belugas for display and research, most originating from western Hudson Bay.

Cumberland Sound field study, 1966–1969

Background

In 1966, the Canadian Dept. of Indian Affairs and Northern Development (DIAND) commenced a harvest of belugas, using fixed nets at strategic sites in Clearwater Fjord, upper Cumberland Sound, with the intention of diversifying the hunting economy. From the beginning of July to early September 1966, all netted animals ($n = 107$) as well as those from several hunting camps ($n = 17$) were sampled by PB. The netted animals represented a cross-section of the population, i.e. no hunting selectivity. Belugas occupy Clearwater Fjord during the ice-free period of July to early September. Observations of full-term foetuses and newborns, revealed that calving took place; one birth was observed. Teeth were collected, although there were no facilities for determining age during this chance field opportunity. However, newborns and age-classes of calves were distinguishable by size, remnants of umbilical cord sheath, body colour, degree of tooth eruption, healed body scars and proximity to netted adult females of known reproductive status. While not a large sample, the spectrum of ages taken during the calving season yielded cross-referenced data, although a qualitative rather than a quantitative nature.

The range of calf sizes was presumed to represent early year-classes, based on side-by-side comparison of morphology, head profile and colour: ‘Beluga in Cumberland Sound of lengths less than 300cm include newborn and as many as four year-classes’ (see Fig. 2; Brodie, 1971). However, it is important to note that in this study (and others), initial colour classification can be somewhat subjective unless compared to a truly white animal. When laboratory interpretation of teeth was later applied to field data, age determination of older animals was based on continuation of the rate at which tooth laminations were deposited in younger animals i.e. those which could be ranked by year-class. Once the initial growth rate of calves to age 4 years was defined in the field, projection to 5 and 6 year-olds was considered justifiable. Based on this, two GLGs (GLG/2) were used as an index of annual growth (Brodie, 1969b).

Sergeant (1959; 1973) had earlier proposed that belugas might deposit multiple GLGs annually, based on comparison of archived teeth with the sperm whale (*Physeter macrocephalus*) and the long-finned pilot whale (*Globicephala melas*). Sergeant (fig. 4 in 1973) provided a photo illustration of beluga GLG sequence, cross-referenced with length and status. Sergeant later stated (1981) that he was unable to explain a mechanism for the formation of GLG/2 in belugas. GLG/2 has since been rejected for the sperm whale (Perrin and Myrick, 1980).

It became evident in 1966 that the population Cumberland Sound was not as large as had been assumed as the basis for the netting project. An aerial (post hunting) near-surface count was conducted on 30 August 1967, resulting in a population estimate of 769 animals for Clearwater Fjord and upper Cumberland Sound, evidence of substantial reduction through generations of commercial and subsistence exploitation (Brodie, 1971; Sergeant and Brodie, 1975). Personal hunting experience of PB in the 1960s indicated a history of sporadic information on catches from distant camps, hunting losses and removal of young animals. This was not unusual for Arctic subsistence hunting economies at that time. However, the population decline was attributed to the high catch rates during episodes of commercial exploitation (Brodie,1971).

Life history parameters

Despite the limitations referred to in the next section, analysis of the Cumberland Sound study (Brodie, 1971) estimated that female sexual maturity was attained at 5 years and at 85% of the physically mature length. Ovulation would occur 9–10 months later during the breeding season in early spring, at age 5.75 years. Earliest maturity was evidenced by a female with a very small (139cm) calf, thus sexually mature late in her fourth year (at 4.75 yr). Multiple ovulations and accessory corpora were typical (see also Robeck *et al.*, 2005) thus corpora numbers are unreliable indicators of production (Brodie, 1971; 1972b). Gestation was calculated to be 14.5 months (*ca.* 442 days), with births in late July–early August (Fig. 1A) followed by 24 months of lactation (Brodie, 1969a), during which time the female becomes pregnant in the spring of the second year of lactation, for a reproductive cycle of 36 months. Estimated gestation was later increased to 15–16 months (458–488 days) in Brodie *et al.* (1981).

In males, Brodie (1971) concluded that sexual maturity was attained at 8 years at 90% of physical maturity, with the first opportunity for breeding estimated to be at 8.75 years the following spring. Physical maturity of both sexes was attained after 10 years.

Tooth eruption began in the second year with partial eruption by the third. Whitening of the skin was estimated to begin after 6 years in females, 7 years in males and was used in the field to establish a minimum age. The animal is physically mature when phasing to white. An age of 21 years was used as age-for-last-birth modelling, following Kleinenberg *et al.* (1964), however belugas of Cumberland Sound were considered capable of births well after age 21. Calf production was estimated to be 43% of that estimated by Bel’kovich and Tarasevich (1964). Net reproductive rate (Ro) was estimated at 6–7 calves during the lifetime of a female (Brodie, 1971). For example, based on successful 3-year reproductive cycles, a female could produce calves at ages: 7, 10, 13, 16, 19, 22 and 25 years. Lifespan in the wild was estimated to range to 30, possibly 35 years (Brodie, 1969b).

Delayed tooth eruption suggests reduced necessity for functional teeth due to extended nursing. It could also indicate a greater reliance on feeding by suction, or that teeth play a greater social role in adulthood (Brodie, 1971; 1985). Beluga teeth do not interdigitate, rather upper teeth abut lower teeth at an angle, resulting in the characteristic wear pattern and effectively sharpening contact areas.

Abundance and management in Cumberland Sound

The 1966–1969 field research and low population estimate renewed interest in the status of Cumberland Sound belugas. A booklet on beluga life-history was designed with graphics and translated into Inuktitut for the hunters, as well as distributed to northern schools (Brodie, 1972a). The Canadian Arctic Resources Committee followed the management/negotiation process (CARC, 1984).

Increased catches in 1976–1977 triggered concern, driven by the lucrative market for beluga food products. Aerial photographic surveys in 1977 (Brodie *et al.*, 1981) suggested a decline in numbers from 1967. Several surveys, by different groups, using different techniques, covering the known area of beluga distribution and relying upon the extensive knowledge and visual skills of the Inuit, did not result in substantial differences with these low estimates, 10–13 years after the 1967 survey of the same areas. The quota for 1980 was set at 40 belugas with the hunters' agreement, a necessary concession for a hunting economy, and further justified at the 1980–82 IWC Scientific Committee sessions. Aerial surveys by DFO in 1985 and 1986 produced surface indices of 398 and 442 respectively that suggested little change since 1980. Thirteen years later, a 1999 survey (DFO, 2002) resulted in an estimated population of 1,547 whales (SD = 240) resulting in an estimated annual increase rate of 55 animals (*ca.* 5%) despite an annual landed catch of 15–50 animals (*ca.* 2–5%). The quota for 2002 was increased to 41. A 2005 update advised that the Cumberland Sound population consisted of 1,211 (932–1,574) mature individuals, above the criterion of 1,000 considered to maintain genetic diversity (DFO, 2005). The 1985–86 surveys did not detect a change after quota implementation in 1980 which is perhaps not surprising given the difficulties in detecting small changes in number. However, the later abundance estimates suggested that management intervention had initiated recovery over the following 19 years. Gross annual reproductive rate appears to be higher than belugas of the St. Lawrence River (Sergeant, 1986). The more recent surveys provided evidence that the Cumberland Sound stock was not food limited, but experienced overexploitation and subsequent increase toward recovery.

Field studies of wild belugas in temporary captivity using tetracycline

A field experiment was conducted in July 1984 and August 1985 in western Hudson Bay, using a total of seven, sub-adult belugas which were injected with tetracycline, held captive over a 10 week period, and released after a tooth extraction. Intramuscular injection of oxytetracycline provided evidence of deposition in all animals and of double deposition in three. This was not used to argue for two laminations per year, but it provided a marker for deposition rate and indicated that amongst wild beluga, there might be an interruption and acquired resources could be retained and

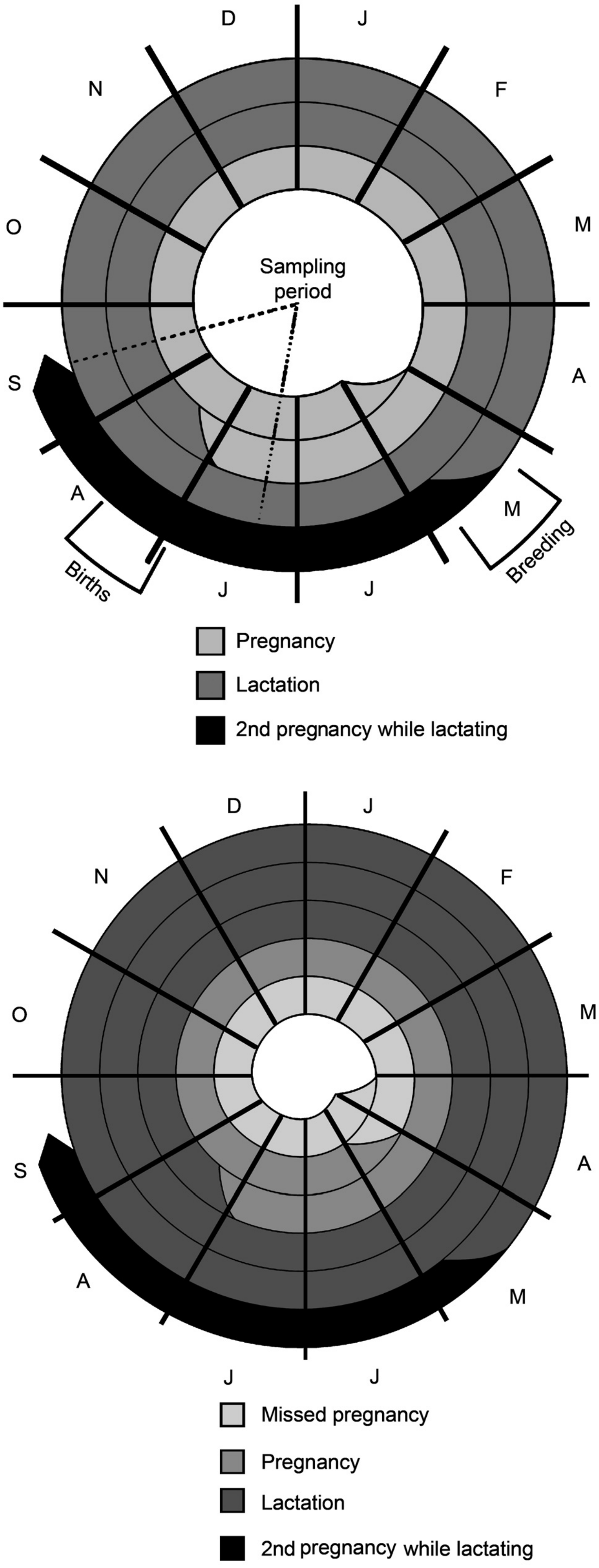

Fig. 1. Reproductive cycle:

(A) Typical of a wild population of belugas in Cumberland Sound (Brodie, 1971) encompassing 36 months. Sampling period incorporates the birthing period, while the breeding period is estimated from the foetal growth curve.

(B) Representative of the wide range of captive beluga reproductive cycles. Oestrus at *ca.* 6 years but without conception, followed by successful breeding in the second year of maturity. Pregnancy followed by an extended lactation period, which may last 3–7 years until conceiving (M. Haulena, pers. obs.), while continuing to nurse the older calf. Note that the sampling/observation period is year-round.

deposited sometime later (Brodie *et al.*, 1990). Lengths of six of the animals and their estimated ages based on tetracycline marks are included for comparison with recent, known-age captive beluga in Fig. 4. All were apparently in agreement, not varying substantially if GLG/2 counts were applied instead.

Background information on the structure of beluga teeth and difficulties in reading in the context of estimating GLG deposition rates

Before discussing the evidence for and against GLG deposition rates in belugas, it is important to review the nature and physiology of the teeth (see Plate 1) and challenges for reading GLGs.

Dentine of beluga GLGs are conical structures, the earliest being three to five-fold greater in height than more recent GLGs. Width of succeeding cones being constant, surface areas of earlier GLGs are greater accordingly. Early GLGs are observed to be thinner in cross-section than later GLGs (Brodie, 1970; figs 1 and 2 in Brodie *et al.*, 1990). However, with greater surface areas, the total volume of early GLGs equals or exceeds more recent GLGs, unlike sperm whales. Early accessory layering may be more relevant than previously assumed. Changes in the pattern of early GLGs as they phase to a lesser cone height are observed in wild belugas. The early dentinal layering sometimes appears to be in pairs of thin laminae. Considering the above arguments, these could form a pair of GLGs should the pattern continue into adulthood. Variation in cone angle can be used to approximate GLG loss in belugas, as described later.

When analysing teeth from captive animals, several authors have relied upon the the junction nodes of dentine and cement (Goren *et al.*, 1987; Hohn and Lockyer, 1999) as evidence of pre- and post-capture growth, since the central GLG structures are sometimes obscured by irregular growth in captivity.

In examining teeth sections, a loss of early GLGs can be identified by examining the characteristics of the remaining GLG pattern and the progressive increase in total angle of deposition of the GLGs from the tip of the tooth to the base. Beluga teeth have interesting characteristics which are unlike sperm whales (illustrated in Scheffer and Myrick, 1980):

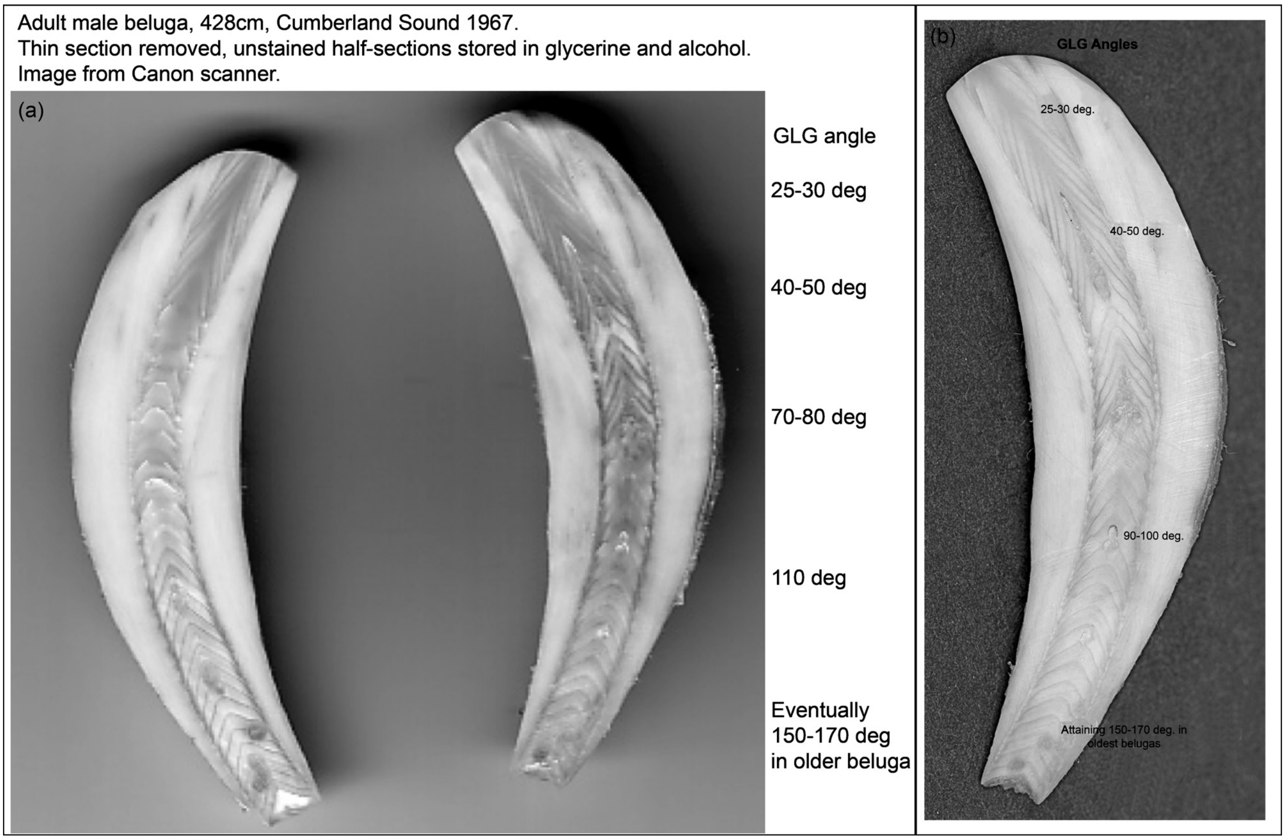

Plate 1.

(a) Tooth section.
Unstained 50 × 13 mm half-section, 428 cm beluga male, Cumberland Sound 1967. Characteristics:
(1) obvious loss of GLGs through tip wear.
(2) greater definition of wild beluga GLGs *vs* captive animals.
(3) constant width of the dentine core (cone base).
(4) increasing dominance of cementum in tooth volume.
(5) three to five-fold greater height of earlier GLG dentine cones *vs* later GLGs.
(6) 1–2 deg. incremental increase in total angle of subsequent dentine GLGs.
(7) equal or greater total tissue volume of earlier dentine cones *vs* later GLGs.
(8) change in pattern as GLGs phase into physical maturity.
(9) potential to approximate earlier dentine GLG loss through wear.
(10) male teeth larger, more robust, with generally thicker GLGs, relative to females.

(b) Right hand unsustained half-section further polished and photographed at higher resolution.

(1) after the initial several GLGs, the width of the dentine core remains constant;

(2) the acute angle of the dentine, relative to the neonatal tooth at the pulp cavity, begins to open by 1–2 degree increments as GLGs are added;

(3) the cementum GLGs are deposited at such an acute angle, almost parallel to the surface of the tooth, that they overlay each other, resulting in their dominance of the thickening tooth cross-section and total volume by 75–80% in older belugas (see fig.2 in Goren *et al.*, 1987);

(4) the dentine layer, which is continuous with the cementum, forms a 'W' in cross-section, with the lengthened outer wings of the 'W' formed by cementum.

GLGs in longitudinal sections of beluga teeth from Cumberland Sound exhibit a general pattern, beginning with a total acute angle at the pulp cavity of 25–30°, increasing by 1–2° increments to 40–50° after 12 GLGs, 70–80° after 18 GLGs, about 110° after 30 GLGs, and then 120° and increasing thereafter until they are often compacted at 150–170° at the base of the tooth. While this could vary between populations, in figs 1 and 2 of Hohn and Lockyer (1999) and fig.1 Stewart *et al.* (2006), the growth pattern and GLG angles appear to be similar to those described here for Cumberland Sound. Of course, should data become available, these values can be adjusted for a specific population.

COMPARISON OF GROWTH RATES WITH THOSE OF CAPTIVE BELUGAS

Determination of age from size alone can be difficult, due to morphological variation in calves and adolescent belugas. Opportunities to handle hundreds of belugas during tagging in Hudson Bay (Sergeant and Brodie, 1969b) and while handling belugas from Cumberland Sound later during the same season, provided evidence of early year-classes and body-size differences between populations (Doidge, 1990; Sergeant and Brodie, 1969a). However, defining vital parameters of belugas from the collection of animals during July–September in Cumberland Sound had limitations, since breeding season and length of gestation were extrapolated from the calving period. In principle, these can be refined through year-round observation of captive belugas. A good understanding of vital rates is important for the management of wild stocks, baseline studies for environmental impact assessments, as well as captive maintenance.

In this paper, case studies based on direct observation of captive animals are compared to the findings of the 1966–1969 field studies in Cumberland Sound and those in Hudson Bay. However, inevitably evidence from tooth laminae is limited, since teeth are not often extracted from captive belugas. The approach taken therefore is to compare growth rates and age of sexual maturity of belugas of known-age, either captured as calves or captive-born.

Early observations of captive belugas for comparison with the Cumberland Sound study

Few belugas were held in captivity during the 1960s. However it is realistic to assume that observations made in the 1970s and 1980s, allow comparison with the growth and maturity estimates for Cumberland Sound in the 1960s.

Lugosi

One of the earlier captive belugas, Lugosi, a male captured in September 1967 in Bristol Bay, Alaska, was maintained at the Vancouver Aquarium (Brodie, 1982). Based on its length (229cm) it was estimated to have been 14–15 months (1.25 yr) at capture i.e. born mid-summer 1966. When Lugosi died in 1980, he had spent almost 13 of 14 years in captivity (91%) and was well known for his wide range of facial expressions and jaw-claps. As a consequence, his teeth were heavily worn, and a section of the tooth provided was too re-worked and obscure in structure for use in assessing laminae. However, body lengths, taken six times following capture, were in close agreement with those of Cumberland Sound, using GLG/2 (Brodie, 1982) suggesting physical maturity after 9–10 years. The data are included in Fig. 4 and appear consistent with growth rates of other known-age males.

As noted earlier, the age at which the body colour begins phasing to white can be a useful (although subjective, especially without direct comparison to a truly white animal) parameter when trying to determine age. It was estimated to occur after 6 years for females and 7 years for males from Cumberland Sound (Brodie, 1971). Aquarium director Murray Newman wrote:

> *'According to a few dated photographs, Lugosi was very white by 1972, and according to my recollections was full, or very near to full length. The animal may have been white before this but I have no more recently dated photos to prove it.'*

Turning white at six years seems early by 1–2 years, given Brodie (1971) although it is clear that no direct comparison with a truly white animal occurred in this case. According to on-site observation, Lugosi appears to have been approaching physical maturity after age six, which seems early given the case of Kayavak at the Shedd Aquarium discussed below.

The age estimate of 1.25 years at 229cm length is consistent with captive beluga calves (Brodie, 1971; Robeck *et al.*, 2005; K. Ramirez and Haulena, pers. obs.) and thus Lugosi is considered known-age. It is apparent from the growth curve in Brodie (1982), and the observations of curator M. Newman, that physical maturity was achieved by 9–10 years, consistent with GLG/2 and half the age of 18–20 years implied by proponents of GLG/1. In fact Lugosi was fully grown well before that age, when he died at 14 years.

Bella

Bella, a female was captured with Lugosi in Bristol Bay Alaska on 8 September 1967. Her length was recorded as 315cm on 26 September, 1967, however the records indicate that, 3 months later on 4 January, 1968, a length of 320cm was recorded (with the notation *'curv.'* – i.e. taken over the body curve rather than linearly, '*lin*'). This suggests that the initial length must have been over the body curve as well (see Doidge, 1990) which is confirmed by subsequent measurements with notation: May 14/68, 307cm ('lin.'); October 16/68, 311cm; February 27/69, 320cm; May 14/69, 320cm; October 09/69, 326 cm. While not annotated, the measurements after 14 May 1968 were taken linearly. Thus the 320cm length does not appear to have been attained until 13.5 months later.

Sergeant, who examined a tooth from Bella who died in 1976 after 8.7 years in captivity, stated:

> *'There is a series of 14 very clear and evenly-spaced layers in early life, followed by recent extensive growth in the dentine which is very irregular. I believe I can count 9 layers in the dentinal-cement junction of this later growth, which happens to coincide with the number of years in captivity… If anyone else can reproduce this count, we have one layer equals one year.'* [It is not known if he was referring only to the period in captivity]. '*In this case Bella should have been an adult at capture, which is reasonable for 10ft. 4 in length, and very light grey-white in skin colour.'*

There is no record of another reader examining this tooth, nor was there a photograph of Bella upon capture. However, as noted above, the length at capture was an overestimate as it was taken along the curve of the back. Alaskan belugas are slightly larger than those of western Hudson Bay and smaller than those of Cumberland Sound. If GLG/2 is used, Bella would have been 7 years old at capture, clearly more than 295cm, apparently less than 307cm, and sexually mature. In his fig. 10, Sergeant (1973) plots the growth of western Arctic belugas for comparison. Bella would appear to fit in the 300–310 cm range for females with 14 GLGs.

In fact, from Sergeant's description above, the total GLGs would be 23, i.e. the 14 clearly resolved, plus an estimated 9 'very irregular' GLGs. Based on GLG/1, if Bella was 7 years old at capture and had spent 8.7 years in captivity one would expect 15.7 GLGs (7 wild + 8.7 captive) and if based on GLG/2, 31.4 GLGs (14 wild + 17.4 captive). Although there was no mention of tip erosion, while the 14 clearly defined GLGs described above would almost satisfy the 15.7 GLGs to comply with GLG/1, this does not account for the additional irregular 9 GLGs.

Based on GLG/1 and assuming that the clearly defined 14 GLGs represented pre-captive growth, Bella would have been 14 years old at capture; this does not appear to be consistent with a length of only 295–307 cm. By comparison, Alex (below) was grey-white at 305cm and age estimated at 5 years; males are larger than females. Under GLG/2 and under the same assumption about pre-captive growth and regular layers, Bella could have been 7 years of age when captured, then held for 8.7 years in captivity.

Alex

Alex, a male from Bristol Bay, was captured in the company of an adult female on 24 August 1961 at 221cm length. This is consistent with the length of yearlings. The estimated weight was reported as 205kg and the estimated age 14 months (1.2 yr). He was held in captivity for 23 years. Sergeant (1973) plotted two points for Alex on a growth curve. Sergeant (fig. 10 in 1973) was advised that Alex was 305cm on 17 May 1965, weighing 448kg and grey-white in colour at 5 years and that he was white by 17 November 1966 at age 6.3 years and 335cm, although 15 months later (19 February 1968) Sergeant observed him and thought him still 'somewhat grey.'

From 28 August 1961 to 6 May 1975, he was held in an outdoor pool at the New York Aquarium. He was then moved 170km to an indoor pool with artificial lighting at Mystic Marineland Aquarium in Mystic, Connecticut, where he remained until his death on 1 June 1984. He was 24 years, 405cm and weighed 1,200kg, and had spent 95% of his life in captivity, the oldest known captive beluga to that date (Goren *et al.*, 1987).

After his death, a well-worn tooth was examined. An estimated 40 dentinal GLGs and 37 in the cementum were identified and the photograph (fig. 2 in Goren *et al.* 1987) illustrates that the tooth section is compacted at the base, and heavily eroded at the tip. There was a loss of early GLGs, evident by the characteristics of the remaining GLG pattern, as well as the progressive increase in total angle of deposition of the GLGs from the tip of the tooth to the base (as discussed in the general section on teeth structure above).

Extrapolation, based on the pattern in Cumberland Sound belugas described above, indicates that about 10–15 GLGs had been eroded from the tip. Added to the 40 GLGs estimated, this gives 50–55 GLGs for a beluga aged 24 years (1.2 yr at capture + 23 yr captivity). Since the cementum layers join with the base of the corresponding dentine layer in a 'W' cross-section, loss of dentinal layers will include a commensurate loss of cementum. Had 10–15 cementum layers eroded, the total cementum GLGs would be 47–52. Lockyer *et al.* (2007), in their table 4, provide age estimates for two older belugas, of 42+ and 46+ GLGs, suggesting tooth erosion and compaction similar to that shown for Alex in Goren *et al.* (1987).

Alex, like Lugosi, can be considered known-age. In spite of 23 captive years of his 24 year lifespan, the pattern of GLGs could be resolved, indicating that two GLGs had been deposited, double that of the 24 GLGs that would have indicated GLG/1. Moreover, Alex's growth record (Fig. 4) and age of physical maturity appears consistent with other known-age belugas and not double the age required to conform with GLG/1.

Allua

Heide-Jørgensen *et al.* (1994) examined four teeth of a female, Allua, captured on 5 August 1969, with another female, Moby, at Seal River in western Hudson Bay. She remained in captivity for 15 years until her death on 26 July 1984 at the Duisberg Zoo, Germany. She was estimated by the captor to be 3 years old and her length on 6 September 1969 was 294cm. In their fig. 7, Heide-Jørgensen *et al.* (1994) indicate where they believe a distinct change in the GLG pattern corresponds to time of capture, although there was no means of validation. Although resolving layers was difficult due to base compaction, they estimated 30–36 GLGs and concluded that GLG/2 was most probable.

For comparison, a 295cm female from western Hudson Bay was estimated to be 5 years old by dentinal GLG/2, and 4.82 years based on tetracycline calibration as discussed below (Brodie *et al.*, 1990). Sergeant (1973) in his fig. 4e, shows the tooth of a young mature female at 295cm with 12 GLGs, aged as six years. Based on known-age belugas (Fig. 2 Robeck *et al.,* 2005), Allua could have been as much as 5.2 years old at capture. However, as discussed below, Tiqa of the Vancouver Aquarium died at known age 3.25 years and length 298cm.

In this case, let us assume that the estimated age at capture

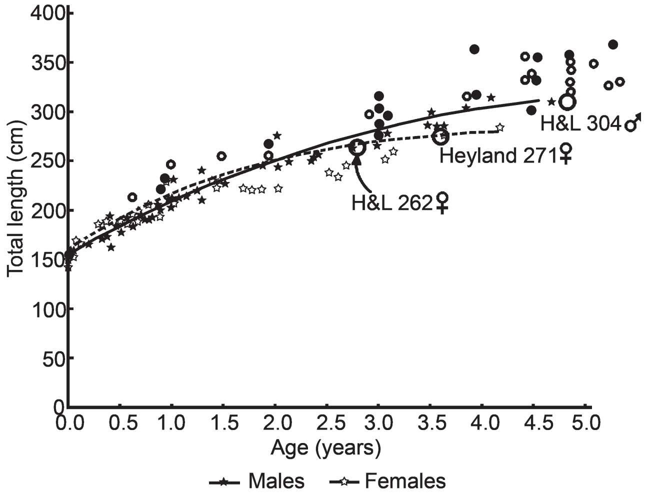

Fig. 2. Early growth rate of known-age captive belugas, based on fig. 6 from Robeck *et al* (2005). The lengths and estimated ages of Cumberland Sound beluga (Brodie, 1971), including 16 newborn, are plotted as well to demonstrate the larger body-size of this population (females are open circles, males are dark circles). Calf ages in 1966, from Brodie (1971) were initially correlated with other parameters. A 271cm female from Heyland and Hay (1976) is plotted according to length. The 262cm female and 304cm male from Hohn and Lockyer (1999) are shown plotted according to length.

(3 yr) was an underestimate and use Sergeant's upper age of 6 years. This provides an estimated age at death of 21 years (6 yr wild + 15 yr captive) i.e. expected GLGs of 21 for GLG/1 and 42 for GLG/2.

The Heide-Jørgensen *et al.* (1994) counts were thus 9–15 GLGs in excess of the 21 required for GLG/1 and 6–12 GLGs short of the required 42 for GLG/2, both contingent upon the accuracy of estimated age at capture of six years. However, using GLG/1 and assuming that 15 of the 30–36 GLGs represented 15 years in captivity, implies that the 294 cm female would have been 15–21 years old at capture. Clearly, 15 and 21 years are excessive age estimates for 294cm and, if plotted on Fig. 4, would be off-scale in length, implying a fraction the body weight for belugas of this age. It also means that she must have spent 50–58% of her life in the wild vs the earlier estimate of 29% for this female, based on lengths of known-age captive animals and Sergeant (1973). This information suggests that the GLG/1 hypothesis is not consistent with the evidence from this female.

Using GLG/2, assuming 30 GLGs represent 15 years in captivity, Allua (with 30–36 GLGs) would have ranged from zero (newborn), to three years old (6 GLGs) at capture. The newborn category is eliminated; three years was the age suggested by the captor. However, as discussed above this may be an underestimate by 2–3 years (or 4–6 missing GLGs), for a total age of 5–6 years (10–12 GLGs) upon capture. Either way, the hypothesis of GLG/2 is not inconsistent with data for this female.

Further evidence of the lack of compatibility with the data for Allua and GLG/1 comes from consideration of her potential life history if she indeed was 15–21 years at capture and using information from Brodie (1971), Robeck *et al.* (2005), direct observations of Aurora(V) and known-age Qila in the Vancouver Aquarium (see below). At 15 years of age, she could have had the potential to produce three calves (at age 7–10–13) and become a grandmother at age 14 years, one year prior to capture; or if 21, could have produced an additional two calves at age 16 and 19, for a total of 5, and become a great-grandmother by age 21 years, just prior to the time she was captured. Lockyer *et al.* (2007) state there is no difference between beluga growth rate in the wild and in captivity.

An age of 21 years was used by Brodie (1971) for a comparison of reproductive potential with Bel'kovich and Tarasevich (1964) whereby a female could have produced the majority of her calves. Robeck *et al.* (2005), concluded that the oldest age for conception, thus far, in a multi-parous captive beluga, was 20 years. There does not appear to be evidence from wild or captive belugas supporting Hohn and Lockyer (1999) or Lockyer *et al.* (2007) with reference to Allua, all being in the direction of GLG/2, as originally determined by Heide-Jørgensen *et al.* (1994).

Review of evidence from captive beluga groups

Robeck *et al.* (2005) combined vital parameter data from disparate groups of belugas born in captivity in nine aquaria, and of known age. From one perspective, animals in captivity have greater potential than the netted and hunted sample in Brodie (1971) for examining life history parameters since they can be repeatedly sampled/observed. However, the captive environment differs from the wild in a number of key ways including the very small number of belugas held in each facility relative to the larger numbers in the wild, which for example could affect breeding synchrony, as noted below.

Robeck *et al.* (2005) concluded that female belugas exhibited luteal concentrations of serum progesterone P at 6.9 years plus or minus 1.5 years (earliest onset at 5.4 years) and first conceived at 9.1 years plus or minus 2.8 years (earliest at 6.3 years). They state:

> '*In captive populations, the inconsistent availability of breeding males may artificially lengthen the period between first estrous and first pregnancy. This is supported by the observation that 67% of the captive females (n = 6) maintained in the presence of a proven breeding male became pregnant at 6 years of age.*' [Robeck *et al.* (2005) p.41].

Of six conceptions, four occurred during the first ovarian cycle at age 6 years, while the oldest age for conception in a multiparous beluga was 20 years. Females are seasonally polyoestrous, with up to two ovulations per season. The youngest male to sire a calf was 9 years old, and all males less than 8 years old were considered sexually immature. Gestation was estimated at 475 days (455–495days). They also concluded that captive belugas seem to follow similar body lengths, but not body growth patterns, when compared to their wild counterparts. Those experienced in maintaining known-age belugas are in an informed position to estimate the age of wild beluga captured as calves. The sections below summarise information on animals born in captivity.

Case studies of captive-born animals

Aurora[4], *Qila, Tiqa, and Nala*

Aurora(V), a female beluga, was captured in Churchill, Manitoba, on western Hudson Bay on 15 August 1990. She

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[4] Note that there is another female of the same name at Mystic, therefore Aurora (V) for Vancouver and Aurora (M) for Mystic.

was measured at approximately 2.5m on 30 August 1990. Using the growth curve for known-age females (Robeck *et al.*, 2005) suggests that she would have been 2.25–3.25 years (thus, born in the wild June 1987 or 1988). In September 1992, at age 4.3–5.3 years, she was 325cm. On 23 July 1995, at an estimated age of 7–8 years, she gave birth to her first calf, Qila. Conception would have therefore occurred *ca.* 15 months prior, at an age of 5.75–6.75 years. Thus after 2.25–3.25 years in the wild, she conceived and gave birth within the timeframe estimated for both wild belugas (Brodie, 1971) and directly observed animals in captivity (Robeck *et al.*, 2005; M. Haulena, pers. obs.). Sergeant (1973, fig. 4e) shows the tooth of a 295cm sexually mature female with 12 GLGs, initial evidence that growth to sexual maturity is not accelerated in a captive environment. Aurora(V) gave birth in 2002 to a male, Tuvaq, who died at age three in 2005.

Qila conceived in early 2001 at 5.75 years but lost the 200mm foetus in September 2001. She successfully gave birth to a female calf (Tiqa) on 10 June 2008, one month before her 13th birthday. Thus Aurora (V) became a grandmother at age 20–21 years, although it could have been as early as 14–15 years, had Qila carried her pregnancy to term in 2002. On 7 June 2009, Aurora(V) subsequently gave birth to a female, Nala who was substantially larger than Tiqa at birth. Nala died on 21 June 2010 at one year, larger than usual (length 243cm, max. girth 172cm and calculated weight 260–270kg). Tiqa died at 3.25 years, length 298cm and axillary girth 189cm.

The above history shows that on a three-year cycle, Qila had the potential to produce three calves (2002, 2005 and 2008) by the age of 13 years (see also Stewart *et al.*, 2006). Had Qila given birth in 2002, the calf (if female), could have been in early pregnancy in 2008 at age six years. Carried to one more generation, that calf would have been born in 2009, making Qila a grandmother at age 14, and Aurora(V) a great-grandmother at 21–22. Examination of adult females in the field, as well as their association with newborn and older calves (Brodie, 1971) indicated that all females were in an active stage of the reproductive cycle, thus the scenario of reproduction described above may be representative of a healthy, wild population (or at least one that was recovering from overexploitation).

Kavna

Data from the Vancouver Aquarium (received in April 2012) provide a profile of a female (Kavna) captured in western Hudson Bay in July 1976. Based on a 3m length estimate and body colour, she was deemed to have been born in 1969. This is consistent with growth-at-age data from Sergeant (1973). Kavna was in early pregnancy when captured, therefore not younger than 6 years (the estimated age at sexual maturity from Brodie), born at the latest in 1970, thus probably primiparous, considering her 3m body length.

On 13 July 1977, she experienced a breech birth, a male (Tuaq) who died four weeks later. In 2009, Kavna was length 380cm and weight 850kg but although always in the presence of a proven breeding male, she had not conceived in 35 years since the single birth.

On 11 July 2007, at an estimated age of 37–38, she lost a tooth which was discovered in the pool. The slender tooth was 57mm × 9mm, some erosion near the tip, tapered to a point at the base, with no evidence of a remaining pulp cavity. An unstained half-section was prepared by PB, allowing for curvature and erosion which required grinding past the midline close to the tip. There were no remnants of a prenatal tooth or neonatal line but the GLG angles indicated that few had been eroded. In the first 19mm there were up to 26–28 laminae of varying thickness (cone angles 25–30°), eventually phasing into 1–2 more characteristic GLGs. Thereafter, the section becomes increasingly obscure with irregular growth: osteodentine nodules, drying fractures, and possible resorption continuing to the pointed base. The interfaces between dentine and cement are visible, although somewhat irregular, while the width of the dentine core diminishes to about 35% that of early growth. There appeared to be several vague GLGs within the marbled tissue 35–45mm from the tip. The duration of irregular tooth metabolism appeared to have been extensive with an incomplete chronology culminating in tooth rejection. By shifting the angle of reflected light, the unusually complex laminae in the first 19mm appear to coalesce into 10–12 units. Allowing for some tip erosion, these may represent 6–7 years of pre-capture GLGs (as noted, changes in GLG structure or pattern may reflect transition from wild to captive, with a possible lag response related to the existing body reserves at capture). Kavna died of cancer 6 August 2012 and at a probable age of 42–43 years, considering her length estimate in 1976. A 54mm × 11mm tooth provided from the necropsy was similar in description, the base reduced to a fine point, with additional tip erosion of earlier laminae. Growth pattern of early laminae was similar to that of the ejected tooth, also being obscured by later irregular growth.

Based on two teeth examined, the laminae pattern in Kavna suggests clear, but complex growth, even prior to capture. Later depositions were obscured by irregular tooth growth and evidence of reworking, which seems to have continued throughout her life, yet she was the longest lived on record, dying at a probable age of 42–43 years. It also suggests that markers, such as tetracycline, might be redistributed during the restructuring, thus providing false readings.

Kayavak

Of the five calves successfully born in captivity at the Shedd Aquarium, Kayavak is of particular interest. She was born to Immiayuk on 3 August 1999 (length 142cm, weight 53kg) and nine years later had reached. 346cm and weighed 534kg (see Fig. 4). On 15 September 2010 at just over 11 years old she measured 343cm and weighed 552kg. The small length difference is attributed to the error incurred when measuring live animals at poolside. Observations indicate that she has not changed in size since 2008 at age nine and when compared to data in Sergeant and Brodie (1969a), this is consistent in size with mature belugas from Churchill, Hudson Bay. (K. Ramirez, pers. obs.). Kayavak was first observed to go into oestrus at 6 years of age, however she has yet to conceive. She had been isolated from the other belugas while being hand fed as a calf, and was later observed to be low in the hierarchy at Shedd; older females did not let her near the adult males. As of January 2011 (age 11.5 years) she continued to show signs of ovulation and has attracted the interest of an adult male, however females continue to prevent her from breeding. While availability of breeding males to females in oestrus has been considered as a limiting factor in conceptions among captive belugas (Robeck *et al.*, 2005), this suggests that social complexity and the dominance of older females over subordinate females must also be considered.

Discussion

As discussed above, the growth of wild belugas has been examined based on apparent year-classes of young animals; adults have been aged (Brodie, 1971) according to dentinal laminations consistent with the lamination rate of calves and sub-adults. In considering this further in this review, captive (age estimated at capture) and born-in-captivity growth rates have also been examined.

With respect to the former, the focus was on two calf males (captured at about 1.2–1.25 years), Alex and Lugosi (see Fig. 4), held in captivity for over 90% of their lives (Brodie, 1982; Goren *et al.*, 1987). As discussed in more detail in a preceding section, information from a number of females was also considered. Bella, captured at an estimated age of 7 years and held in captivity for 8.7 years (55% of her life); Allua, a female, captured at an age ranging from 3–6 years, and held in captivity for 15 years, around three-quarters of her life (Heide-Jørgensen *et al.*,1994); and Moby, who appeared to have lived for some 34 years, of which 30 (80%) were in captivity.

With respect to the latter, as detailed in the previous section, there are now both first and second-generation captive born animals. These represent the first belugas with a fully-known history, albeit in captivity. Age of sexual maturity for males and females in captivity is consistent with findings of wild belugas in Cumberland Sound. Primiparous belugas captured in early pregnancy, as well as calves and sub-adults later conceiving and giving birth in captivity, are consistent in size and age with those of known age in captivity and in the wild (Brodie, 1971). Pregnancies in captivity are contingent upon the availability of proven breeding males (Robeck *et al.*, 2005), and in one case, a consequence of exclusion of a mature but subordinate female, by other females. Kayavak, a female sexually mature at six and nearing 12 years old at Shedd Aquarium (Fig. 4) appears to have been physically mature since nine (K. Ramirez, pers. obs.). Beluga females appear capable of at least seven complete reproductive cycles in their lifetime, and potentially four generations, by age 28 years.

REVIEW OF PAPERS SUGGESTING GLG/1

In light of the preceding sections, the paper now considers the research and arguments that have been advanced for one GLG per year (GLG/1). The implications over GLG/2 are obvious – it doubles the duration of all life stages, including lifespan and age at attainment of sexual maturity. The focus is on a comparison of archived data to direct observations of wild and captive belugas (see Figs 2 and 4).

Hohn and Lockyer (1999)

The findings of Hohn and Lockyer (1999) have influenced subsequent studies of beluga growth and age determination (Lockyer *et al.*, 2007; Luque *et al.*, 2007; Stewart *et al.*, 2006). The authors examined tooth deposition rates based on archived teeth of two belugas from Hudson Bay, captured at lengths of 262cm (SW-DL-7903, female) and 304cm (Churchill, male). Both animals were held in captivity for almost 8 years (7.92 and 7.83 years, respectively) until their deaths. The female had been administered tetracycline orally for clinical purposes at a dose of 9 grams, twice daily over a week period, 4.2 years before her death. The issue of tetracycline is dealt with in the discussion. This section focusses on the authors' numbers of GLGs for these two animals. Based on the best counts of GLGs and assuming GLG/1, the authors concluded that the female was 18 years old and the male 23 years old at time of death. In table 2 of a later paper by Lockyer *et al.* (2007) the average count of five readers for the male was increased to 27.8 (SD 3.63) while the average count of five readers for the female was 18.20 (SD 2.17). To avoid confusion related to this manuscript submitted in 1999, it should be noted that there exists two versions (Hohn and Lockyer, 1999[5]) with similar text, however with different figures and position of the tetracycline mark.

Assuming GLG/1, then the 262cm female was about 10.1–10.3 years old at capture, while the 304cm male was 15.2–20 years at capture. However, when compared with the growth curves (Fig. 2) for known-age captive animals (Robeck *et al.*, 2005), the implied ages are around 2.75 years for the female and 4.9 years for the male, substantially lower than those based on GLG/1 and casting doubt on that hypothesis.

However, using an estimated age of 12.7 years for the male (4.9 years wild from the growth-curve estimate plus 7.83 years in captivity), the expected number of GLGs assuming GLG/2 would be 25.4. This is comparable to the best count of 23 (Hohn and Lockyer, 1999) or the mean of 27.8 (Lockyer *et al.*, 2007).

Similarly, using an estimated age of 10.65 years for the female (2.75 years from the growth curve plus 7.9 years in captivity), the expected number of GLGs assuming GLG/2 would be 21.3. This represents a shortfall but is still comparable to their best count of 18.2 (SD 2.17) GLGs.

While the rationale is unclear, the authors rounded down the previously documented times of almost 8 years in captivity (7.92 and 7.83 years) to '7 complete years', thereby shifting the difference to the precapture age. Based on the increased precapture ages of 11 and 21 years, the annual increase in length from newborn to ages 11 and 21 would be 10cm and 7cm respectively using a growth curve from Stewart (1994) for Arviat in the western Hudson Bay. However, this represents only a small fraction of the observed growth in the first year alone based on wild (Cumberland Sound) and captive data, ranging from 60–80cm (figs 2 and 4 in Brodie, 1971). This would in fact require an almost straight-line growth trajectory from newborn to ages 11 and 21, completely inconsistent with the observed early growth of known-age belugas. In addition, the appearance and interpretation of the tooth sections for the female (figs. 1–2 in Hohn and Locker) implies that *ca.* 65%–75% of the volume of tooth deposition occurred before capture; this has not been observed in calves and sub-adults of that size.

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[5] One version was submitted at the meeting and a revised version after the meeting – both versions are available from the office of this journal.

Fig. 3. From Heyland and Hay (1976), showing Doug Heyland kneeling immediately behind a 271cm juvenile female beluga at Cunningham Inlet, Canadian Arctic. The beluga, described as brown in colour (possible sun exposure), was estimated to be three years old. For comparison, the 262cm female (from Hohn and Lockyer, 1999) was 9cm shorter and estimated 80–90% the mass of the 271cm juvenile shown. Hohn and Lockyer deduce that the 262cm juvenile was 10–11 years old at capture.

For further comparison, Heyland and Hay (1976) included a photograph (Fig. 3 here and plotted in Fig. 2) of a 271cm juvenile female beluga stranded in July 1974 in Cunningham Inlet. It was initially assessed on site to be 3–4 years old by its length, morphology and body colour. Sergeant later examined the teeth, provided by the authors, counting 5–6 GLGs. Fitting the 271cm length to the female growth curve from Cumberland Sound would place the calf at 2.5–3 years of age whereas fitting to the known-age growth curve in Robeck *et al.* (2005) gives an estimate of 3.6 years. The difference can be attributed to a possible size difference in Cunningham Inlet belugas or to natural individual variation in age-at length.

The female reported by Hohn and Lockyer (1999) was 9cm shorter than this 271cm stranded juvenile female. A 262cm calf in the wild (Brodie, 1971) would have some very small teeth just beginning to pierce the gum, and may have been weaned the previous year. Clearly it would not have been sexually mature whereas if it had been 11 years old at capture, based on Brodie (1971) and Robeck *et al.* (2005) it could have previously given birth at age 7 and have been multiparous by age 10. Similarly, if the male was 21 years at capture (Lockyer *et al.*, 2007) it should already have been sexually and physically mature – this seems implausible for an animal captured at a length of 304cm. Similar conclusions are reached taking into account the length-range of known-aged Nala and Tiqa, described above. We also have to consider the impractical size and weight of adult belugas when attempting live-capture in the field. Given the work of Brodie (1971) and Robeck *et al.* (2005), we believe that the pre-capture ages and histories implied by Hohn and Lockyer (1999) are considerably in error, maybe by as much as 400%.

Radiocarbon-14 dating in Stewart *et al.* (2006)

Stewart *et al.* (2006) used bomb radiocarbon 14 (^{14}C) dating from fallout in 1958 (e.g. see Levin *et al.*, 2009) to calibrate beluga age estimates. Archived teeth from nine belugas were used. Three representing the pre-bomb era (from animals of unknown sex and length) were obtained from 1890s

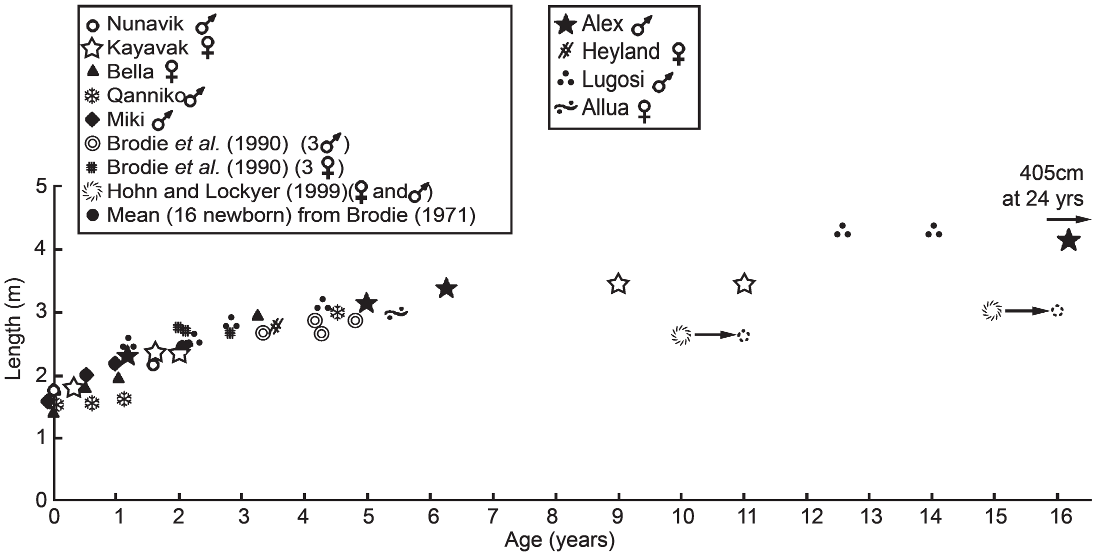

Fig. 4. Early growth rates of known-age belugas and wild belugas with estimated ages.

Kayavak, Bella, Qannik, Miki and Nunavik were born in captivity. Kayavak at age 9 years, was sexually mature at 6, of low social status, and has yet to conceive at age eleven and appears to be physically mature. Wild belugas from Brodie *et al* (1990) are included for comparison, based on known length and their ages estimated here from tetracycline markers. The two older animals (262cm female and 304cm male) are plotted, based on known length and their extrapolated age at capture according to Hohn and Lockyer (1999). By comparison, the 262cm female which they implied was 10–11 years old is 79cm shorter than (known-age) 9 year-old Kayavak, and *ca.* 49% of her known weight. The 304cm male, based on their age estimate of at least 15 years, would be *ca.* 75% the weight of the younger, 9 year old Kayavak and 35–40% that of an adult male of that age. They imply that an annual increase in length from newborn would average *circa* 10 cm, or 15% the observed growth in the first year. If the adjusted age of '7 complete years' in captivity is used for both, the points shift to 11 and 16 years respectively, as indicated. Recent data, in Table 2 of Lockyer *et al.* (2007) implies the 304cm male was 20 years old at capture (20 yr vs 5 yr), a four-fold increase in age, relative to known-age beluga. Growth data for captive Hudson Bay-origin, adult male belugas are not yet available, thus Lugosi and Alex are included here to illustrate the mature male growth curve. Both were from Alaska, intermediate between Hudson Bay and Cumberland Sound (Sergeant and Brodie, 1969b; Doidge, 1990).

archaeological sites on Somerset Island in the high Arctic. Six (5 females and 1 unknown; all unknown length) were from belugas that had been hunted in 1991–2001 from southern Baffin Island. In short, the authors concluded that belugas attain sexually maturity at twice the age and live twice the age estimated for Cumberland Sound (Brodie, 1971). Those conclusions were almost exclusively based on material micro-milled from the archived teeth of nine belugas of unknown length, with the sex known for five in the post-bomb era.

The authors did provide information on technical difficulties, possible sources of error and how they accounted for these in reaching their conclusions. This information provided part of the basis for the critique presented below. The main factors considered are: (1) technical difficulties with the prepared teeth; (2) assumptions about lags in the absorption of ^{14}C; (3) the physiology of transfer of ^{14}C from prey to beluga and from beluga mothers to calves; and (4) implications of their results in relation to population dynamics.

Technical difficulties

Stewart *et al.* (2006) stated that during their analysis it became apparent that resin had permeated teeth that were embedded for sectioning and that corrections were applied to account for this. With reference to the complexities in the use of ^{14}C vs direct observation, Ubelaker and Buchholz (2006) had stressed caution with respect to lag response, as well as the choice of tissues used, bone and hard tissues. I consulted Buchholz over the techniques used in Stewart *et al.* (2006) and he commented as follows:

'My problems with the paper are the incomplete methods and the corrections they used to remove large amounts of dead carbon from embedded samples. None of the samples embedded in epoxy are suitable for these measurements. The corrections seem arbitrary, and can be used to obtain whatever answer you want. You can make GLG/1 fit the late 1950s rise with a suitable correction. Ignoring all data after 1982 is not justified. If the corrections are accurate, they should work for the entire curve, not just a segment. Hence, the data have significant problems.' (Bucholz, pers. comm.)

The study seems thus to have been initially compromised in such a way as to affect the interpretation of the results although the authors point out that including the post-1982 data would change the fit very little. It also underscores the difficulties the authors appear to have in rationalising lag responses in their findings (see below).

If ^{14}C is present in the teeth, can it be assumed that the animal was alive during the radiocarbon event?

A fundamental assumption made in their analysis is that the ^{14}C originated in the lifetime of the belugas for which the teeth were examined, i.e. the late 1950s. They stated that bomb radiocarbon is a reliable dated marker if it remains static in the GLG throughout the subsequent life of the animal. They also stated that there was no evidence for ontogenetic effects, suggesting that the bomb signal was not diluted by subsequent growth over a period of up to 40 years. This fundamental assumption that animals exhibiting the signal must have been alive in the late 1950s requires serious evaluation in the light of the biology of belugas and their prey. The ^{14}C study by Stewart *et al* (2006) did not consider the dynamics of reproduction and the possibility of transfer of any radioactive marker from the mother to the foetus during pregnancy, nor do their citations refer to mammals.

Most fish produce large numbers of very small eggs containing genetic material and a small energy reserve, By contrast, mammals such as the beluga transfer a substantial portion of their body mass to foetal development and subsequent lactation. Where there are multiple live-births in fish and elasmobranchs, unlike belugas, individual young do not achieve 50% the weight of the mother through further transfer of resources, factors to consider in ^{14}C analysis.

Belugas produce relatively large, single calves, followed by long-term nursing. If ^{14}C is present in the beluga food-base and sequestered in their body tissue, it follows that radiocarbon in the mother would continue to be transferred and sequestered in the tissue of the foetus and nursing calf. As with all cetaceans, belugas feed more intensively during pregnancy, acquiring disproportionately large reserves (Brodie, 1975), which could further magnify their ^{14}C burden acquired during the peak fallout period.

From this perspective, foetal growth can be seen as a continuation of growth of the adult, in terms of sequestering ^{14}C from maternal tissue. This is a period when tissue is remobilised and incorporated into the foetus, including any such markers. There is no evidence that a barrier to the sub-atomic particles ^{14}C exists (Goren and Gerstner, 1965), given that there is apparently no atomic particle barrier during the sequestering of radiocarbon from prey. The forming foetal teeth would thus incorporate the radiocarbon marker in their collagen matrix (Goren and Gerstner, 1965; Liden and Angerbjorn, 1999). Beluga newborn are large (64–94kg, Brodie, 1971) relative to the muscle/skeletal body core of their mothers, being approximately 30% of her core weight at birth. By weight, as much as 40% of a beluga consists of integument and blubber, and even more in pregnant animals (Sergeant and Brodie, 1969a, fig.12). A disproportionately large amount of core tissue would therefore be transferred from the mother to the foetus during gestation.

In the wild, birth is followed by two years or more of nursing, during which the calf does not appear to rely heavily on foraging (thus a calf born in 1958 during the peak ^{14}C fallout would ingest relatively little contaminated prey). However, it is known that proportional burdens of organochlorines are transferred from mother to calf during lactation (Addison and Brodie, 1973; 1977; 1987) and there is no reason not to assume that this would also be the case for ^{14}C if present in the mother: a newborn calf gains an additional 189 kg over two years of nursing, in spite of losses through thermal maintenance and propulsion. By this stage, the total weight of a 2 year old calf would approximate the core weight of the mother and half her total weight. It seems probable that any pulse of ^{14}C acquired by females in the 1950–60s (Levin *et al.*, 2009) would be proportionately transferred to their young. We assume that subsequent tooth growth draws on tissue containing radiocarbon.

Thus the fundamental assumption of Stewart *et al*. (2006) may not be correct. A perfectly plausible (indeed more plausible) explanation is that they were actually measuring a spike of bomb ^{14}C which had been transferred across one generation and incorporated into body tissue, skeleton and forming teeth of the foetus and nursing calf. The chronology of ^{14}C dilution and decay would continue, albeit in a second-generation animal, and would continue to be detectable against the reference background of the pre-bomb era (Levin *et al.*, 2009). Dilution of ^{14}C would be relative to the amount of body tissue transferred from the mother to the foetus and nursing calf, a probable range of 25–50%, depending on the relative size of the calf versus age-related weight of the mother. Since the total ^{14}C burden of a pregnant beluga may be magnified through disproportionate intake of prey, the actual burden transferred to the foetus and nursing calf may approximate that of a non-breeding beluga present during the peak of radiation fallout.

Stewart *et al.* (2006) concluded that GLG/2 was inconsistent with the data and could be rejected since it resulted in a delay of almost 20 years from the 1958 initiation of the bomb signal. However, as shown above that depends on an assumption, feasibly erroneous, that the animals must have been alive at the time of the signal. In addition, the atmospheric bomb test in China in 1980 produced considerable ^{14}C, and with a 1–2 year lag in its appearance in the biosphere (McNeely, 1994). Such a lag must also be taken into account for the 1958 event along with the lag response from generational transfer of radiocarbon and the more general uncertainty generated by methodological issues including the problem with resin.

In their discussion, they also noted that feeding at higher trophic levels or on long-lived prey would reduce the rate of increase of the signal and extend it over a longer period. They attributed this cause to their observation for the teeth that the radiocarbon signal initially appeared on the 'correct' date although subsequent incorporation extended into the 1980s rather than the early 1970s. We note that at least an equally plausible explanation is that this was a consequence of ^{14}C transfer from mother to calf, thus extending the radiocarbon signal by one or more generations.

A further general complication relates to the fact that 'dilution' will differ between males and females. Sexually mature females can transfer markers to the foetus and nursing calf, whereas males have no such outlet (Addison and Brodie, 1987). Thus while both male and female calves of the post-bomb era would have received similar burdens from their mothers, a female calf may later dilute her burden via reproduction. One would therefore expect dilution factor differences between the sexes over a 40 year period (of the post event samples, five were female and one was of unknown sex). A lack of change in levels reported by Stewart *et al*. (2006) of the five females sampled from the 1990s, suggests that they apparently produced few, if any, offspring during their lifetimes. This seems improbable if their ages (22 to 60 years with an aggregate productive lifespan of about 170–200 years, according to the authors with GLG/1) are correct. Dilution will occur during reproduction and it seems even less likely that that this would have occurred during a period when the animals appeared to be increasing after intensive exploitation and so would be expected to have an increased reproductive rate (see below).

Implications of their results in relation to population dynamics

In reviewing the strengths and weaknesses of their interpretation of the results in the light of the GLG/1 and GLG/2 hypotheses, Stewart *et al.* (2006) also referred to life history parameters. They noted that an assumption that belugas live twice as long as previously assumed would necessarily result in twofold changes in growth rate, age of maturity and longevity. However, they commented that 'differences in other life-history parameters were not so simple'. In particular, they noted that the net production rate (the average number of newborn expected over the life of a newborn female) increased by 14% in a simulated population under an assumption of GLG/1 rather than GLG/2, whereas the intrinsic rate of increase declined by almost 40% under the same assumption.

They also considered the implications for production of GLG/2 and GLG/1. Under GLG/2 they commented that a female (maturing at age 6) could have given birth to 3 calves and any daughters would have produced one calf each by the time the first female would reach maturity under a GLG/1 scenario, i.e. maturity at age 12. They further commented that although females live some 30 years longer under the GLG/1 scenario, the 'population cannot compensate for its late start'. In fact, only the first calf (if female) would have been able to produce offspring under the above GLG/2 scenario. However, an obvious implication of their comment on the inability to 'compensate' (as noted above they simulated that the intrinsic rate of increase declines by almost 40% under a GLG/1 assumption) is the need to consider how populations have recovered in the wild as part of a holistic view of the merits of the two hypotheses.

In spite of the inconsistencies which they objectively described for their study, the authors concluded that the lifespan of belugas is double that proposed under GLG/2. Although not explicitly stated, one consequence is that the period of growth to sexual and physical maturity also doubled. Unfortunately, we do not consider that the authors sufficiently examined the implications of their conclusion of GLG/1 in the broader sense, i.e. relating to the whole animal and cross-reference of life history parameters with direct field observations and with known-age belugas in captivity.

In terms of the implications for growth, while recognising the inherent difficulties in estimating abundance and determining statistically significant trends in cetacean populations, it is informative to look at the available information from the Cumberland Sound population based on surveys by the Department of Fisheries and Oceans (DFO) of Canada. A substantial (>5%) annual increase in numbers has been reported (DFO, 2002; 2005); a doubling of the population since the early 1980s. There is no indication that only part of the Cumberland Sound population was observed by field observers and by experienced hunters who selected the early survey areas. More recent surveys covered the same area (DFO, 2002). It also seems unlikely that the Cumberland Sound stock has been recently augmented (doubled) by the arrival of large numbers of productive belugas from a distant population; the COSEWIC (2004) assessment of belugas, states that genetic, distributional and abundance information reinforce the historical view that the belugas of Cumberland Sound form a discrete population. This does not fit well with the population dynamics scenario provided by Stewart, *et al.* (2006) for GLG/1.

Lockyer *et al.* (2007)

In March 2001, a workshop was attended by the five authors of the resulting report (Lockyer *et al.*, 2007). Archived teeth from ten belugas, held in captivity for a range of years, were the focus of the study. The workshop focused on GLG counts, with little reference to other life-history parameters and the existing body of understanding, based on known-age captive belugas. The ten animals were originally captured in western Hudson Bay; duration in captivity was known for all as was length at capture for all except Winston. Colour reported at capture was given for 6 animals; the difficulties of interpreting these subjective colours by different people and without truly white animals for comparison have been discussed above and were recognised by the authors. The study concluded that GLG/2 was a plausible hypothesis for only four of the specimens; the six specimens for which it was deemed infeasible were Allua, Moby, Winston, No-See-Um, Big Mouth, SW-DL-7903 and Immiayuk (these are re-examined below), based largely on minimum agreed GLG counts given in their table 3 and associated estimated negative ages at capture. The authors concluded that 'an annual deposition rate was most likely' but also recognised that further work was required to improve age validation and standardised reading in the species. In particular, they noted the difficulties of accounting for missing layers, e.g. due to crown wear, and also mentioned that the ages for two of the animals were unrealistically large (Aurora(M) and No-See-Um) even when minimum ages were used. As noted earlier, examination of the change in total GLG angle at the pulp cavity may provide an approximation of GLG loss, e.g. when applied to the worn tooth of Alex (Goren *et al.,*1987).

We would note that it does not seem appropriate to use 'estimated negative ages at capture' in conjunction with minimum estimates to rule out a hypothesis for cases when those estimates are considered minimum because of tooth wear, i.e. even the authors themselves noted it is impossible to know how many layers have been lost.

Allua

Allua was one of the animals examined in Heide-Jørgensen *et al.* (1994) and discussed above. We do not repeat the arguments above but note that the earlier discussion revealed that the case of Allua was not incompatible with GLG/2. Incidentally, Lockyer *et al.*'s table 4 (with 'maximum' GLGs) did not suggest incompatibility with GLG/2.

Moby

Moby was a female captured with Allua on 5 August 1969. She was 280cm long on 6 September 1969 and died in June 1999, at a length of 355cm, after 29.9 years in captivity. Even under GLG/2, this appears to have been one of the oldest belugas in captivity; 34.1 years (4.2 years wild + 29.9 years captive). Lockyer *et al.* (2007), in their table 4, estimated a maximum of 42+ GLGs (their minimum estimate in their table 3 was 38+), with evidence of tooth erosion (no neonatal line was present). Based on GLG/1, Moby would have been a minimum of 12 years old at capture (42years minus 29.9years), perhaps substantially older and probably multiparous when tooth wear is factored in. Even at 12 years this would suggest she should have been physically mature (Fig. 4). Clearly, as she grew a further 75cm in captivity, she was not. Based on 280cm in Figs 2 and 4, she would have been about 4.2 years (births in June). Since she was almost 30 years in captivity, with little margin for error based on her age estimate at capture (see Fig. 4), thus she was realistically 34 years old at death and subject to tooth wear, as was the much younger, 24 year old Alex. It is implausible that she was 38+ years to 42+ years old (using GLG/1) since even these are substantial underestimates when tooth erosion is factored in. Interpretation is confounded by both tooth wear and perhaps complications in layer formation of animals that have spent so long in captivity.

Winston

Winston was a male who spent 14.25 years in captivity but for whom there was no length at capture. He was 380cm at death. The tooth was worn (neonatal line was not present) and thus it seems inappropriate to use this animal to rule out GLG/2. The 14.5 years in captivity is almost accounted for (using GLG/2) by the 27+ GLGs estimated. In fact, the negative ages reported in their tables 3 and 4 were minus 3.5 and minus 1.5 and thus few GLGs would need to be missing, especially if he had been captured as a calf, as were the majority in the study.

No-See-Um

No-See-Um was a male captured at 257cm who died 21.7 years later at 402cm. He also had a worn tooth (no neonatal line). While for the minimum GLG count their estimated age at capture was minus 1.4 years (their table 3), for the maximum (their table 4) the estimated age at capture was 2.6+. Rather than see this as an argument against GLG/2, the case of No-See-Um rather suggests the implausibility of the GLG/1 hypothesis due to the implausibly high ages at capture (21+ or 23+, their tables 3 and 4 respectively) this gives given the length at capture. The unrealistically high age at capture was also noted by the authors. A realistic age estimate would be: 3.2 years at capture, plus 21.7 in captivity, dying at an age of 24.9 years, thus 49.8 GLGs (GLG/2) compared to Lockyer *et al.*'s table 4 maximum estimate of 46+ indicating tooth wear.

Big Mouth

Big Mouth was a male who was 348cm at capture and whose reported colour was white. He lived 13 years in captivity and was 406cm at death. In this case there was no evidence of tooth wear and a neonatal line was seen. For the minimum GLG count the estimated age at capture for GLG/2 was minus 2; clearly implausible. However, for the maximum count the estimated age was 6 years. Alex, referred to above and believed to be captured as a yearling was estimated to be 6.3 years at 335cm. Thus while the evidence cannot be said to point strongly in favour of GLG/2 in this case, it similarly cannot be said to reject it.

The ages at capture for GLG/1 were 11 years and 19 years; if the estimated age for Alex is correct at 335cm, then an argument can be made that these are too high. In particular, if he was 19 years when captured then he would be expected to be sexually and physically mature. In fact he grew an extra 58cm. Similarly, another male Lugosi also described above died in captivity at known age 14 years at length 427cm, being 5 years younger than 19 year old Bigmouth at capture.

Alex and Lugosi were from Bristol Bay, Alaska, the nearest size category to those of western Hudson Bay. Based on Fig. 4, a realistic age for Bigmouth would be 7–8 years at capture, plus 13 years captive, dying at age 20–21 years. Furthermore, mention of manageable size of calves in the introduction alludes to a practical problem in the field, that of safely handling a captive adult male weighing 1,000–1,500kg, Lugosi and Alex as examples. Bigmouth, at supposed 19 years, would simply be too large, as well.

In summary, this case favours the hypothesis of GLG/2.

SW-DL-7903

This female was considered carefully in an earlier section of the paper reviewing Hohn and Lockyer (1999). Without repeating the discussion, we concluded that this animal favoured GLG/2 and that GLG/1 was implausible. In addition, this animal was treated with tetracycline just under 4 years after capture (Lockyer *et al.*'s table 5). The mark in the teeth was seen at GLG 14 (7 years assuming GLG/2) – this is close to expected given the earlier discussion that she was 2.75 years at capture (from the growth curve). This was not mentioned in their table 5 which commented (incorrectly) that the tetracycline information was consistent with GLG/1.

Immiayuk

Immiayuk was captured on 28 July 1989 at a length of 267cm, and was reportedly medium grey in colour. She was given tetracycline in late August 1989. She died after 10.4 years in captivity at length 388cm after 'first' calving (their table 5). No tooth wear was reported and a neonatal line was present. Lockyer *et al.* report a tetracycline mark at GLG7, 8 or 9 depending on the reader. They reported a minimum of 20 and a maximum of 27 GLGs (their tables 3 and 4, respectively).

Four possible scenarios are considered below.

(1) *GLG/2 and 20 GLGs*. This implies that she was born in the aquarium 4.8 months after her recorded capture date and 3.8 months after her tetracycline treatment. Clearly, this is implausible.

(2) *GLG/1 and 20 GLGs*. This implies that she was 9.6 years old at capture – this is a little greater than the maximum 9 GLG for the tetracycline mark but could be characterised as 'not inconsistent with it' given normal errors. She would be sexually mature. From known-age captive animals, a 9.6 year old female would be substantially larger than 267cm. It would also be very light grey to white in colour. Kayavak (discussed above), was born in captivity and at nine years old was 346cm and 534kg (see Fig. 4). Locker *et al.* report two males who were described as white when captured at 304cm (Churchill) and 348cm (Big Mouth). The idea that she was 9.6 years old at capture is implausible.

(3) *GLG/1 and 27 GLGs.* This implies that she was 16.6 years old at capture. She would have been sexually mature, near physical maturity and been white in colour. The tetracycline mark would have indicated treatment 7.6–9.6 years before capture. The length-age arguments applied under scenario (2) are even more exaggerated here. This scenario is also implausible.

(4) *GLG/2 and 27 GLGs*. This implies that she was 3.1 years at capture with tetracycline treatment occurring at 3.2 years of age or 6.4 GLGs. This is not incompatible with the minimum of 7 GLGs for the mark provided. The estimated age at capture is also consistent with information from known-age captive belugas (see Fig. 2). It also means that she reached sexual maturity while in captivity giving birth at age 13.6 years. Her estimated age at length is also consistent with the discussion of SW-DL-7903 and the juvenile depicted in Fig. 3, of the photo from Heyland and Hay (1976). From several strands of evidence this seems the most plausible scenario; indeed it is the only plausible scenario for this animal.

Discussion

The above holistic review of the ten cases in Lockyer *et al.* (2007) reveals that in fact the hypothesis of GLG/2 is consistent with a suite of information in all of the cases. In fact, there are five cases where the hypothesis of GLG/1 is either implausible or provides a much poorer explanation of the information than GLG/2: Allua, No-See-Um, Big Mouth, SW-DL-7903, Immmiayuk. Thus on the basis of the ten cases alone, the hypothesis of GLG/2 is at least clearly preferable. This is discussed further under Conclusions below.

While Lockyer *et al.* did consider some additional information, this was rather limited. In particular, this relates to not fully considering information on length-at-known age from captive animals and information on the age of known animals in the early years of life from hunting data that are not dependent on teeth readings and consideration of age/length at attainment of sexual and physical maturity. In addition to the discussions of individual cases above, which reveal a number of serious inconsistencies with the GLG/1 hypothesis, Lockyer *et al.* (2007) appear largely to ignore work on captive animals without providing robust arguments to support the conclusion. This includes the work of Robeck *et al.* (2005) which is consistent with that of Brodie (1971)where they note that the authors provide 'at least a rough estimate' of length at age for 'very young' animals up to age 5 years. In fact, the estimates were not rough (they were based on known-age captive-born individuals or those identified as 1–2 years in the field) and 5 years approaches the age at which females may become sexually mature in captivity and in the wild (Brodie, 1971). In this context the 'apparent contradiction' they refer to between the monitored lengths at age for captive individuals and their (GLG/1 based) much older estimated ages relative to body length for Aurora(M) and No-See-Um disappears for the GLG/2 hypothesis as discussed above.

It is, of course, important to examine arguments related to the comparability of information from captive and wild animals. Stewart *et al.* (2006), in response to the findings of Robeck *et al.* (2005) commented that captive animals might mature earlier in the absence of food stress. That animals mature somewhat earlier (in age rather than length due to increased growth rate) in response to good food conditions is a reasonable hypothesis in line with the traditional concept of density-dependence (alongside increases in other reproductive parameters as well as increased survivorship). What is much more unlikely is that in nine separate aquaria, captive born (or captured at calf) belugas, all accelerate their rate of growth to exactly twice the rate of free-ranging animals, without any period of adjustment to captivity. If food limitation is the ultimate governing factor determining the carrying capacity of belugas, then this would not occur at heavily-reduced population sizes when one might expect increased *per capita* food supply. If captive animals mature at earlier ages due to good food supply, then one might consider that captive animals are similar to wild animals in populations that have been reduced by overexploitation. For example, there is no evidence of food limitation or poor condition in the recovering population of Cumberland Sound belugas discussed earlier.

With respect to layering in the teeth, Lockyer *et al*. (2007), as others, discussed the possibility that GLGs in captive belugas might not reflect the extremes of feeding and migration in the wild. They noted that this may result in less defined layers in captive animals as has been noted above; tooth sections from captive animals are generally more difficult to read than from wild animals. In addition, that the tooth section from the male beluga Lugosi of the Vancouver Aquarium was difficult to resolve, could possibly attributed to wear from his social displays of jaw claps (Brodie, 1982). However, the authors then go on to suggest that this may ‘preclude’ using data from captive animals to calibrate GLG deposition in free-ranging ones. Given that their study was based on only a limited sample of teeth from captive animals then this could be argued to cast doubt on their own rather firmly stated conclusions. It also seems inconsistent with their recommendation that captive belugas be used for planned studies using tetracycline injections, which therefore assumes similar growth patterns of wild and captive animals.

In fact, Sergeant and Brodie (1969a) tagged 1,700 wild beluga of which 93 were injected with tetracycline injections as discussed by Brodie (1969b) while Geraci and St. Aubin (Brodie *et al*., 1990) held tetracycline injected belugas for several weeks, extracting a tooth before release. Length-at-age estimates from the latter tetracycline study confirm the rapid early growth of known-age belugas shown in Fig. 4.

Finally, despite Lockyer *et al.*’s (2007) conclusion that their results ‘clearly indicated that an annual deposition rate was most likely’, elsewhere in the paper they were more circumspect. Interestingly, they stated that the most ‘compelling’ evidence was the radiocarbon study of Stewart *et al.* (2006) that is critiqued above. They also recognised that loss of GLGs due to wear was an alternative explanation in several cases for which they had deemed GLG/2 implausible. Importantly, they recognised that in terms of management, the GLG/2 hypothesis should also be considered. They also made a number of recommendations to resolve ‘the controversy of either one or two GLGs/y.’

Allometric relationships amongst odontocetes

Luque *et al.* (2007) briefly reviewed the then available evidence for deposition rates in beluga teeth. Their main focus was on a comparison of estimated age at maturity for 22 delphinoid odontocete species. While it is not clear how carefully they reviewed the evidence for each species, which was primarily taken from Gygax (2000, *in* Luque *et al.*, 2007) they used single point estimates. They then used a robust regression approach to develop an age at maturity vs length at maturity relationship. From this they took an age at maturity value of 5 years for beluga (based on GLG/2) and a value of 10 years based apparently on Hohn and Lockyer’s (1999) paper as evidence for GLG/1. They also referred to Robeck *et al.*’s (2005) estimate as 9 years stating that this may not be representative of wild populations. They concluded that while the 5-year estimate fell just within the 95% prediction limit of the allometric relationship, the 10-year estimate fell closer to the predicted line and within the 95% confidence band (in fact only 5 of the 22 species fell within the 95% band).

While the allometric approach is interesting, it does not take into account a number of factors including the confidence intervals around the ages and lengths at sexual maturity reported or the different environments of the various odontocete species which may influence life history strategies (the narwhal and beluga are almost unique in this regard). In addition, the best estimate for mean age at attainment of sexual maturity given here is 5.75 years rather than 5 years, while Robeck *et al.*’s estimate of 9 years (which they stated as giving credence to GLG/1 and an age at maturity of 10) was related to first conception and was characterised as plus or minus 2.8 years. Robeck *et al.* state quite clearly that the majority of captive females conceived at age 6 years, when in the presence of proven breeding males. In summary, despite their conclusion that the available evidence supported GLG/1, their review was not particularly informative.

Aspartic acid racemization (AAR)

One relatively new aging technique that has become more widespread is that of aspartic acid racemization (AAR). It was first tried for cetaceans in the early 1980s (Bada *et al.*, 1980; Bada *et al.*, 1983; Nerini, 1983). More recently, Garde *et al.* (2007) used AAR to examine age determination of narwhals (*Monodon monoceros*), social odontocetes that live in a similar environment to belugas. The results indicated that female and male sexual maturity in narwhals was 6–7 years and 9 years respectively, similar to the captive belugas in Robeck *et al.* (2005), wild belugas from Cumberland Sound (Brodie, 1971) and recent direct observations of captive belugas described here. However the maximum estimate of age for one female narwhal was 105–125 years, considerably higher than estimates for belugas for either GLG/1 or GLG/2. Bowhead whales have also been found to reach very high ages, but in this case corroborative evidence exists from whaling equipment found in the animals (George *et al.*, 1999; Rosa *et al.*, 2011). Rosa *et al.* reviewed a number of factors that need to be considered when interpreting results from this technique and *inter alia* stress the need for calibration work for the technique to occur for the same species and the need to recognise the relationship between racemisation rate and temperature. As several authors have noted, marine mammals demonstrate a gradient of body core temperature and there is a –2°C to +18°C temperature range in beluga seasonal habitats (Brodie and Påsche, 1985; 2001; Brodie, 1975).

CONCLUSIONS

In this paper we have examined the evidence for deposition rate in beluga from a holistic viewpoint, incorporating field-based, life-history research, captive animal research that incorporates and cross-references the available parameters. The review highlights the value of collaborative research between field scientists and scientists maintaining animals in captivity with direct observation. It is clear that the only way to examine the question of deposition rate in tooth laminations is through such a holistic approach. Merely examining a limited suite of information or relying on new but not fully understood techniques can result in misinterpretation and lead to unjustified or overly-stated conclusions, with potentially serious consequences in terms of conservation and the provision of management advice.

We used a holistic approach to critically review: (1) evidence from the reading of a limited number of teeth of animals that died in captivity; and (2) evidence from the relatively new technique, in the context of cetaceans, of use of radiocarbon dating from specific events such as atomic weapons testing.

With respect to the former, our review shows that the hypothesis of GLG/2 is consistent with information from a number of approaches whilst the hypothesis GLG/1 revealed some serious inconsistencies with data from other sources. While it is important to try to resolve inconsistencies, it appears that the only way to do this for the GLG/1 hypothesis was for the proponents to use rather complex arguments and the application of correction factors that are not rigorously justified. Aside from the issue of radiocarbon dating, the difficulties with the Lockyer *et al.* (2007) study related to teeth can be summarised as follows:

(i) reliance mainly on a single approach (an archived tooth) and on older belugas with greater numbers of GLGs, thus increasing the possibility of errors;

(ii) incomplete consideration of GLG loss through erosion or behaviour in captivity – which will underestimate numbers of GLGs;

(iii) attributing without good evidence GLGs into the pre-captive period to compensate for the apparent excess numbers produced in captivity, a portion of the tooth that is often eroded – resulting in substantially over-estimated pre-capture ages;

(iv) use of teeth from several captive belugas with poorly understood pre-capture histories;

(v) poor cross-referencing of real-time events recorded of known-age captive belugas.

The above factors, singly or in combination, increase the potential for compounding errors. It is possible to designate early year-classes without the use of GLGs as was done in the field (Brodie, 1971), by direct observation in captive animals (Robeck *et al.*, 2005) and as updated with more recent data in Fig. 4.

With respect to (2) above, the evidence from radiocarbon dating that was seen as the most important by Lockyer *et al.* (2007) has been shown to be problematic, especially with respect to the transfer of ^{14}C from mothers to calves as well as the influence of resin in the tooth due to the preparation method. Contaminants sequestered by belugas will continue to be transferred through several generations, unless otherwise metabolised, or diluted in the case of ^{14}C. Elevated levels of ^{14}C may reflect the background of contamination from a previous generation. This could be examined by looking at the teeth (or bone) of earlier and recent, captive, mature belugas that could have received generational transfers of ^{14}C. These include:

Moby: Female conceived in 1964 and born in 1965, captured in 1969 and held in captivity for 29.9 years. One of the oldest verifiable belugas at 34.1 years, and born after the peak of bomb radiocarbon levels. However, her mother would have been at least 7 years old, possibly older, born in mid 1940s–1958 and exposed to bomb radiocarbon levels, feeding intensively when pregnant during the late 1950s. If 7 years old, the mother could have been born during peak ^{14}C fallout, therefore Moby's grandmother may have acquired the ^{14}C burden.

Alex: Male conceived in 1959 and born in 1960, captured in 1961 and died in 1984. Born two years after the peak of ^{14}C fallout, therefore his mother may have acquired the greater radiocarbon burden.

Lugosi: Male conceived in 1965 and born in 1966, captured in 1967 and died in 1980. Possible that his mother, if giving birth at age seven, could have been born one year after peak ^{14}C fallout, potentially a generational transfer from her mother.

Bella: Female estimated conceived in 1959 and born in 1960, captured in 1967 and died in 1976. Her mother must have been at least 7 years old, born *circa* 1940–1953, thus exposed to high levels of ^{14}C while feeding intensively when pregnant.

Kavna: Female probably conceived in 1968–1969 and born in 1969–1970, captured in July 1976, died in 2012. At birth, the youngest her mother could have been would be 7 years, born in 1962, but even at 11 years, Kavna's mother would have been born after the 1958 peak ^{14}C fallout. It is possible that Kavna's mother, or her grandmother, could have been exposed to the initial ^{14}C burden, initiating a generational transfer of radiocarbon.

Therefore, belugas of known-age, or with realistic age estimates, and having achieved adulthood during the late 1960s to the 1980s, were born after peak ^{14}C fallout. Yet, they were as old, or older, than those hunted 10–20 years later in the 1990s, and used in the ^{14}C study by Stewart *et al.* (2006). Generational transfer, later fallout to 1980, tissue contamination and application of corrections may explain the discrepancies (B. Buchholz, pers. comm.).

There are clear differences for the two deposition rate hypotheses: belugas are sexually mature by either 6 or 12 years for females and by 9 or 18 years for males. The Cumberland Sound study was based on field observations of full-term foetuses, newborns, juveniles, sub-adult, and calving adults. Often the teeth exhibited better resolved GLGs and the animals were younger with less potential for error in age determination. There are, of course, body-size differences between various populations (Sergeant and Brodie, 1969a). However, these are modest compared to the twofold and greater differences in all life processes and production being discussed. Comprehensive data on younger animals were key to understanding the initial trajectory of the growth curve and the age of sexual maturity in females. The young age spectrum from the wild is readily compared to their counterparts of known age in captivity. The body of direct observation from wild and captive beluga established thus far, indicates mean age at attainment of sexual maturity of females at 5.75 years, and of males at 8.75 years. Physical maturity seems to occur after 10 years, and average lifespan around 30–35 years.

The implications of the two hypotheses for conservation and management are great. GLG/1 implies *inter alia* appropriate numbers of females, either pregnant and/or lactating, whose ages can be verified at 35–70 years, or greater. The implications for recovery of populations (as seen at Cumberland Sound) are quite different for the two hypotheses with GLG/1 having a much lower intrinsic rate of growth. A qualitative evaluation of the Cumberland Sound scenario supports the GLG/2 scenario. Recovery would therefore require considerably greater survivorship than considered by Stewart *et al.* (2006) and/or a decrease in the length of the reproductive cycle from three years to two.

A more sophisticated population modelling exercise would be valuable to further explore the implications of life history parameters for specific populations for which good abundance data over time are available.

While dedicated age determination studies using tetracycline can be effective if used in a controlled experiment (e.g. Brodie *et al.*, 1990), at this time we place greater confidence on direct and cross-referenced observations of known-age, wild and captive animals, in real time, rather than extrapolations.

Biological and environmental factors can clearly affect life history traits and the north circumpolar habitat does appear to have resulted in growth and behavioural adaptations, especially among highly social odontocetes. Belugas have adapted to this demanding environment, to the exclusion of most other cetaceans. The only other odontocete to survive in a similar habitat is the narwhal (*Monodon monoceros*). However, narwhals have not been successfully maintained in captivity and comparisons with free-ranging animals are not possible (Hay, 1980). Comparisons of biological parameters and teeth from high Arctic populations of beluga with those found in the quite different environment of the St. Lawrence River should be explored.

In conclusion, we believe that the suite of data now available from captive belugas and studies of younger, known-age animals, are consistent with GLG/2 and do not support GLG/1.

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REFERENCES

Addison, R.F. and Brodie, P.F. 1973. Occurence of DDT residues in beluga whales (*Delphinapterus leucas*) from the Mackenzie Delta, NWT. *J. Fish. Res. Bd Can.* 30(11): 1733–36.

Addison, R.F. and Brodie, P.F. 1977. Organochlorine residues in maternal blubber milk, and pup blubber from grey seals (*Halichoerus grypus*) from Sable Island, Nova Scotia. *J. Fish. Res. Bd Can.* 34(7): 937–41.

Addison, R.F. and Brodie, P.F. 1987. Transfer of organochlorine residues from blubber through the circulatory system to milk in the lactating grey seal (*Halichoerus grypus*). *Can. J. Fish. Aquat. Sci.* 44: 782–86.

Bada, J.L., Brown, S. and Masters, P.M. 1980. Age determination of marine mammals based on aspartic acid racemization in the teeth and lens nucleus. *Rep. int. Whal. Commn (special issue)* 3: 113–18.

Bada, J.L., Mitchell, E. and Kemper, B. 1983. Aspartic acid racemization in narwhal teeth. *Nature, Lond.* 303: 418–20.

Bel'kovich, B.M. and Tarasevich, M.N. 1964. Biology and behaviour. pp.276–91. *In*: Kleinenberg, S.E., Yablokov, A.V., Bel'kovich, V.M. and Tarasevich, M.N. (eds). Beluga (*Delphinapterus leucas*). *Investigation of the Species*. Izdatel'stvo Nauka, Moscow.

Brodie, P. and Påsche, A. 1985. Thermoregulation and energetics of fin and sei whales based on postmortem, stratified temperature measurements. *Can. J. Zool.* 63: 2267–69.

Brodie, P.F. 1969a. Duration of lactation in Cetacea: an indicator of required learning? *Amer. Midland Nat.* 82(1): 312–14.

Brodie, P.F. 1969b. Mandibular layering in the *Delphinapterus leucas* and age determination. *Nature* 221: 956–58.

Brodie, P.F. 1970. Life history of the white whale, *Delphinapterus leucas* (Pallas) in the waters of Baffin Island, Canada. PhD thesis, Dalhousie University, Halifax, NS. vii + 127ppp.

Brodie, P.F. 1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Bay, population. *J. Fish. Res. Bd Can.* 28(9): 1309–18.

Brodie, P.F. 1972a. *The Growth of the White Whale.* Fisheries Development Section, Government of the Northwest Territories. 10pp. [In English and Inuktitut].

Brodie, P.F. 1972b. Significance of accessory corpora lutea in odontocetes with reference to *Delphinapterus leucas*. *J. Mammal.* 53(3): 614–16.

Brodie, P.F. 1975. Cetacean energetics, an overview of intraspecific size variation. *Ecology* 56(1): 152–61.

Brodie, P.F. 1982. The beluga (*Delphinapterus leucas*); growth at age based on a captive specimen and a discussion of factors affecting natural mortality estimates. *Rep. int. Whal. Commn* 32: 445–47.

Brodie, P.F. 1985. The acoustical Arctic aquabat. *BBC Wildl.* 3(12): 559–62.

Brodie, P.F., Geraci, J.W. and St Aubin, D.J. 1990. Dynamics of tooth growth in beluga whales, *Delphinapterus leucas*, and effectiveness of tetracycline as a marker for age determination. pp.141–48. *In*: Smith, T.G., St Aubin, D.J. and Geraci, J.R. (eds). *Advances in Research on the Beluga Whale, Delphinapterus leucas*. Canadian Bulletin of Fisheries and Aquatic Sciences 224, Department of Fisheries and Oceans, Ottawa.

Brodie, P.F., Parsons, J.L. and Sergeant, D.E. 1981. Present status of the white whale (*Delphinapterus leucas*) in Cumberland Sound, Baffin Island. *Rep. int. Whal. Commn* 31: 579–82.

Brodie, P.F. and Påsche, A. 2001. Body temperature variation in grey and harbour seals (*Halichoerus grypus* and *Phoca vitulina*), based on post-mortem measurements of young and adult animals. pp.363–67. *In*: Mazin, J.M. and De Buffrenil, V. (eds). *Secondary Adaptations of Tetrapods to Life in Water*. Verlag Dr Friedrich Pfeil, Munchen, Germany.

CARC. 1984. *Marine mammal management in the Eastern Arctic: a case study of manager/user interactions at Cumberland Sound, Baffin Island to 1980. Researched by Stephen Challis, research assistant Arctic Ocean Programme*. Presented at the University of Ottawa, 11 June 1984. 36pp. [Available from: *davidg@carc.org, jangly@carc.org*.]

COSEWIC. 2004. Committee on the Status of Endangered Wildlife in Canada. Assessment and update status report on the beluga whale *Delphinapterus leucas* in Canada. 70pp. [Available from: *cosewic/cosepac@ca.gc.ca*]

DFO. 2002. Cumberland Sound beluga. *Fisheries and Oceans Canada Stock Status Report E5-32 (2002)*. 11pp.

DFO. 2005. Can. Sci. Advisory Secretariat. Proc. Series 2005/011. 94pp.

Doidge, D.W. 1990. Age-length and length-weight comparisons in the beluga, *Delphinapterus leucas*. *Can. Bull. Fish. Aquat. Sci.* 224: 59–68.

Garde, E., Heide-Jørgensen, M.P., Hansen, S.H., Nachman, G. and Forchammer, M.C. 2007. Age-specific growth and remarkable longevity in narwhals (*Monodon monoceros*) from west Greenland as estimated by aspartic acid racemization. *J. Mammal.* 88(1): 49–58.

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.

Goren, A.D., Brodie, P.F., Spotte, S., Ray, G.C., Kaufman, H.W., Gwinnett, A.J., Sciubba, J.J. and Buck, J.D. 1987. Growth layer groups (GLGs) in the teeth of an adult belukha whale (*Delphinapterus leucas*) of known age: evidence for two annual layers. *Mar. Mammal Sci.* 3(1): 14–21.

Goren, A.D. and Gerstner, R. 1965. Autoradiographic localization in fetal oral tissues of maternally stored calcium 45. *J. Dental Research* 44: 1272–77.

Gygax, L. 2000. Group size and behavioural ecology in the Superfamily Delphinoidea (*Delphinidae,*
Phocoenidae, Monodontidae). PhD thesis, University of Zurich, Zurich, Switzerland.

Hay, K.A. 1980. Age determination of the narwhal, *Monodon monoceros* L. *Rep. int. Whal. Commn (special issue)* 3: 119–32.

Heide-Jørgensen, M.P., Jensen, J., Larsen, A.H., Teilmann, J. and Neurohr, B. 1994. Age estimation of white whales (*Delphinapterus leucas*) from Greenland. *Medd. Grnl. Biosci.* 39: 187–93.

Heyland, J.D. and Hay, K. 1976. An attack by a polar bear on a juvenile beluga. *Arctic* 29: 56–57.

Hohn, A.A. and Lockyer, C. 1999. Growth layer patterns in teeth from two known-history beluga whales: reconsideration of deposition rates. Paper SC/51/SM4 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 17pp. [Paper available from the Office of this Journal].

Kleinenberg, S.E., Yablokov, A.V., Belkovich, V.M. and Tarasevich, M.N. 1964. *Beluga, Delphinapterus leucas. Investigations of the Species*. Nauka, Moscow. 131pp. [English Translation, Israel Program for Scientific Translation, Jerusalem, 1969].

Levin, I., Naeglar, T., Kromer, B., Diehl, M., Francey, J.R., Gomez-Pelaez, A.J., Steele, L.P., Wagenbach, D., Weller, R. and Worthy, D.E. 2009. Observations and modelling of the global distribution and long-term trend of atmospheric 14CO2. *TELLUS B* 1 October 2009. 51pp. [Available from: *ingeborg.levin@inp.uni-heidelburg.de*]

Liden, K. and Angerbjorn, A. 1999. Dietary change and stable isotopes: a model of growth and dormancy in cave bears. *Proc. Biol. Sci.* 266(1430): 1779–83.

Lockyer, C., Hohn, A., Doidge, D.W., Heide-Jørgensen, M.P. and Suydam, R. 2007. Age determination in belugas (*Delphinapterus leucas*): a quest for validation of dentinal layering. *Marine Mammals* 33(3): 293–304.

Luque, S.P., Higdon, J.W. and Ferguson, H. 2007. Dentine deposition rates in beluga (*Delphinapterus leucas*): an analysis of the evidence. *Aquat. Mamm.* 33(2): 241–45.

McNeely, R. N. 1994. Long-term environmental monitoring of 14C levels in the Ottawa region. *Environmental International* 20(5): 675–79.

Nerini, M.K. 1983. Age determination of fin whales (*Balaenoptera physalus*) based upon aspartic acid racemisation in the lens nucleus. *Rep. int. Whal. Commn* 33: 447–48.

Overstrom, N.A. 1991. A resident belukha whale (*Delphinapterus leucas*) in Long Island Sound. *In*: Reynolds, J.E. and Odell, D.K. (eds). *Marine Mammal Strandings in the United States: Proceedings of the Second Marine Mammal Stranding Workshop*, 3–5 December 1987, Miami, Florida. NOAA Technical Report-NMFS 98: 356–378.

Perrin, W.F. and Myrick, A.C. 1980. *Report of the International Whaling Commission (Special Issue 3). Age Determination of Toothed Whales and Sirenians*. International Whaling Commission, Cambridge, UK. 229pp.

Robeck, T.R., Monfort, S.L., Calle, P.P., Dunn, J.L., Jensen, E., Boehm, J.R., Young, S. and Clark, S.T. 2005. Reproduction, growth and development in captive beluga (*Delphinapteris leucas*). *Zoo Biol.* 24: 29–49.

Rosa, C., Zeh, J., George, J.C., Botta, O., Zauscher, M., Bada, J. and O'Hara, T.M. 2011. Age estimates based on aspartic acid racemization for bowhead whales (*Balaena mysticetus*) harvested in 1998–2000. Paper SC/63/BRG5 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 14pp. [Paper available from the Office of this Journal].

Scheffer, V.B. and Myrick, A.C. 1980. A review of studies to 1970 of growth layers in the teeth of marine mammals. *Rep. int. Whal. Commn (special issue)* 3: 51–63.

Sergeant, D. 1986. Present status of white whales *Delphinapterus leucas* in the St. Lawrence Estuary. *Naturaliste Canadien (Revue Ecologique et Systématique*) 113: 61–68.

Sergeant, D.E. 1959. Age determination of odontocete whales from dentinal growth layers. *Norsk Hvalfangsttid.* 48(6): 273–88.

Sergeant, D.E. 1973. Biology of white whales (*Delpninapterus leucas*) in Western Hudson Bay. *J. Fish. Res. Bd Can.* 30(8): 1065–90. [Abstract in French].

Sergeant, D.E. and Brodie, P.F. 1969a. Body size in white whales, *Delphinapterus leucas*. *J. Fish. Res. Bd Can.* 26: 2561–80.

Sergeant, D.E. and Brodie, P.F. 1969b. Tagging white whales in the Canadian Arctic. *J. Fish. Res. Bd Can.* 26(8): 2201–05.

Sergeant, D.E. and Brodie, P.F. 1975. Identity, abundance, and present status of populations of white whales, *Delphinapterus leucas*, in North America. *J. Fish. Res. Bd Can.* 32(7): 1047–54.

Stewart, R.E.A., Campana, S.E., Jones, C.M. and Stewart, B.E. 2006. Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates *Can. J. Zool.* 84: 1840–52.

Ubelaker, D.H. and Buchholz, B.A. 2006. Complexities in the use of bomb-curve radiocarbon to determine time since death of human skeletal remains. *Forensic Science Communications* 8(1): 1–8.

Long-term site fidelity and seasonal abundance estimates of common bottlenose dolphins (*Tursiops truncatus*) along the southwest coast of Florida and responses to natural perturbations

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ABSTRACT

Information characterising site fidelity and abundance for common bottlenose dolphins (*Tursiops truncatus*) along the southwest coast of Florida is important for defining stock structure for management purposes. Long-term site fidelity and ranging patterns of bottlenose dolphins in Charlotte Harbor and Pine Island Sound, Florida were investigated using photo-ID data collected during 566 boat-based surveys from 1982 through 2007. Seasonal abundance estimates were generated from seven multi-week field seasons during 2001 through 2006, before and after a major hurricane and red tide event occurred in the area. In total, 1,154 distinctive dolphins were identified up to 34 times each with 84% of individuals resighted on more than one day. Multiple year residency rates were high with 81% of dolphins sighted in at least two years and 30% over ten or more years. Seventy-six percent of individuals with sightings on two or more days were observed in both summer and winter. Of 249 dolphins sighted on ten or more days in the study area, 83% were never observed outside the study area, indicating strong site-fidelity. Two years after a devastating Category 4 hurricane in 2004 and following two years of *Karenia brevis* harmful algal blooms, 94% of dolphins were observed in the same region within the study area and abundance estimates remained stable. Documenting range and site fidelity patterns of individuals over long periods of time is helpful for characterizing population structure and for examining changes attributable to environmental factors and perturbations such as hurricanes, harmful algal blooms and climate change.

KEYWORDS: COMMON BOTTLENOSE DOLPHIN; PHOTO-ID; SITE FIDELITY; ABUNDANCE ESTIMATE; MARK-RECAPTURE; CLIMATE CHANGE; NORTH AMERICA; NORTHERN HEMISPHERE

INTRODUCTION

Conservation strategies under the US Marine Mammal Protection Act (MMPA) aim to preserve marine mammal stock structure, specifying that '…population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part…' (US Marine Mammal Protection Act of 1972). Defining populations or stocks of marine mammals can be challenging due to the animals' often complex lives, large aquatic ranges and in some cases, continuous species distribution along coastlines. Stock identification can be derived from many types of information, including distribution and movements, population trends, morphological differences, genetic differences, contaminant and natural isotope loads, parasite differences and oceanographic habitat differences (Wade and Angliss, 1997).

Many marine mammals exhibit a distinct population structure, which may be most evident in their patterns of movement (Taylor, 2005). Stock boundaries for all US cetacean species have been designated by the National Marine Fisheries Service (NMFS) for stock assessment purposes, but in many cases there is uncertainty in the biological accuracy of these boundary decisions (Taylor, 2005). In the US Gulf of Mexico, 33 bay, sound and estuarine stocks were provisionally defined for common bottlenose dolphins (*Tursiops truncatus*), based primarily on geographical features rather than on documented movement patterns, genetics, or other kinds of biological data for the dolphins using the waters (e.g. Waring *et al.*, 2011). The focus stocks reported on in this paper, Lemon Bay (NFMS stock B21) and Gasparilla Sound, Charlotte Harbor, and Pine Island Sound (NMFS stocks B22–23) inhabit these estuaries and sounds in the southeastern portion of the Gulf. In addition to the bay, sound and estuarine stocks, NMFS has also defined three Northern Gulf of Mexico coastal bottlenose stocks (Western, Northern and Eastern) based on differences in climatic, coastal and oceanographic characteristics (Waring *et al.*, 2011).

Data for identifying bay, sound and estuarine bottlenose dolphin stocks and their interactions with Gulf coastal stocks are incomplete for much of the Gulf coast. However, information that is available indicates variability in stock structure across sites relative to residency to specific geographic regions. In order to optimise the utility of local residency as a guide for defining stocks relative to geographic features, several basic criteria should be met:

(1) residency should be pervasive throughout the study area;

(2) animals in the bay system should be resident to the area year-round, or they should be clearly identifiable as transients or seasonal residents, and therefore scored as members of different stocks;

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(3) residency should be long-term and stable through multiple generations; and

(4) provisional stock boundaries should contain most of the range of each of the putative residents.

With only a few exceptions, very few provisional stocks have been studied sufficiently to be able to examine them relative to all of these criteria.

The basic assumptions of stock identification based on residency in defined geographic regions have been examined in several areas of the Gulf through photographic identification (photo-ID) and tagging and tracking studies to document dolphin ranging patterns. Many of the findings to date support the concept of site fidelity for Gulf of Mexico dolphins in bays, sounds and estuaries, with year-round, multi-year residency exhibited by at least some individuals at nearly every site where photo-ID or tagging studies have been conducted (Texas: Bräger, 1993; Bräger *et al.*, 1994; Fertl, 1994; Maze and Würsig, 1999; Shane, 1980; Würsig and Lynn, 1996. Florida: Balmer *et al.*, 2008; Quintana-Rizzo and Wells, 2001; Wells, 1994). Typically, residents exhibit only limited movements through passes to the Gulf of Mexico, emphasising use of bay, sound or estuarine waters (Fazioli *et al.*, 2006; Irvine *et al.*, 1981; Maze and Würsig, 1999; Shane, 1980). This limited use of Gulf waters can be reflected in the ecology of the dolphins. For example, Barros and Wells (1998) noted that squid were not found in the diets of resident Sarasota Bay, Florida, dolphins, in contrast to the diets of non-resident dolphins stranded on nearby Gulf beaches. Stable isotope analyses further demonstrate dietary differences between dolphins using bays vs. Gulf of Mexico waters (Barros *et al.*, 2010). Residency patterns are somewhat more variable in certain regions of the Gulf such as northern Florida and the panhandle. In a more open estuarine system, the Cedar Keys, Florida region, Quintana-Rizzo and Wells (2001) identified a variety of residency patterns based on re-sighting rates ranging from 'frequent' to 'rare'. Balmer *et al.* (2008) identified year-round resident bottlenose dolphins in St. Joseph Bay, Florida, but also noted seasonal influxes of non-residents, including two radio tagged individuals that were tracked over 70km from their tagging location within the St. Joseph Bay region. These results suggested overlap between the St. Joseph Bay estuarine stock and the Northern Gulf of Mexico Northern stock. In northwestern Florida, NMFS has identified seven bay, sound and estuarine stocks adjacent to the Northern and Eastern Coastal stocks (Waring *et al.*, 2011) and several studies have suggested overlap between coastal and estuarine stocks, making stock delineations difficult.

In contrast to northwestern Florida, decades of research by the Sarasota Dolphin Research Program (SDRP), along the central west coast of Florida, involving photographic identification, tagging, tracking and genetic studies has led to documentation of strong site fidelity and long-term residency for many of the dolphins using these waters (Wells, 1994). In Sarasota Bay, research has been underway since 1970 to document population structure, ecology and demographics (Irvine *et al.*, 1981; Irvine and Wells, 1972; Scott *et al.*, 1990; Wells, 1991; 2003; 2009; Wells *et al.*, 1980). Over this period, on average, 89% of the sightings of resident dolphins occurred within Sarasota Bay (Wells, in review). Of those residents present in 2007 known to be at least 15 years old, 96% had been observed in the area over a span of at least 15 years, with some observed for as many as 37 years (Wells, In review).

Within Sarasota Bay, long-term (42 year) studies have monitored five concurrent generations of bottlenose dolphins totaling approximately 160 members (Wells, 2009). This long-term research has anchored our knowledge of bottlenose dolphin population ecology along the west coast of Florida and resulted in key behavioral observations and genetic findings that have led to the identification and description of biologically-based population units known as 'communities'. These communities are defined as regional societies of dolphins sharing ranges and social associates, but exhibiting genetic exchange with other social units (Wells *et al.*, 1999; Wells *et al.*, 1987). In some cases, communities can be considered to be essentially equivalent to stocks, with an explicit biological basis (Taylor, 2005). In addition to Sarasota Bay, dolphin communities have been identified just north in Tampa Bay, based on ranging and social association patterns and repeated identifications of some animals over several decades (Urian *et al.*, 2009; Wells *et al.*, 1996b). Bottlenose dolphin communities have also been identified for areas south of Sarasota Bay, including Lemon Bay, Gasparilla Sound, Charlotte Harbor and Pine Island Sound, suggesting the occurrence of long-term residency (Shane, 1990a; 2004; Wells *et al.*, 1996a; Wells *et al.*, 1997).

Building on data collected since 1982, recent research along the west coast of Florida has provided an opportunity to examine residency patterns relative to provisional stock boundaries and seasonal abundance trends. In 2001, intensive photo-ID surveys were initiated throughout Lemon Bay, Charlotte Harbor and Pine Island Sound (CHPIS) over multiple years and through multiple seasons to provide a basis for defining residency in this region and comparing population structure to provisional stock boundaries based largely on geography (Waring *et al.*, 2011). The more recent surveys have also provided unique opportunities for 'natural experiments' to test the strength of stability of residency patterns and trends in abundance in response to natural catastrophic events, including a devastating Category 4 hurricane and a series of severe *Karenia brevis* (red tide) harmful algal blooms, with resulting effects on water quality and dolphin prey species (Sallenger *et al.*, 2006; Stevens *et al.*, 2006; Tomasko *et al.*, 2006). The resulting data provide the first description of bottlenose dolphin population structure in CHPIS and allow for an evaluation of current stock designations.

METHODS

Study area

The Charlotte Harbor and Pine Island Sound study area (CHPIS) includes the enclosed bay waters eastward of the chain of barrier islands from the north end of Lemon Bay southward to San Carlos Bay as well as the shallow Gulf coastal waters around the passes between the barrier islands (Fig 1). The study area covers approximately 750 square kilometers and is composed of a variety of habitats, including highly productive seagrass meadows and mangrove shorelines, deep passes between barrier islands, dredged

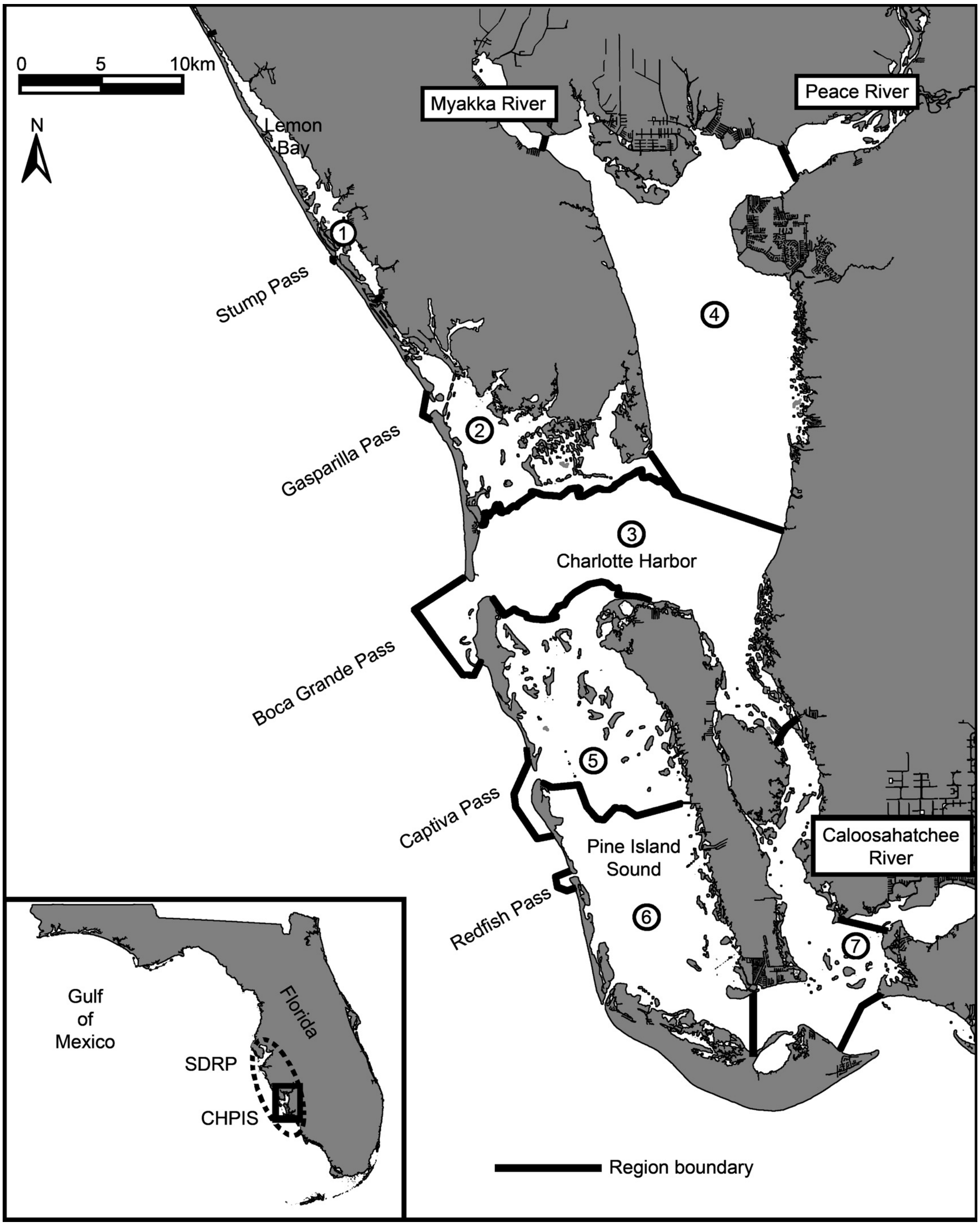

Fig. 1. Charlotte Harbor/Pine Island Sound (CHPIS) study area showing region boundaries, passes, barrier islands, rivers and bodies of water. On the inset map the larger Sarasota Dolphin Research Program (SDRP) study area is enclosed within a dashed line and smaller CHPIS study area is enclosed within a solid line.

channels, river mouths and open bays. The study area was divided into seven regions for assessment of survey effort, site fidelity and distribution following the segmentation scheme used in earlier Charlotte Harbor and Pine Island Sound surveys (Wells *et al.*, 1996a; Wells *et al.*, 1997) (Fig 1). Region 1, Lemon Bay, equates to NMFS stock designation B21, and Regions 2–7, including Gasparilla Sound, Charlotte Harbor, and Pine Island Sound are the same as NMFS stocks B22–23 (Waring *et al.*, 2011; Wells *et al.*, 1997).

Study background

Research on bottlenose dolphins in CHPIS has been conducted through both boat-based and aerial surveys since 1970. Tagging efforts occurred during 1970–71 (Irvine and Wells, 1972) and in 1984 (Wells, 1986). Aerial surveys designed to determine bottlenose dolphin abundance were conducted in CHPIS during 1975/76 (Odell and Reynolds, 1980) and by NMFS during 1980/81, 1983–86 and 1994 (Blaylock, 1995; Scott *et al.*, 1989; Thompson, 1981). A one-year study of the behavior and ecology of dolphins in southern Pine Island Sound and around Sanibel Island was initiated in 1985 (Shane, 1990a; 1990b) and opportunistic sighting data were collected through 1996 (Shane, 2004). Preliminary photo-ID began in 1982, but systematic surveys with the goal of determining trends in abundance were not conducted in the region until 1990 (Wells *et al.*, 1996a; Wells *et al.*, 1997). Surveys focused on the Charlotte Harbor region during 1990–94 (Wells *et al.*, 1996a) and on Pine Island Sound during 1996 (Wells *et al.*, 1997). The data reported here were collected during seasonal photo-ID surveys in Charlotte Harbor and Pine Island Sound conducted from 2001 through 2007 as well as long-term findings from combined datasets over all years.

Field effort and survey methodology

Building on the multi-week, multi-boat photo-ID surveys conducted during 1990–94 and 1996 (Wells *et al.*, 1996a; Wells *et al.*, 1997), as well as opportunistic surveys between major field sessions, seven seasonal multi-week surveys of CHPIS were conducted during September 2001–September 2006 using three vessels each day. The field sessions will be referred to as: September/October 2001 (summer 2001); January/February 2002 (winter 2002); September 2002 (summer 2002); February 2003 (winter 2003); September 2003 (summer 2003); February 2004 (winter 2004); and September 2006 (summer 2006). The survey design for these multi-week surveys used both line transects spaced 1km apart (followed with the aid of a GPS in open water areas) and contour transects (followed using a chart and depth contours in narrower areas). Both line transects and contour transects were randomly selected each day without replacement and conducted under Beaufort Sea State two or less when possible until the entire study area (all seven Regions) was completely surveyed (the Mark portion of the survey). The recapture portion of the survey was started 1.4 ± 0.5 SD days later on average. Both the Mark and Recapture survey segments took on average 8.0 ± 3.0 SD days each to complete. In addition, other opportunistic photo-ID survey and biopsy darting efforts were conducted between 2001 and 2007.

Surveys were conducted from 6–7m outboard-powered boats. Survey crews typically included a minimum of three people per boat and observer positions were rotated approximately every 60 minutes. While searching for dolphin groups, the boats operated at the slowest possible speed that would still allow the vessel to plane, typically 30–35km hr^{-1}, depending on the vessel. When groups were encountered, the boat slowed to match the speed of the dolphins and moved parallel to the group to obtain photographs.

Every dolphin group encountered along a survey route was approached for identification photographs (Scott *et al.*, 1990; Würsig and Jefferson, 1990). The research vessel remained with each dolphin group until the dorsal fin of each member of the group was photographed, or until conditions precluded complete coverage of the group. Prior to September 2003, primarily Nikon film camera systems with zoom-telephoto lenses (up to 300mm), motor drives, data backs and Kodachrome 64 color slide film were used. In February 2003, Nikon D100 digital camera systems with 80–300mm zoom-telephoto lenses were used complementary to the Nikon film camera systems on some surveys. Starting September 2003, only digital cameras were used.

A suite of data including date, time, location, activities, headings and environmental conditions were recorded for each sighting. In addition, minimum, maximum and best point estimates of numbers of total dolphins, calves (dolphins < about 80–85% adult size, typically swimming alongside an adult, a subset of the total number of dolphins) and young-of-the-year (as a subset of the number of calves) were also recorded.

Analysis of photographs

Each dorsal fin in a photograph was graded by two independent graders to characterise photographic quality and dorsal fin distinctiveness (Read *et al.*, 2003). Slides were examined using a high power (15x) loupe eyepiece. Digital photos were downloaded, labeled and cropped in *ACDSee* and/or *Adobe Photoshop*. Photograph quality rank was based on focus clarity, contrast, angle, portion of fin showing and percent of photograph frame filled (Q1 = excellent quality; Q2 = average quality; Q3 = poor quality). Dorsal fin distinctiveness was ranked on the strength of fin markings: D1 = dolphins with major fin markings, very distinctive fins with features evident in distant or poor quality photographs; D2 = dolphins with minor fin markings, fins with difficult to distinguish features in distant or poor photograph; D3 = dolphins with clean or non-distinctive fins. Dolphins with either a D1 or D2 fin were considered ‘marked’.

The best photograph of each individual with a D1 or D2 fin within each sighting was compared to our established SDRP Photo-Identification Catalog which includes individuals from Tampa Bay, Sarasota Bay, CHPIS and near-shore Gulf of Mexico coastal waters. When a match was made with a fin in the SDRP catalog, all photos were labeled with the dolphin’s unique code. The entire catalogue was searched by two staff members before a new animal was added to the catalog with a new code. As of August 2012, there were 3,425 marked individuals in the SDRP catalog, including the 276 dolphins identified by Shane (2004). Sexes of marked dolphins were determined through genetic analysis of skin samples obtained during biopsy darting efforts or visual examination during tagging efforts. In addition, marked dolphins were classified as female if they were sighted on three or more days with a calf surfacing alongside. All sighting and environmental data including identified individuals were entered into an Access database.

Sighting frequency and span of years seen

In order to examine sighting frequency and span of years seen, all photos (Q1, Q2, and Q3) of marked (D1 or D2) individuals sighted within the study area were used. The sighting frequency of all dolphins sighted since 1982 was limited to include only one sighting per individual per day within the study area. The span of years over which an individual was observed in the study area was calculated using only sightings by SDRP or Shane during 1982–2007 within the CHPIS study area.

Residency, site fidelity and ranging patterns

Residency patterns across years were determined by scoring the number of dolphins in the yearly catalogue during consecutive multi-week field season years (2001–04) that were identified in previous or subsequent years. Dolphins sighted in only a single survey year, and not in previous or subsequent years, were considered non-residents. Individuals were defined as year-round residents if they were sighted in at least one summer and one winter field season.

To quantify long-term site fidelity and ranging patterns in Charlotte Harbor and Pine Island Sound, individuals sighted on ten or more days within the study area were identified. The sighting locations of these individuals within the study area were examined to determine the prevalence of an individual's distribution pattern to a particular Region (1–7). In addition, the percentage of days sighted outside the study area was calculated.

Between the February 2004 and September 2006 surveys, several catastrophic events occurred in the CHPIS study area. These events provided opportunities to test the strength of site-fidelity and residency. On 13 August 2004, the eye wall of Category 4 Hurricane Charley passed through Regions 3, 4 and 5. These Regions, as well as the eastern half of Region 2, sustained devastating habitat damage (Stevens *et al.*, 2006). Beginning in February 2005, a severe *Karenia brevis* red tide harmful algal bloom impacted much of the west coast of Florida, including CHPIS, lasting for 11 months. Red tide impacted the CHPIS area again during September and October of 2006. This study examined how these combined events influenced site-fidelity by comparing sighting locations of dolphins observed at least ten days with at least one sighting before and after the hurricane and red tide events.

Abundance estimation

The number of dolphins inhabiting the study area was estimated for the seven primary field sessions conducted from September 2001 through September 2006. These data can be utilised to compare to other areas along Florida's west coast as well as establish baseline abundance estimates for the defined B22 and B23 Northern Gulf of Mexico bay, sound and estuarine stocks currently defined by NMFS (Waring *et al.*, 2011). The methods for estimating abundance in this study were based on similar studies performed on coastal and estuarine bottlenose dolphins (Balmer *et al.*, 2008; Chilvers and Corkeron, 2003; Read *et al.*, 2003; Speakman *et al.*, 2010; Williams *et al.*, 1993; Wilson *et al.*, 1999). The closed mark-recapture models (Seber, 1982) and robust design models (Pollock, 1982) used in this study follow the assumptions: (1) a demographically and geographically closed population (for abundance estimation), (2) homogeneity of capture probabilities; (3) marks are recognised on recapture; and (4) marks are not lost during the study period. These were reasonable assumptions for this study area as documented by previous mark-recapture studies conducted in this region (see Wells *et al.*, 1996a; Wells *et al.*, 1997). For all mark-recapture models only marked individuals with a D1 or D2 distinctiveness ranking and sightings with photo quality scores of Q1 or Q2 were utilised.

A Chapman modification of the Lincoln-Petersen model was used for the simplest mark-recapture abundance calculation (Chapman, 1951; Thompson *et al.*, 1998) where the mark period (n_1) was during the first set of completed transects and the recapture (n_2) was the second set of completed transects. Each (n) refers to the number of individuals photographically captured in each set and (m_2) refers to the number of individuals that were counted in both the mark and recapture period. The abundance estimate (N_c), variance (var N_c) and standard error (SE) were calculated as described in Chapman (1951):

$$N_c = ((n_1 + 1)(\mathrm{n}_2 + 1)/(m_2 + 1)) - 1$$

$$\mathrm{var}\ N_c = (n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)/(m_2 + 1)^2(m_2 + 2)$$

$$\mathrm{SE} = (\mathrm{var}\ N_c)^{0.5}$$

A robust 'Markovian Emigration' population model to estimate abundance (see Balmer *et al.*, 2008 for a discussion of model suitability selection criteria and description for this type of application) was used because it permits abundance estimates to be determined during multiple, short-term survey periods within a closed population model (*Mt*) and uses the Jolly-Seber open population model to estimate survivorship, emigration rates and capture-recapture probabilities between the short term survey periods (reviewed in Pine *et al.*, 2003; Pollock, 1982). Total abundance estimates of the entire CHPIS population (distinctive (D1 and D2) plus non-distinctive (D3)) were calculated using the Delta method (see Read *et al.*, 2003; Williams *et al.*, 1993; Wilson *et al.*, 1999).

RESULTS

Survey effort, group size and sighting frequency

Survey effort through the entire SDRP study area was essential for identifying northerly bounds for CHPIS residents. A total of 34,545 group sighting records were compiled during 1970 through 2007 with over 6,425 boat survey days within the entire SDRP programme study area of Tampa Bay, Sarasota Bay, CHPIS and the nearshore Gulf of Mexico coastal waters. As a subset of the above effort, 573 (9%) boat days occurred within the CHPIS study area, although the most intensive efforts in the region did not occur until 1990 (Fig. 2). Annual CHPIS survey effort relative to the rest of SDRP study area involved seven boat days (2%) in the 1970s, five (1%) in the 1980s, 223 (8%) in the 1990s and 338 (13%) in 2000–07.

Short-term site fidelity, at least, was suggested from early tagging studies. Few resightings during 1970/71 of tagged dolphins in CHPIS were documented because much of the field work was concentrated in Sarasota Bay and vicinity (Irvine and Wells, 1972). In addition, field efforts emphasised capture-release, allowing for only incidental resighting opportunities, and the durations of early tag attachments were limited, with a high rate of tag loss. The only documented re-identifications during this period involved two adult females tagged in northern Lemon Bay on 19 July 1971 and re-identified from fin scars two weeks later, within 1km of the original tagging site.

Most of the dolphins identified in CHPIS were observed on multiple occasions. Overall, 3,256 groups were approached ranging in size from one to 40 individuals (average group size = 5 ± 4.5 SD). Calves were present in 47% of dolphin groups (average group size with calves = 7 ± 5.2 SD; without calves = 3 ± 2.6 SD). In total, 1,154 different marked dolphins were identified within study area boundaries between 1982 through 2007. Of these, 139 (12%) were seen once, 766 (66%) were seen on two to nine days and 249 (22%) were seen on 10 or more days in the study area (Fig. 3).

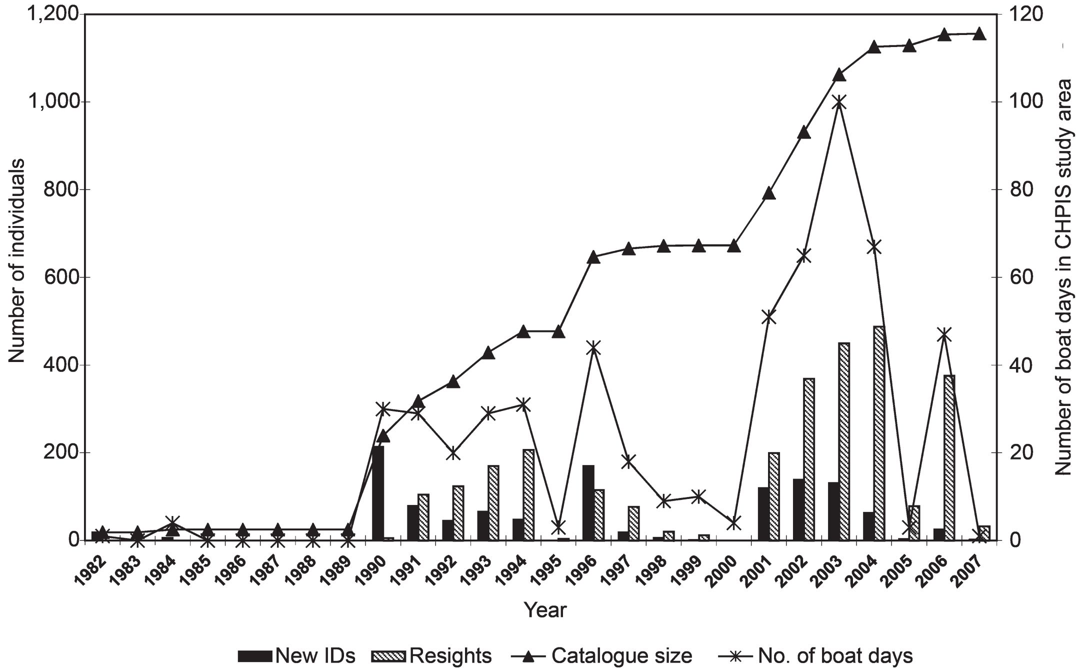

Fig. 2. Number of individuals (new and resights) sighted during all photo-identification efforts, discovery curve for dolphins in the study area and boat day effort.

Most of the dolphins in Charlotte Harbor and Pine Island Sound were identified by the end of the 2003 field seasons (Fig. 2). Understandably, the rate of discovery of new dolphins stabilised by the end of consecutive years with multi-week field seasons (1990–1994 and 2001–04, 2006) and increased when effort was expanded into new Regions (1996) or with the addition of winter field seasons (2002, 2003 and 2004).

Residency, site fidelity and ranging patterns

Overall, residency was defined on the basis of sightings in more than one year, and 937 individuals (81.2% of the total catalogue) met this criterion (Fig. 4). Of these, 332 individuals (28.8% of the total catalogue) were sighted over a span of two to four years and are considered short-term residents, 261 (22.6% of the total catalogue) were sighted during five to nine years and are considered moderate-term residents and 344 (29.8% of the total catalogue) were observed over ten or more years and are considered long-term residents. Two hundred and seventeen individuals (18.8%) were observed only within a single year (non-residents, or dolphins observed at the beginning or end of their residency). For dolphins that were sighted at least twice, most (76%) were year-round residents and were observed in at least one summer and one winter field season (Fig. 5).

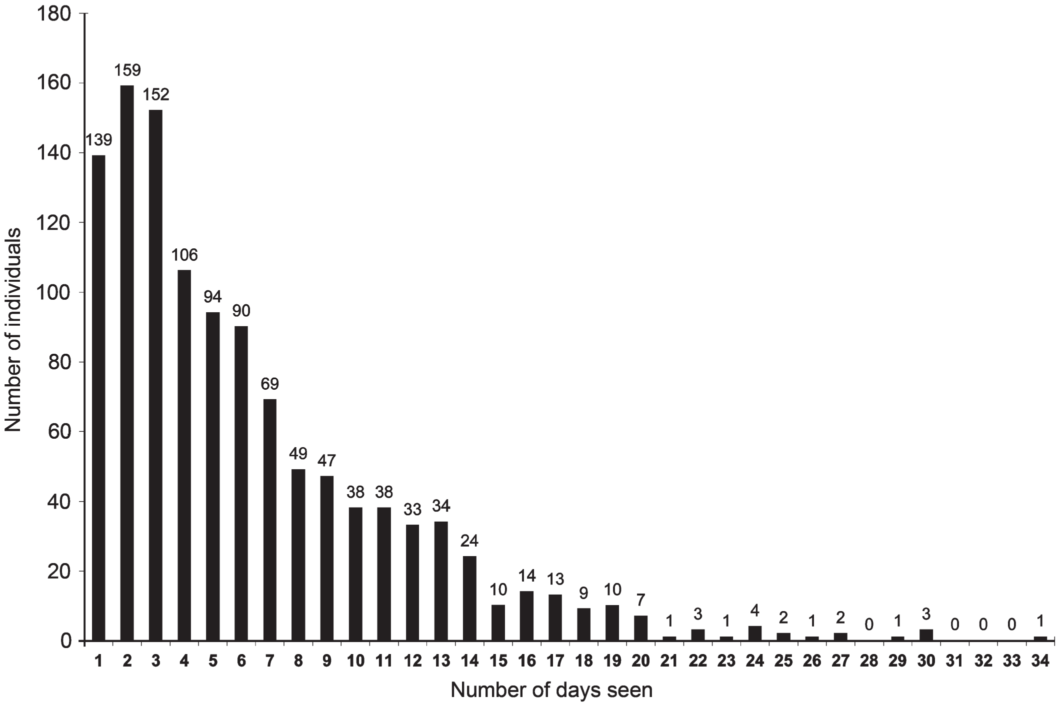

Fig. 3. Sighting frequency of individuals in the CHPIS study area 1982 to 2007

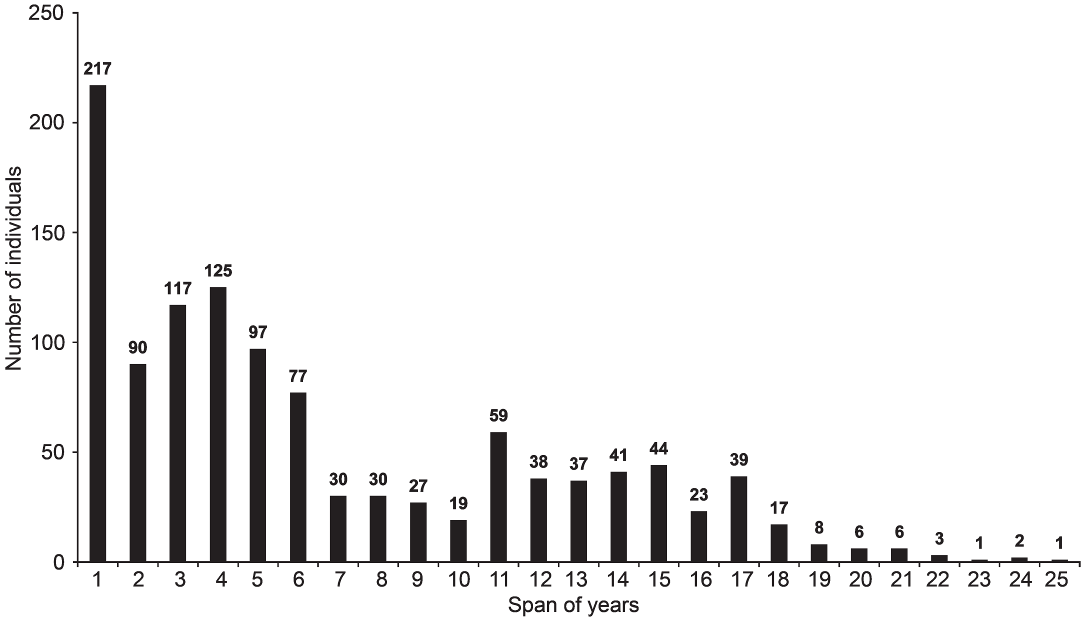

Fig. 4. Span of years seen within the CHPIS study area for 1,154 individuals.

In total, 249 dolphins were resighted on ten or more days in the study area and for further analyses are considered the ‘10+ sight’ group, including 71 females, 30 males and 148 of unknown sex. Individuals from the 10+ sight group were resighted over a span of 3–24 years. Re-sighting patterns of these dolphins suggest strong site fidelity to CHPIS. Over 96% (240) had more than 80% of their sightings in the study area. More than 83% (207) were never observed outside of the ~750 km^2 CHPIS study area. Only nine individuals (3.6%) had at least 20% of their sightings outside of the study area.

Sighting distributions of all individuals in the SDRP catalogue sighted in the Gulf coastal waters adjacent to the CHPIS study area were compared to those of individuals sighted both in and out of the CHPIS study area to assess the frequency of occurrence of Gulf dolphins inside the study area. In total, 287 individuals were sighted at least once in adjacent Gulf coastal waters but were never observed within the study area, and 180 individuals were sighted both in and out of the study area, with 66 of these observed on ten or more days. Of these 66 dolphins, 22 had more than 50% of their sightings outside the study area. These 22 dolphins were observed to the north of the study area in either Sarasota Bay (an area with intensive monthly survey effort) or Tampa Bay.

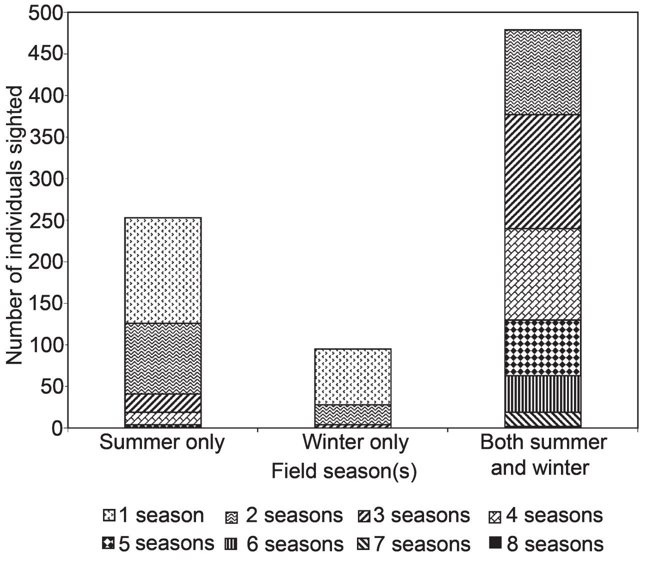

Fig. 5. Number of individuals seen in summer only, winter only, or both summer and winter field seasons within the CHPIS study area.

On a smaller scale, dolphins from the 10+ sight group demonstrated varying degrees of site-fidelity to particular Regions within the CHPIS study area. More than half (57%) were sighted in just one or two Regions in the study area. Only 2.4% were observed in five or more Regions. Table 1 shows the distribution of sightings of these dolphins across the Regions. From the 10+ sight group, four dolphins were seen exclusively in Region 1 (Lemon Bay, NMFS stock B21), while the remaining 245 were seen in Regions 2–7 (Gasparilla Sound, Charlotte Harbor, Pine Island Sound, San Carlos Pass, NMFS stock B22–23). Not surprisingly, dolphins were typically observed most frequently in adjacent regions.

Hurricane Charley in 2004 and subsequent red tides in 2005/06 did not appear to have long-term impacts on individual site fidelity within the study area. Of the 192 dolphins seen on at least ten days and with sightings both before and after Hurricane Charley, 94.3% (181) were resighted within the same Region. Examples of this Regional and long-term site fidelity for four of these individuals are illustrated in Figure 6 and they are representative of the site fidelity patterns of the other 177 dolphins.

Dolphins using the CHPIS region are typically seen in multiple consecutive years and only a small percentage (<10%) of those observed are not sighted in multiple years. Years 2002 and 2003 were used to calculate residency on a percentage basis (since those years included multi-week surveys with previous and subsequent multi-week survey years including the entire CHPIS study area). For the 508 dolphins identified in 2002, 252 (49.6%) were observed in 2001 and 371 (73.0%) in 2003. For the 581 dolphins

Table 1

Number of dolphins from the 10+ sight group that were observed in each Region. The bold values in the matrix represent the number of individuals seen exclusively in that Region. The other values represent the number of individuals that share sightings amongst the Regions.

	# IDS	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6	Region 7
Region 1	**39**	**4 (10%)**	29 (74%)	18 (46%)	3 (8%)	7 (18%)	1 (3%)	1 (3%)
Region 2	**79**	29 (37%)	**2 (3%)**	64 (81%)	30 (38%)	30 (38%)	8 (10%)	3 (4%)
Region 3	**145**	18 (12%)	64 (44%)	**0 (0%)**	58 (40%)	86 (59%)	40 (28%)	14 (10%)
Region 4	**65**	3 (5%)	30 (46%)	58 (89%)	**6 (9%)**	21 (32%)	7 (11%)	6 (9%)
Region 5	**147**	7 (5%)	30 (20%)	86 (59%)	21 (14%)	**1 (1%)**	92 (63%)	17 12%)
Region 6	**112**	1 (1%)	8 (7%)	40 (36%)	7 (6%)	92 (82%)	**6 (5%)**	26 (23%)
Region 7	**30**	1 (3%)	1 (10%)	14 (47%)	6 (20%)	17 (57%)	26 (87%)	**0 (0%)**

identified in 2003, 371 (64.0%) were observed in 2002 and 406 (70.0%) in 2004. Thirty nine dolphins (7.7%) were only seen in 2002 and 58 (10.0%) were only seen in 2003.

Abundance estimates

The number of marked dolphins directly counted during each of the seven primary field seasons ranged from a low of 223 in winter 2002 to a high of 345 in winter 2004 (Table 2). The calculated distinctiveness (or marked proportion) rate ranged from 62% in winter 2002 to 78% in winter 2004 (Table 2). Seasonal abundance estimates derived from both the Lincoln-Petersen and robust design models (Markovian) and adjusted by the Delta method ranged from the lowest estimate, in summer 2001 ($N = 636$, 95% CI = 532–793) to the highest in summer 2002 ($N = 848$, 95% CI = 706–1,036) (Fig. 7). During summer 2006, two years after Hurricane Charley, the estimate was 826 (95% CI = 710–989) (Fig. 7).

DISCUSSION

From a conservation and management perspective, quantitative information about the site fidelity, residency, ranging patterns and abundance trends of dolphins using a particular geographic area is helpful for defining management approaches. Our findings indicate that a large majority of the dolphins that use Charlotte Harbor and Pine Island Sound appear to be both long-term and year-round residents with strong regional site fidelity. This supports the NMFS designation of this area as a geographic management unit. Most of the resident CHPIS dolphins have never been observed outside study area boundaries to the west and north despite intensive SDRP survey effort in these regions. The Gulf and bay waters to the south of CHPIS have not been extensively surveyed for bottlenose dolphins and should be an area considered for future studies. Our residency findings from 2001–07 are consistent with, and expand upon, earlier findings from the CHPIS area (Wells *et al.*, 1996a; Wells *et al.*, 1997) as well as other nearby west coast Florida estuaries such as Tampa Bay (Urian *et al.*, 2009; Wells *et al.*, 1996b) and Sarasota Bay (Wells, 1986; Wells, 1994; Wells, 2009). Findings from multiple complementary studies have supported this differentiation through genetic analyses (Duffield and Wells, 2002; Duffield and Wells, 1991; Sellas *et al.*, 2005; Wells, 1986) and stable isotopes (Barros *et al.*, 2010). The similarity of site fidelity and residency patterns of bottlenose dolphins in west Florida estuaries, as well as the overall low level of movement of individuals between these bordering estuaries, is remarkable. These findings extend the mosaic of long-term resident bottlenose dolphin communities along the west coast of Florida from at least Old Tampa Bay, through Pine Island Sound, a distance of nearly 200 km of contiguous inshore waters.

The observed level of site fidelity in CHPIS supports the general approach of the National Marine Fisheries Service to identify bay, sound and estuarine stocks at least in part on the basis of ranging patterns relative to geographic features. However, our findings suggest that current management unit boundaries may not be entirely appropriate. In particular, there was a lack of evidence to support the current identification of the NMFS management unit B21 (Lemon Bay) as being discrete from B22–23 (Gasparilla Sound, Charlotte Harbor, and Pine Island Sound). The data indicate that most dolphins using Lemon Bay range between the two management units. Of the 249 dolphins sighted 10 or more times within CHPIS, 39 of these individuals were seen in Lemon Bay but only four of these dolphins were seen in Lemon Bay exclusively. The remaining 35 individuals ranged through both B21 and B22–23. Therefore, combining B21 with B22–23 is recommended, until such time as more detailed analyses may yield further information on fine scale stock structure, as has been done recently for a comparable 852 km^2 estuarine system to the north, Tampa Bay (Urian *et al.*, 2009). Similar to Tampa Bay dolphins, CHPIS dolphins typically range into adjacent Regions within the larger CHPIS ~750km^2 study area complex but not throughout the entire area (87.9% in three or fewer Regions).

Based on the above findings, dolphins in the CHPIS study area meet the assumptions needed to estimate abundance using closed population models. By using a dorsal fin grading system to characterise photographic quality and dorsal fin distinctiveness (i.e Read *et al.*, 2003) and a rigorous two person photo-ID cross-checking system, we have minimized the possibility of marks not being detected for recapture and increased the chances of changed fins being detected. Individuals with more subtle D2 fin markings were seen over the same span of time and with similar numbers of sightings as D1 individuals with more extensive fin markings, meeting the assumption of homogeneity of recapture.

Our most recent (2006) best estimate of abundance for the combined B21–22–23 management unit is 826 dolphins (95% CI = 710–989). Abundance of dolphins in CHPIS remained relatively stable across years and seasons during 2001 through 2006. The 2001–06 abundance estimates are much greater than that reported for 1994 in NMFS Stock Assessment Reports for the CHPIS study area. The best estimates of dolphin abundance from NMFS aerial surveys

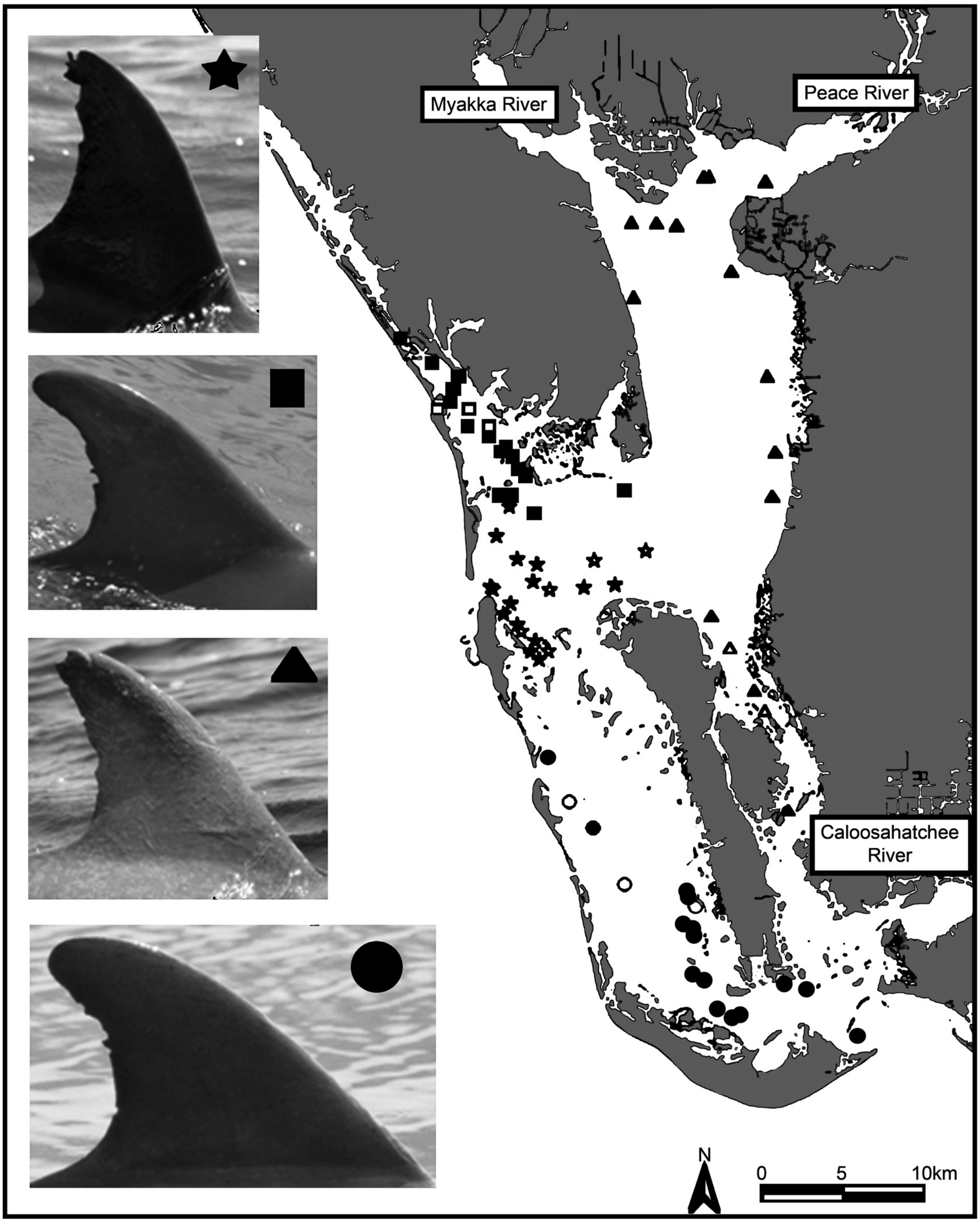

Fig. 6. Sighting distributions of four individuals, RHNO (star), SMRF (square), SNST (triangle) and WVPN (circle) both before and after Hurricane Charley (13 August 2004). Closed symbols represent sightings prior to Hurricane Charley and open symbols represent sightings after Hurricane Charley.

Table 2

Number of marked (D1 or D2 grade) individuals sighted, distinctiveness rate, and estimate of total number of dolphins in CHPIS study area during each field season.

Field season	Summer 2001	Winter 2002	Summer 2002	Winter 2003	Summer 2003	Winter 2004	Summer 2006
Number of marked dolphins identified	247	223	322	283	328	345	330
Distinctiveness rate	0.69	0.62	0.65	0.71	0.75	0.78	0.70
Mark-proportion estimate of marked + unmarked dolphins	358	360	495	399	437	442	471
Total abundance estimate (Robust Markovian) of marked + unmarked dolphins	636	848	892	777	757	868	826
Standard deviation	65.3	83.7	82.8	82.5	62.6	72.6	70.3
Coefficient of variation	0.10	0.10	0.09	0.11	0.08	0.08	0.09
Upper 95% confidence limit	793	1,036	1,086	974	903	1,034	989
Lower 95% confidence limit	532	706	757	645	654	746	710

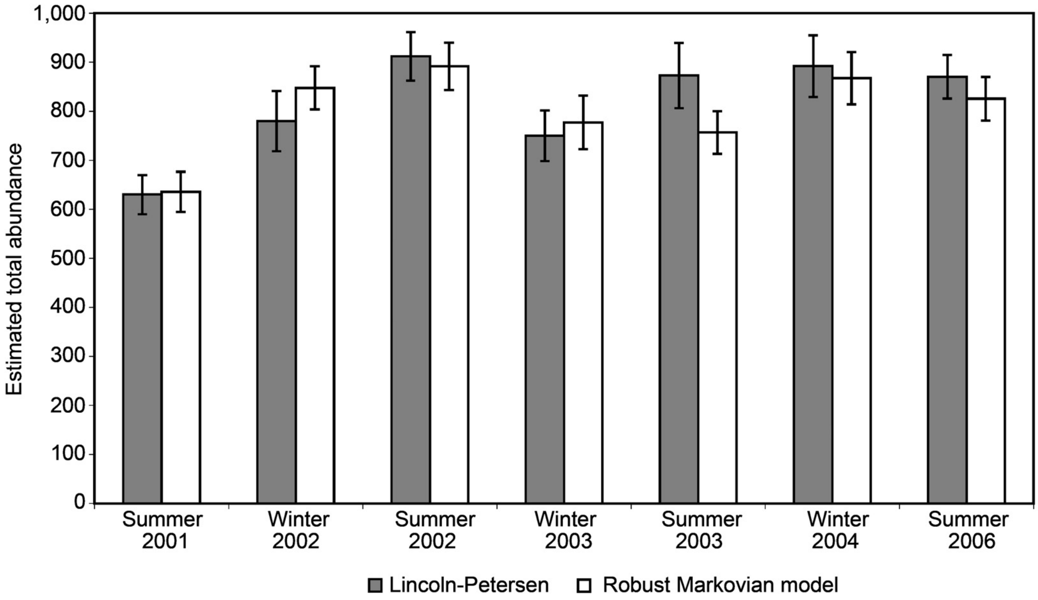

Fig. 7. Population size (±SE) estimated using closed (Lincoln-Petersen) and robust (Markovian Emigration) models for each survey season.

as of 1994 was 0 for Lemon Bay (B-21), and 209 for Charlotte Harbor, Pine Island Sound and Gasparilla Sound (B22–23) (Waring *et al.*, 2011). During SDRP's previous boat-based photo-ID efforts, abundance estimates in Charlotte Harbor (Regions 1–5) were relatively stable between 1990–94, with a minimum estimate of 238 (95% CI = 198–278) in 1992 and a maximum estimate of 385 (95% CI = 341–429) in 1994 (Wells *et al.*, 1996a). The abundance estimate for Pine Island Sound (Regions 6 and 7) in 1996 was 247 (95% CI = 228–266) (Wells *et al.*, 1997). Abundance estimates from the current study exceed those from previous aerial and vessel surveys in the region, but it is unclear whether this represents a true increase or if it is an artifact of field and analytical methodological differences across the decades.

The dolphins in CHPIS showed no evidence of long-term impacts from large-scale environmental perturbations. In 2004, Hurricane Charley devastated the shoreline, terrestrial flora and man-made structures along its path, changed the physiography of the estuary, and washed tremendous quantities of biological and chemical pollution into CHPIS. Major red tide events impacted the region in 2005 and 2006, killing massive quantities of fish. In spite of these perturbations, dolphin abundance in 2006 was within, or slightly greater than the 2001–04 abundance estimates, and 94% of dolphins were re-sighted within their previous ranges. Sharks and other fish in the CHPIS system and nearby estuaries were also found to resume normal patterns following hurricanes (Heupel *et al.*, 2003; Locascio and Mann, 2005; Ubeda *et al.*, 2009).

The apparent resilience and stability of the dolphins of CHPIS to multiple potentially catastrophic natural perturbations is noteworthy in light of reported responses elsewhere. Miller *et al.* (2010) suggested that Mississippi Sound experienced an increase in bottlenose dolphin reproduction in the two years following Hurricane Katrina, but the time series used by Miller and colleagues is too brief to confirm changes beyond the normal multi-year cycle of interannual reproductive variability. For comparison, annual bottlenose dolphin fecundity in Sarasota Bay, Florida, can vary by nearly an order of magnitude from one year to another (Wells and Scott, 1990), a range of variability greater than the changes in calf encounters reported by Miller *et al.* (2010). Elliser and Herzing (2011) reported dramatic changes to the social structure of bottlenose dolphins over the Little Bahama Banks in response to passage of two major hurricanes over a three week period in 2004. The long-term resident community experienced the disappearance of 30% of its members with the storms. Subsequently, approximately the same number of individuals immigrated into the population, and a new social structure was established.

Bottlenose dolphin responses to *K. brevis* blooms vary depending on the strength, duration and spatial coverage of the bloom, among other factors. In the northern Gulf of Mexico, several recent federally declared Unusual Mortality Events involving the deaths of hundreds of bottlenose dolphins have been tentatively attributed to poisoning from toxins from harmful algal blooms, perhaps through an eosinophilia syndrome (Balmer *et al.*, 2008; Schwacke *et al.*, 2010). The severe and prolonged 2005 *K. brevis* bloom encompassed much of the central and southwest coast of Florida. Elevated levels of mortality of manatees (*Trichechus manatus latirostris*), bottlenose dolphins and marine turtles during this time led to the declaration by US federal agencies of a Multi-species Unusual Mortality Event. While dolphin mortalities involving non-residents increased near Sarasota Bay, none of the long-term resident Sarasota Bay dolphins were found to have died from brevetoxins (Wells, in review). Instead, Sarasota Bay dolphins demonstrated sublethal responses, including emigration of shorter-term residents, and changes in group size, habitat use and social behavior (Wells, in review; McHugh *et al.,* in press). Lagged responses to decreases in prey species availability of 90% or more (Gannon *et al.*, 2009) led to declines in body condition for some vulnerable dolphin age/sex classes, and likely contributed to an increase in lethal interactions with anglers through depredation of bait and catch (Powell and Wells, 2011; Wells *et al.*, 2008). Latent impacts of the red tide are thought to include the deaths in 2006 of 2% of the long-term resident dolphins of Sarasota Bay from ingestion of recreational fishing gear (Powell and Wells, 2011). Increased interactions between anglers and dolphins in the CHPIS area have been noted in recent years. Mortality rates on the order of 2% might not have been detectable through our abundance estimation approach. Such a rate of additional loss, maintained over years, would not be sustainable.

The work reported here provides the necessary information for identifying biologically meaningful bottlenose dolphin management units in the bays, sounds and estuaries of southwestern Florida. The documented long-term stability and site-fidelity in spite of severe natural environmental perturbations pave the way for more detailed studies applying additional tools and information such as genetics, social association patterns, habitat use patterns, stable isotopes and environmental contaminant concentrations to define fine scale stock structure in this region. Long-term studies of well-defined, biologically meaningful population units facilitate potential detection of impacts from a variety of sources, including natural perturbations, human activities including oil spills and climate disruption.

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REFERENCES

Balmer, B.C., Wells, R.S., Nowacek, S.M., Nowacek, D.P., Schwacke, L.H., McLellan, W.A., Scharf, F.S., Rowles, T.K., Hansen, L.J., Spradlin, T.R. and Pabst, D.A. 2008. Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *J. Cetacean Res. Manage.* 10(2): 157–68.

Barros, N.B., Ostrom, P., Stricker, C. and Wells, R.S. 2010. Stable isotopes differentiate bottlenose dolphins of west central Florida. *Mar. Mamm. Sci.* 26: 324–36.

Barros, N.B. and Wells, R.S. 1998. Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *J. Mammal.* 79(3): 1,045–59.

Blaylock, R.A. 1995. A pilot study to estimate abundance of the US Atlantic coastal migratory bottlenose dolphin stock. NOAA Tech. Mem. (SEFSC-362): 9pp.

Bräger, S. 1993. Diurnal and seasonal behaviour patterns of bottlenose dolphins (*Tursiops truncatus*). *Mar. Mammal Sci.* 9: 434–40.

Bräger, S., Würsig, B., Acevedo, A. and Henningsen, T. 1994. Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Galveston Bay, Texas. *J. Mammal.* 75(2): 431–37.

Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. *Univ. Calif. Publ. Statist.* 1: 131–60.

Chilvers, B.L. and Corkeron, P.J. 2003. Abundance of Indo-Pacific bottlenose dolphins, (*Tursiops truncatus*), off Point Lookout, Queensland, Australia. *Mar. Mammal Sci.* 19(1): 85–95.

Duffield, D. and Wells, R.S. 2002. The molecular profile of a resident community of bottlenose dolphins, *Tursiops truncatus*. pp.3–11. *In*: Pfeiffer, C.J. (eds). *Molecular and Cell Biology of Marine Mammals*. Krieger Publishing Company, Melbourne, FL.

Duffield, D.A. and Wells, R.S. 1991. The combined application of chromosome, protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. *Rep. int. Whal. Commn (special issue)* 13: 155–69.

Elliser, C.R. and Herzing, D.L. 2011. Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, *Tursiops truncatus*, after two major hurricanes. *Mar. Mamm. Sci.* 27: 39–59.

Fazioli, K.L., Hofmann, S. and Wells, R.S. 2006. Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). *Aquat. Mamm.* 32: 212–22.

Fertl, D. 1994. Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *Texas J. Sci.* 46(4): 299–317.

Gannon, D.P., Berens, E.J., Camilleri, S.A., Gannion, J.G., Brueggen, M.K., Barleycorn, A., Palubok, V., Kirkpatrick, G.J. and Wells, R.S. 2009. Effects of *Karenia brevis* harmful algal blooms on nearshore fish communities in southwest Florida. *Mar. Ecol. Prog. Ser* 378: 171–86.

Heupel, M.R., Simpfendorfer, C.A. and Hueter, R.E. 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *J. Fish. Biol* 63: 1,357–63.

Irvine, A.B., Scott, M.D., Wells, R.S. and Kaufmann, J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fish. Bull.* 79(4): 671–88.

Irvine, B. and Wells, R.S. 1972. Results of attempts to tag Atlantic bottlenose dolphins (*Tursiops truncatus*). *Cetology* 13: 1–5.

Locascio, J.V. and Mann, D.A. 2005. Effects of Hurricane Charley on fish chorusing. *Biol. Lett.* 1: pp.362–65.

Maze, K.S. and Würsig, B. 1999. Bottlenose dolphins of San Luis Pass, Texas: occurrence patterns, site fidelity, and habitat use. *Aquat. Mamm.* 25(2): 91–103.

Miller, L.J., Mackey, A.D., Hoffland, T., Solangi, M. and Kuczaj, S.A. 2010. Potential effects of a major hurricaneon Atlantic bottlenose dolphin (*Tursiops truncatus*) reproduction in the Mississippi Sound. *Mar. Mamm. Sci.* 26: 701–15.

Odell, D.K. and Reynolds, J.E. 1980. Abundance of the bottlenose dolphin, (*Tursiops truncatus)*, on the west coast of Florida. NTIS PB80-197650. US Dept. of Commerce, Springfield, Virginia.

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J. and Rice, J.A. 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries* 28: 10–23.

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.* 46: 757–60.

Powell, J.R. and Wells, R.S. 2011. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Mar. Mamm. Sci.* 27: pp.111–29.

Quintana-Rizzo, E. and Wells, R.S. 2001. Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into social organization. *Can. J. Zool.* 79: 447–56.

Read, A.J., Urian, K.W., Wilson, B. and Waples, D.M. 2003. Abundance of bottlenose dolphins in the bays, sounds and esturies of North Carolina. *Mar. Mammal Sci.* 19(1): 59–73.

Sallenger, A.H., Stockdon, H.F., Fauver, L., Hansen, M., Thompson, D., Wright, D.W. and Lillucrop, J. 2006. Hurricanes 2004: an overview of their characteristics and coastal change. *Estuaries and Coasts* 29: 880–88.

Schwacke, L.H., Twiner, M.J., De Guise, S., Balmer, B.C., Wells, R.S., Townsend, F.I., Rotstein, D.C., Varela, R.A., Hansen, L.J., Zolman, E.S., Spradlin, T.R., Levin, M., Leibrecht, H., Wang, Z. and Rowles, T.K. 2010. Eosinophilia and biotoxin exposire in bottlenose dophins (*Tursiops truncatus*) from a coastal area impacted by repeated mortality events. *Environ. Res.* 110: 548–55.

Scott, G.P., Burn, D.M., Hansen, L.J. and Owen, R.E. 1989. Estimates of bottlenose dolphin abundance in the Gulf of Mexico from regional aerial surveys. NOAA-NMFS, SEFSC Miami Lab. Contr. CRD-88/89-07, February 1989 (unpublished). 24pp + appendices. [Available from: *www.nmfs.gov*].

Scott, M.D., Wells, R.S. and Irvine, A.B. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. pp.235–44. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, California. 653pp.

Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd ed. Charles Griffin and Company Ltd., London. i–xvii+654pp.

Sellas, A.B., Wells, R.S. and Rosel, P.E. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conserv. Genet.* 6: 715–28.

Shane, S.H. 1980. Occurrence, movements and distribution of bottlenose dolphins, *Tursiops truncatus*, in southern Texas. *Fish. Bull.* 78: 593–601.

Shane, S.H. 1990a. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. pp.245–66. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, Californa. 653pp.

Shane, S.H. 1990b. Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. pp.541–58. *In*: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, California. 653pp.

Shane, S.H. 2004. Residence patterns, group characteristics, and association patterns of bottlenose dolphins near Sanibel Island, Florida. *Gulf of Mexico Science* 22: 1–12.

Speakman, T.R., Lane, S.M., Schwacke, L.H., Fair, P.A. and Zolman, E.S. 2010. Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *J. Cetacean Res. Manage.* 11(2): 153–62.

Stevens, P.W., Blewett, D.A. and Casey, J.P. 2006. Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of hurricane Charley. *Estuaries and Coasts* 29: 997–1,003.

Taylor, B.L. 2005. Identifying units to conserve. pp.149–62. *In*: Reynolds, J.E., Perrin, W.F., Reeves, R.R., Montgomery, S. and Ragen, T.J. (eds). *Marine Mammal Research: Conservation Beyond Crisis*. The Johns Hopkins University Press, Baltimore, Maryland.

Thompson, N.B. 1981. Estimates of abundance of *Tursiops truncatus* in Charlotte Harbor, Florida. NOAA/NMFS/SEFC/Miami Laboratory, Fishery Data Analysis Technical Report. [Available from: *www.nmfs.gov*].

Thompson, W.L., White, G.C. and Gowan, C. 1998. Monitorng vertebrate populations. *Academic Press, San Diego, California*: 365pp.

Tomasko, D.A., Anastasiou, C. and Kovach, C. 2006. Dissolved oxygen dynamics in Charlotte Harbor and its contributing watershed, in response to hurricane Charley, Frances, and Jeanne-impacts and recovery. *Estuaries and Coasts* 29: pp.932–38.

Ubeda, A.J., Simpfendorfer, C.A. and Heupel, M.R. 2009. Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. *Environ. Biol. Fish.* 84: 293–303.

Urian, K.W., Hofmann, S., Wells, R.S. and Read, A.J. 2009. Fine-scale population structure of bottlenose dolphins, *Tursiops truncatus*, in Tampa Bay, Florida. *Mar. Mamm. Sci.* 25: 619–38.

Wade, P.R. and Angliss, R.P. 1997. Report of the GAMMS Workshop, April 3–5, 1996, Seattle, Washington. *NOAA Technical Memorandum NMFS* OPR-12. [Available from: *www.nmfs.gov*].

Waring, G.T., Josephson, E., Maze-Foley, K. and Rosel, P.E. 2011. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments 2010. NOAA Tech Memo NMFS NE. 598pp.

Wells, R.S. 1986. Structural aspects of dolphin societies, PhD thesis, University of California, Santa Cruz, CA. 234pp.

Wells, R.S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. pp.199–205. *In*: Pryor, K. and Norris, K.S. (eds). *Dolphin Societies, Discoveries and Puzzles*. University of California Press, Berkeley, California. 397pp.

Wells, R.S. 1994. Determination of bottlenose dolphin stock discreteness: application of a combined behavioural and genetic approach. pp.16–20. *In*: Wang, K.R., Payne, P.M. and Thayer, V.G. (eds). *Coastal Stock(s) of Atlantic Bottlenose Dolphin: Status Review and Management. Proceedings and recommendations from a workshop held in Beaufort, NC, 13–14 September 1993*. NOAA Technical Memorandum NMFS-OPR-4. 120pp.

Wells, R.S. 2003. Dolphin social complexity: lessons from long-term study and life history. pp.32–56. *In*: de Waal, F.B.M. and Tyack, P.L. (eds). *Animal Social Complexity: Intelligence, Culture, and Individualised Societies*. Harvard University Press, Cambridge, MA. 640pp.

Wells, R.S. 2009. Learning from nature: bottlenose dolphin care and husbandry. *Zoo Biol.* 28: pp.1–17.

Wells, R.S. In review. Social structure and life history of common bottlenose dolphins near Sarasota Bay, Florida: insights from four decades and five generations. In: J. Yamagiwa and L. Karczmarski (eds). Springer, New York. *Field Studies of Primates and Cetaceans: Understanding and Conserving Complex Mammalian Societies*.

Wells, R.S., Allen, J.B., Hofmann, S., Bassos-Hull, K., Fauquier, D.A., Barros, N.B., DeLynn, R.E., Sutton, G., Socha, V. and Scott, M.D. 2008. Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Mar. Mammal Sci.* 24(4): 774–94.

Wells, R.S., Bassos, M.K., Urian, K.W., Carr, W.J. and Scott, M.D. 1996a. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Charlotte Harbor, Florida: 1990–1994. *NOAA Tech. Mem.* NMFS-SEFSC-384: 36pp.

Wells, R.S., Bassos, M.K., Urian, K.W., Shane, S.H., Owen, E.C.G., Weiss, C.F., Carr, W.J. and Scott, M.D. 1997. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Pine Island Sound, Florida: 1996. Final Contract Report to National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL. Contract No. 40-WCNF601958. 86pp. [Available from: *www.nmfs.gov*].

Wells, R.S., Boness, D.J. and Rathburn, G.B. 1999. Behaviour. pp.324–421. *In*: Reynolds, J. and Rommel, S. (eds). *Biology of Marine Mammals*. Smithsonian Institution Press, Washington and London. 578pp.

Wells, R.S., Irvine, A.B. and Scott, M.D. 1980. The social ecology of inshore odontocetes. pp.263–317. *In*: Herman, L.M. (eds). *Cetacean Behaviour: Mechanisms and Functions*. John Wiley & Sons, New York. xiii+463pp.

Wells, R.S. and Scott, M.D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Rep. int. Whal. Commn (special issue)* 12: 407–15.

Wells, R.S., Scott, M.D. and Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. pp.247–306. *In*: Genoways, H. (eds). *Current Mammalogy*. Plenum Press, New York. 519pp.

Wells, R.S., Urian, K.W., Read, A.J., Bassos, M.K., Carr, W.J. and Scott, M.D. 1996b. Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Tampa Bay, Florida: 1988–1993. *NOAA Tech. Mem.* NMFS-SEFSC-385: 25pp. [Available from: *www.nmfs.gov*].

Williams, J.A., Dawson, S.M. and Slooten, E. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool.* 71: 2,080–88.

Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl.* 9: 288–300.

Würsig, B. and Jefferson, T.A. 1990. Methods of photo-identification for small cetaceans. *Rep. int. Whal. Commn (special issue)* 12: 43–52.

Würsig, B. and Lynn, S. 1996. Movements, site fidelity and respiration rates of bottlenose dolphins on the central Texas coast. *NOAA Tech. Mem.*: NMFS-SEFSC-383. 111pp.

Defining the appropriate ‘Unit-To-Conserve’ under the International Whaling Commission’s Revised Management Procedure

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ABSTRACT

Identifying the appropriate ‘Unit to Conserve’ (UTC) is critical to the success of any management scheme. While the need to define the UTC appropriate to the IWC’s Catch Limit Algorithm (CLA) has long been recognised by its Scientific Committee, little progress has been made on this issue. The CLA was rigorously tested prior to its adoption. However, most of those original performance trials focused on single-population scenarios or two-population scenarios with no ongoing dispersal. None of the trials considered the performance of the CLA across a range of dispersal rates. In this study, the performance of the CLA under a variety of population structure scenarios is examined. This is the first study to investigate the levels of connectivity (i.e. dispersal rate) for which populations require separate management to meet the conservation goals of the CLA. All the trials consisted of two populations that were managed as a single stock for 100 years. Both historical and modern hunts were spatially-biased so that population 1 was the primary target of hunting. Parameters that varied among trials were the relative carrying capacities (*K*) of the populations, the dispersal rate between them, maximum sustainable yield rate ($MSYR_{1+}$), and the precision in simulated abundance estimates. All of these parameters had strong effects on the conservation performance of the CLA. Trials with a low $MSYR_{1+}$ (1%) generally ended with the abundance of population 1 below 0.54*K*, regardless of the dispersal rate or relative carrying capacities of the two populations. The same was true of trials in which the carrying capacity of population 1 represented only 10% of the total landscape carrying capacity and the CV of the abundance estimates was low, even when dispersal between populations was high ($5 \times 10^{-3} yr^{-1}$) and $MSYR_{1+}$ was 4%. The results suggest that the appropriate UTCs under the RMP are likely to exchange dispersers at high enough rates that they will be difficult to delineate using existing methods. These results also highlight the value of spatially-diffuse hunting patterns that avoid potential overhunting of unrecognised stocks.

KEYWORDS: CONSERVATION; UNIT TO CONSERVE; MANAGEMENT PROCEDURE; SUSTAINABILITY; STOCK IDENTITY

INTRODUCTION

The success of most management schemes hinges on accurate identification of the management units the scheme is intended to conserve. The dispersal rates at which ‘Units to Conserve’ (UTCs) should be defined will depend on the management objectives those units are intended to meet (Palsbøll *et al.*, 2007; Taylor, 2005; Taylor *et al.*, 2010; Waples and Gaggiotti, 2006). For instance, in the United States, the two major pieces of legislation aimed at conserving marine mammals are the Endangered Species Act (ESA), and the Marine Mammal Protection Act (MMPA). These Acts have different goals and hence require different levels of connectivity between their respective UTCs; the ESA aims to prevent the extinction of species, while the MMPA aims to maintain populations as ‘functioning elements of their ecosystems’. To achieve the goal of the ESA requires identification and management of units that contribute to the evolutionary potential of the species (Waples, 1991). Units that experience gene flow at the rate of one disperser or fewer per generation have been suggested as meeting this criterion because such a low level of gene flow could allow for the development of local adaptations (Gardenfors *et al.*, 2001; Taylor, 2005; Taylor *et al.*, 2010). Units with this level of connectivity are typically referred to as ‘Evolutionarily Significant Units,’ or ESUs (Moritz, 1994; Waples, 1991). The more ambitious conservation goal of the MMPA, on the other hand, requires separate management if two units are demographically independent (Angliss and Wade, 1997). Specifically, simulations have shown that separate management is necessary even for populations exchanging dispersers at rates in excess of 1% per year if the goals of the MMPA are to be met (Taylor, 1997). Units at this level are referred to as ‘Demographically Independent Populations,’ or DIPs (Taylor, 1997; Waples and Gaggiotti, 2006).

The IWC agreed to use the Revised Management Procedure (RMP) to manage commercial whaling of baleen whales on their feeding grounds, should commercial whaling be allowed to resume (IWC, 1994). Catches are determined by the Catch Limit Algorithm (CLA), which was subjected to extensive performance testing to ensure robustness considering the three competing management objectives of maximising catch, minimising variability in catch and adequately conserving populations (IWC, 1991; 1992b; 2007). During the development of the CLA, testing was done to examined performance when two populations were erroneously managed as one stock (‘stock’ is the name given to management units in the RMP framework) and when one stock is managed as two (Smith *et al.*, In press). The two-population trials included scenarios in which dispersal (i.e. permanent movement of individuals from one breeding population to another) occurred between adjacent populations at a rate of 0.5% per year as well as cases with no dispersal. These trials confirmed that the conservation

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performance of the CLA is poor when two populations are erroneously combined into a single stock and hunting is concentrated on only one of the populations (IWC, 1991), but that stock definition errors are partially mitigated by dispersal between populations (IWC, 1992a). However, the trials did not investigate a range of dispersal rates to determine the critical level of dispersal above which the conservation goal of the RMP can be met even if two populations are combined into a single stock, i.e. they did not provide insight into the question of what is the appropriate UTC under the RMP. The RMP includes options (variants) such as catch cascading and catch capping to account for stock structure uncertainty, and evaluations of the consequences of stock definition errors have been conducted as part of selecting among these variants for individual stocks based on case-specific *Implementation Simulation Trials* (e.g. IWC, 2004; 2007; Punt and Donovan, 2007). However, the case-specific nature of *Implementation Simulation Trials* limits their utility for drawing general conclusions regarding the circumstances under which management as separate stocks is necessary to adequately protect populations.

In this study the performance of the CLA under a variety of population structure scenarios is examined. Two populations are erroneously managed as a single stock in all of our simulations. Performance is measured as the probability that the abundance of both populations is greater than 54% of carrying capacity (i.e. $0.54K$) by the end of each simulation. $0.54K$ was the Protection Level in the New Management Procedure, and the probability of taking whales when a stock was below $0.54K$ was taken into consideration when selecting among CLA variants. The performance of the CLA is evaluated as a function of the relative sizes of the two populations and the dispersal rate between them. Our results provide insight into the critical level of dispersal above which two populations can be managed as a single stock without compromising the conservation goal of the RMP. The results will provide guidance to researchers attempting to define stocks for individual species being managed under the RMP, as well as to those seeking to develop new approaches to defining stocks for use under the RMP.

METHODS

The TOSSM package (Martien *et al.*, 2009) was used to evaluate the performance of the CLA in the face of unrecognised population structure. A series of simulations were conducted in which two populations were combined into a single management unit (MU). A single catch limit was calculated by the CLA for the MU and was therefore based on the combined abundance of both populations. The entire catch limit was removed each year and, if possible, was taken entirely from 'population 1'. If there were insufficient individuals in population 1 to meet the catch limit, the balance of the catch limit was taken from population 2. Hunted animals were chosen at random, without respect to age or sex.

All simulations were initialised with both populations at K. The combined carrying capacity of the two populations (K_{TOT}) was set to 7,500 in all simulations. In the first year of each simulation, population 1 was depleted to $0.3K$ and population 2 to $0.99K$[3]. The two populations then underwent 100 years of simulated management, with both populations combined into a single MU. Abundance in the MU was estimated and the catch limit re-calculated every five years during this management period. We performed 100 replicates of each simulation.

Preliminary analyses showed that our results were strongly dependent on the coefficient of variation (CV) of the abundance estimate for the MU. In the TOSSM package, CV is modeled according to the formula

$$CV = 0.1\sqrt{x/n}$$

where N is the estimated abundance of the MU and x is the the abundance at which CV = 0.1[4].

Taylor *et al.* (2007) found that CVs for stocks of large baleen whales in US territorial waters ranged from 0.08 (western North Pacific humpback whales) to 0.73 (CA/OR/WA minke whales), with an average of 0.29. Values of x were chosen such that when both populations in the MU were at carrying capacity, the CV was 0.30, 0.17, or 0.04 (Fig. 1). The highest of these values represents a typical level of precision, while the middle value represents a realistic high precision case[5]. The lowest CV examined is unlikely to apply or to be achieved for large whale species except in cases of mark-recapture estimates with high effort, but allows full characterisation of the behavior of the CLA. Higher values of CV were not examined. Doing so would have resulted in adequate protection under virtually all population structure scenarios because the CLA reduces catches when abundance estimates are imprecise, and would therefore not have contributed to the objective of identifying the population structure scenarios under which the CLA failed to adequately protect populations if population structure went undetected.

TOSSM simulations must be initialised with a dataset generated by the R package 'rmetasim' (Strand, 2002). An array of datasets with various parameterisations were generated using 'rmetasim' for this study. The three parameters varied in these datasets were: (1) the maximum sustainable yield rate ($MSYR_{1+}$); (2) the carrying capacities of the two populations (always summing to 7,500); and (3) the annual dispersal rate between the two populations. A full description of all population parameters used when generating these datasets is included in Appendix 1.

Two main sets of trials were performed. The first set of trials was performed to determine the effect of dispersal rate on conservation performance, which we defined as recovering the most vulnerable population to $0.54K$[6]. In these trials, the carrying capacity of each population was set at K = 3,750 (half of the total for the landscape). These trials

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[3] These values were chosen to be consistent with those used during development and testing of the CLA (IWC, 1991)

[4] This is a simplification of the way CVs are generated by the control program used to test the CLA (IWC, 1991), but captures the essence of that data generation process.

[5] The guidelines to the RMP impose a minimum CV of 0.15 because performance of the CLA can be poor when the CV is underestimated (IWC, 1992b).

[6] Recovery to 0.54K, which is approximately MSYL, was a measure of conservation performance used during the development of both the CLA and the algorithm for calculating catch limits under the MMPA.

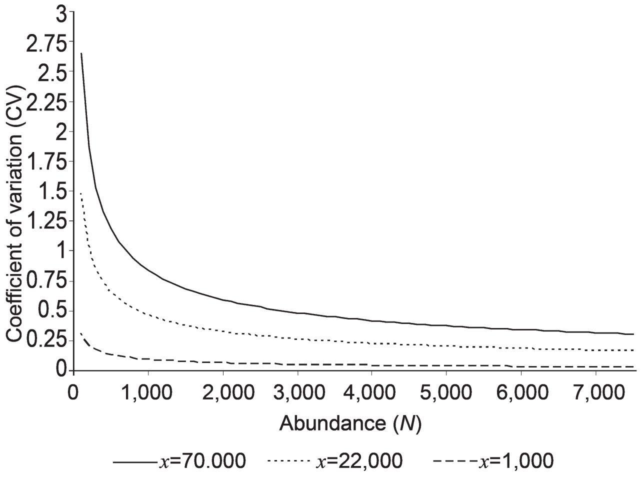

Fig. 1. Relationship between abundance and *CV* for the three values used for the *CV* tuning parameter (x). The values chosen for x result in *CV*s at $N = 7{,}500$ of 0.3 ($x = 70{,}000$), 0.17 ($x = 22{,}000$) and 0.04 ($x = 1{,}000$).

were conducted using the highest CV scenario ($x = 70{,}000$; Fig. 1). Four dispersal rates (5×10^{-6}yr^{-1}, 5×10^{-5}/yr^{-1}, 5×10^{-4}yr^{-1}, and 5×10^{-3}yr^{-1}) were examined. These rates span the range of dispersal rates typically of interest when defining units to conserve (Palsbøll *et al.*, 2007; Taylor *et al.*, 2010). Simulations using these four dispersal rates were performed for $\text{MSYR}_{1+} = 4\%$ and $\text{MSYR}_{1+} = 1\%$.

The second set of trials explored the effect of the CV of the abundance estimates on conservation performance across five levels of relative population carrying capacity. In these trials, the parameters held constant were dispersal rate (5×10^{-3}yr^{-1}) and MSYR_{1+} (4%). For each of the three CV curves shown in Fig. 1, the relative carrying capacities of the two populations were varied so that population 1 comprised 10, 20, 30, 40, or 50% of the total landscape carrying capacity.

For each trial, the abundance trajectory for population 1 and the total catch during RMP hunting was summarised. Only the abundance of population 1 is presented because a spatial bias in hunting resulted in this population being more heavily impacted by hunting than population 2. This spatial bias simulated a situation in which whalers attempt to minimise effort by concentrating their effort close to a home port. Population 1 is assumed to be a coastal population and therefore the first encountered when whalers leave port. Population 2 is adjacent to population 1, but further offshore. The spatial bias in hunting during the historic hunting phase of the simulations is reflected in the initial depletion of population 1 (it is depleted to 0.3*K* prior to the first application of the CLA). The extent of spatial bias in removals during the management period is controlled in the TOSSM package by the 'harvest.interval' argument. Hunting always occurs initially in the harvest interval closest to the coast and then proceeds steadily offshore upon depletion of the animals in each interval (Martien *et al.*, 2009). For all of our simulations the landscape was divided into ten equally-sized harvest intervals.

Two single-stock simulations were ran and the results were compared with those from previous analyses to confirm that the CLA as implemented in the TOSSM package was working correctly. These trials each consisted of a single population with a carrying capacity of 7,500 that was initially depleted to 0.3*K*. MSYR_{1+} was set at 1% in one trial and 4% in the other. Thus, these trials correspond fairly closely to the R1 and R4 base-case trials used during the development of the CLA (IWC, 1991), except that MSYR refers to the 1+ rather than mature component of the population, MSYL does not occur at 0.6*K* for our trials but instead occurs at 0.518*K* and 0.547*K* for the $\text{MSYR}_{1+} = 1\%$ and 4% trials, respectively, and the abundance estimates are generated slightly differently[7]. These single-stock trials were run for 500 years, with median abundance (across 100 replicates) recorded at years 100 and 500.

RESULTS

Population 1 always recovered to greater than 0.54*K* (Fig. 2) after 100 years of CLA management when the initial carrying capacities of the two populations were equal to half of the total landscape *K*, and MSYR_{1+} was set at 4%. However, this was not the case when MSYR_{1+} was set at 1%. Population 1 did not generally recover in these trials. The exception to this was when the dispersal rate, *d*, equaled 5×10^{-3}yr^{-1}. This dispersal rate resulted in better conservation performance (Fig. 2), with population 1 recovering to above 0.54*K* in 69% of replicates. The abundance trajectories for the three lowest dispersal rates ($d = 5 \times 10^{-6}$ to 5×10^{-4}) were fairly consistent (Fig. 2). The depletion of population 1 in the $\text{MSYR}_{1+} = 1\%$ trials resulted in lower total catches than in the $\text{MSYR}_{1+} = 4\%$ trials (Table 1).

Table 1

Median cumulative catch as a function of MSYR_{1+} and dispersal rate.

	Dispersal rate			
MSYR_{1+}	5×10^{-6}	5×10^{-5}	5×10^{-4}	5×10^{-3}
4%	2,855	2,775	2,850	2,900
1%	1,590	1,660	1,700	1,825

The CVs for the abundance estimates strongly affected the population trajectories, as did the relative carrying capacities of the two populations (Fig. 3). Population 1 did not recover to 0.54*K* with high probability with the lowest CV regardless of the relative sizes of the populations, except when the carrying capacity for population 1 was half of the total when this probability was 0.73 (Fig. 3, upper panels). In contrast, Population 1 did recover in most trials with the two higher CVs, except when population 1 constituted only 10% of the total landscape *K* initially. The impact of higher CVs on population recovery rates was not unexpected; the CLA sets the catch limit as the 40.2th percentile of a posterior distribution for the catch limit; greater uncertainty in abundance estimates thus results in a wider posterior distribution for the catch limit and hence a lower catch limit overall. The results in Fig. 3 are based on the most optimistic assumptions regarding MSYR_{1+} (4%) and dispersal rate (5×10^{-3}yr^{-1}).

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[7] In principle, 0.54K is 10% less than the nominal MSYL of 0.6K, suggesting that the threshold for defining management success should be 10% lower than the 0.518K and 0.547K. However, the linkage between 0.54K and MSYL (if not the entire rationale for the linkage) is no longer used explicitly in testing of management strategies.

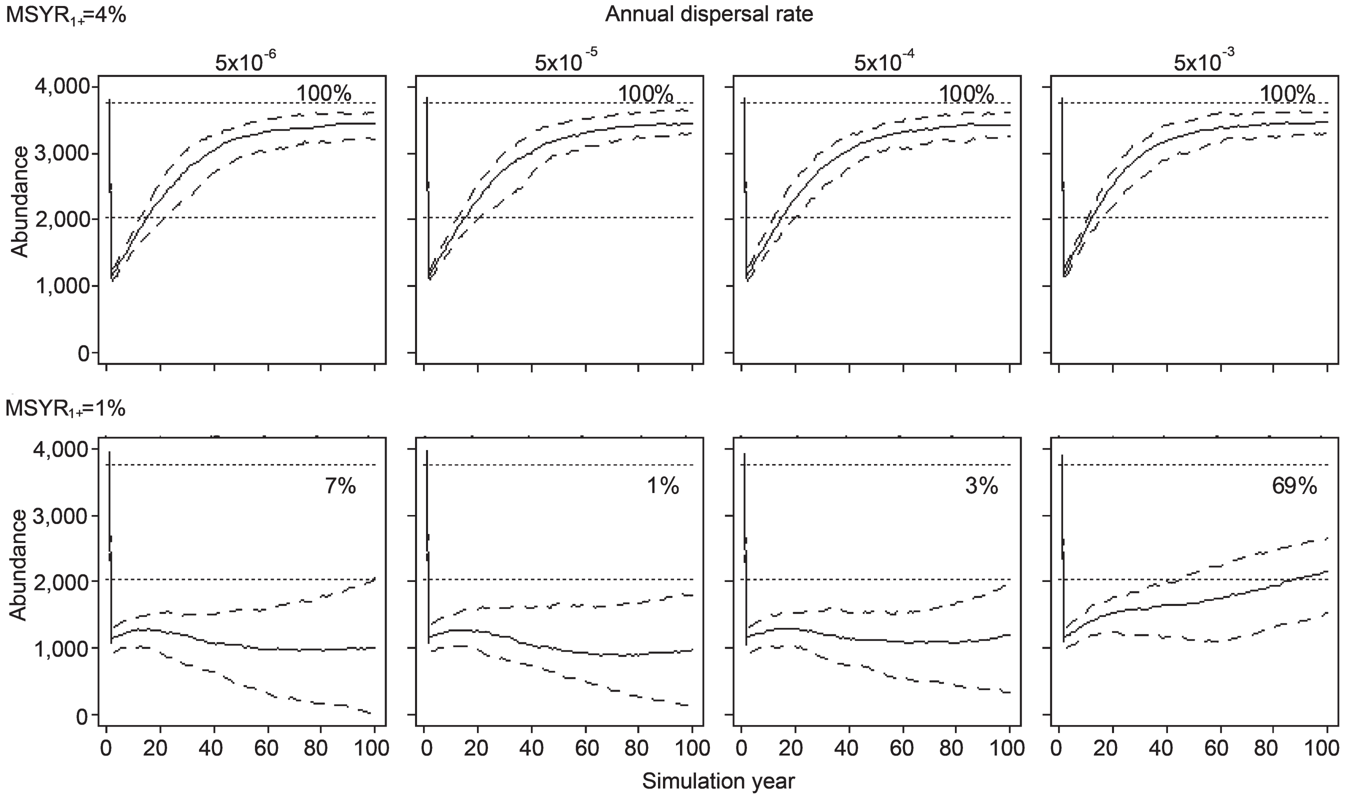

Fig. 2. Time-trajectories of total (1+) population size for population 1 (*P1*) as a function of MSYR$_{1+}$ (4% and 1%) and dispersal rate (ranging from 5×10^{-6} to 5×10^{-3}yr^{-1}). Median (solid line) and 5th and 95th percentiles (dashed lines) are shown. The carrying capacity for each population was 3,750 (upper dotted line), and the CV at carrying capacity was 0.3. The percentage of replicates whose final abundance was greater than 0.54*K* (lower dotted line) is shown on each panel.

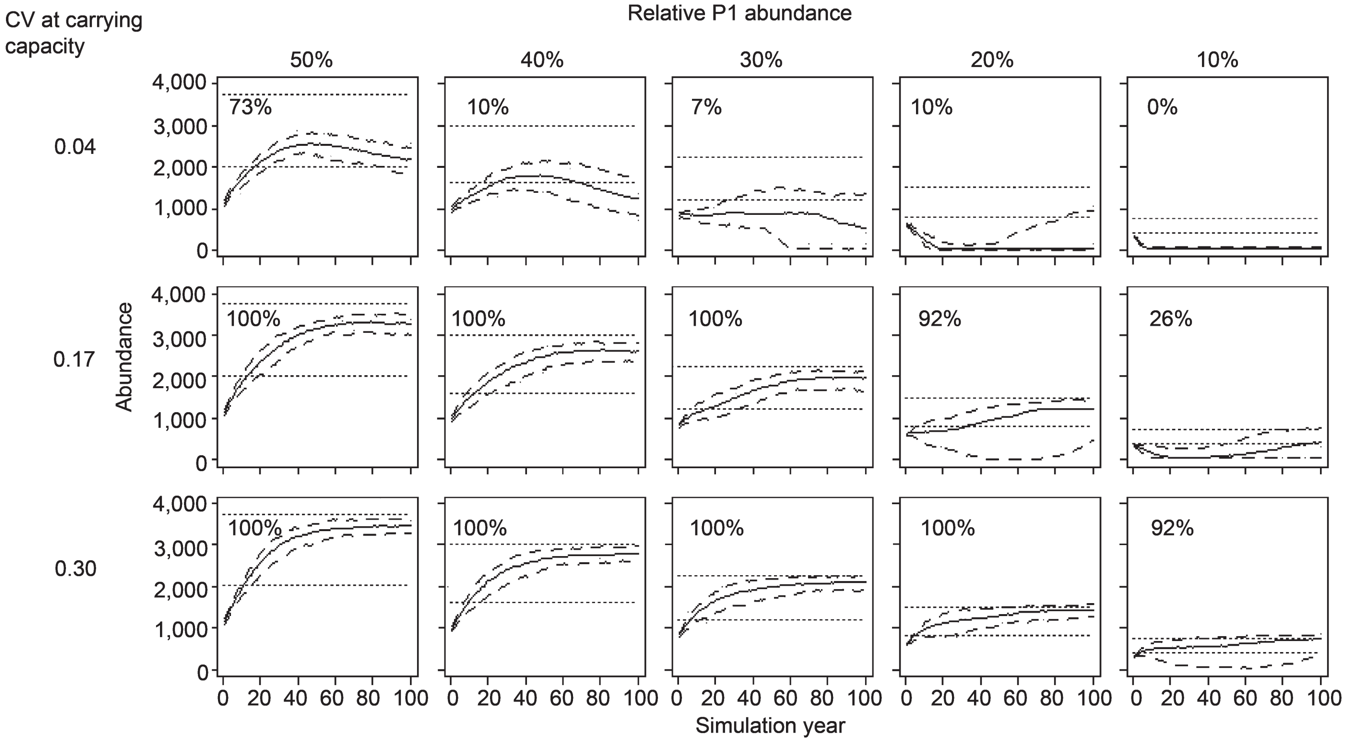

Fig. 3. Time-trajectories of total (1+) population size for population 1 (*P1*) as a function of the fraction which this population constitutes of the entire landscape carrying capacity and the CV at carrying capacity. Median (solid line) and 5th and 95th percentiles (dashed lines) of abundance are shown, along with *K* (upper dotted line) and 0.54*K* (lower dotted line). Dispersal rate and MSYR$_{1+}$ were set to 5×10^{-3}yr^{-1} and 4%, respectively. The percentage of replicates whose final abundance was greater than 0.54*K* is shown on each panel. MSYL for these simulations is 0.547*K*.

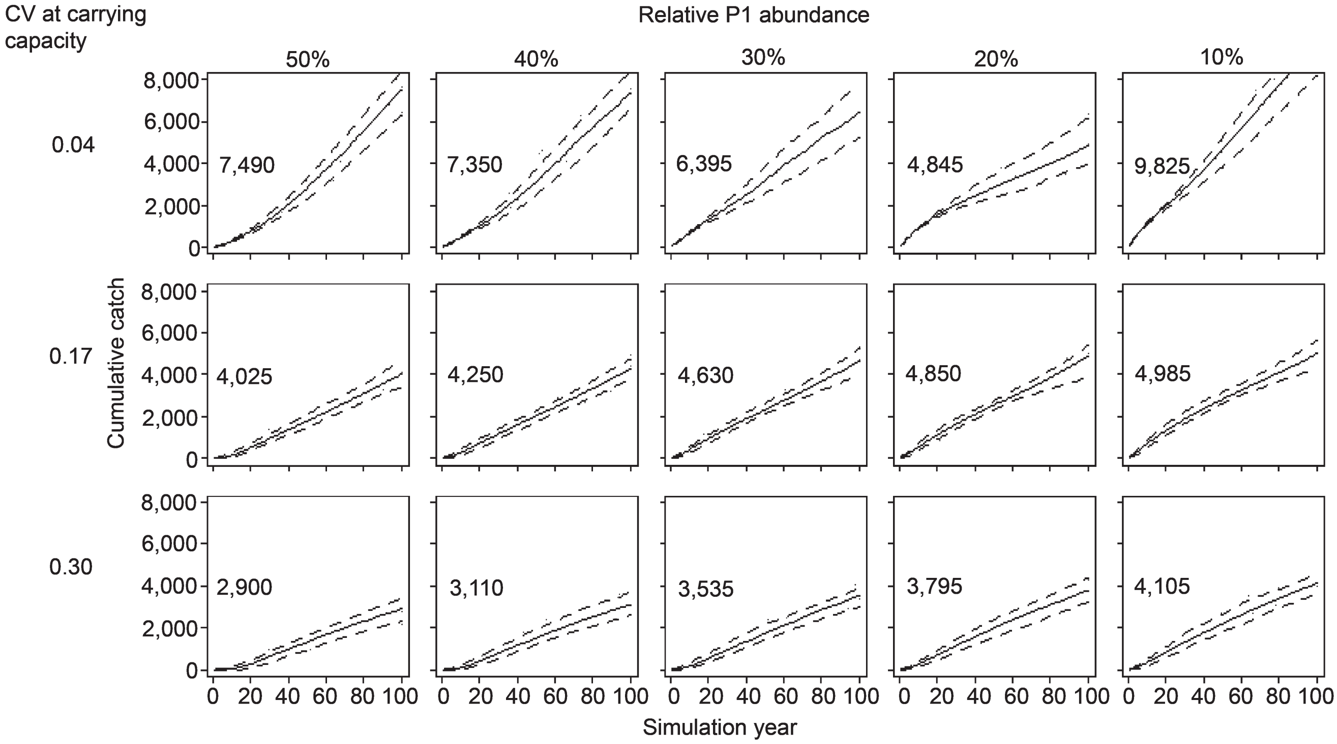

Fig. 4. Cumulative catch as a function of the fraction which population 1 constitutes of the entire landscape carrying capacity and the CV at carrying capacity (see Fig. 1). Median (solid line) and 5th and 95th percentiles (dashed lines) are shown. Dispersal rate and $MSYR_{1+}$ were held constant at $5 \times 10^{-3} yr^{-1}$ and 4%, respectively. Median total catch in year 100 is shown on each panel.

The total catch decreased as the CV of the abundance estimates increased (Fig. 4), as expected. Total catch increased as the relative initial abundance of population 1 decreased for the two higher CVs. The pattern was largely reversed in simulations using the lowest CV (cases in which population 1 fails to recover to MSYL), with total catch decreasing as the relative abundance of population 1 decreased from 0.5 to 0.2. However, the total catch more than doubled as the relative size of population 1 was further reduced from 20% to 10% of the landscape *K*.

The results of the single-stock trials were not inconsistent with those published by Butterworth and Punt (1994) (Table 2)[8], indicating that the CLA is correctly implemented in the TOSSM package. Comparisons between our results and the graphical summaries of Aldrin *et al.* (2006) also provide support for the CLA working correctly within TOSSM.

DISCUSSION

Failure to manage populations separately resulted in poor conservation performance of the CLA for many of the parameter combinations examined, including some with dispersal as high as 0.5% per year, the highest value examined. Thus, it is necessary to separately manage populations between which annual dispersal rates are relatively high, at least from an evolutionary perspective, to protect and sustain populations of large whales. The fact that the conservation performance of the CLA is sensitive to errors in stock definition was demonstrated early in the development of the algorithm (IWC, 1991). However, because performance across a range of dispersal rates was examined, this study provides new insights into the critical level of dispersal below which two populations warrant management as separate stocks. Our results indicate that the 'unit-to-conserve' of relevance to the RMP is much more similar to the 'Demographically Independent Populations' (DIPs) of the MMPA than to the 'Evolutionarily Significant Units' (ESUs) of the ESA (Taylor, 2005; Taylor *et al.*, 2010). This is not surprising, given that the management objective of the RMP (i.e. maintaining sustainable fisheries) is focused on an ecological rather than an evolutionary scale (Waples and Gaggiotti, 2006).

Defining stocks that adequately protect populations managed under the RMP is likely to be challenging, especially if catches are not spread out spatially (e.g. using techniques such as catch cascading). In recent decades, genetic data have emerged as the most powerful tool available for defining units to conserve (Taylor *et al.*, 2010) and hence for identifying hypotheses for consideration when developing *Implementation Simulation Trials* (*IST*s) for RMP testing. However, dispersal rates on the order of $5 \times 10^{-3} yr^{-1}$ result in very low levels of genetic differentiation. Most existing analytical methods are unable to detect such low levels of differentiation (Chen *et al.*, 2007; Latch *et al.*, 2006; Martien *et al.*, 2009; Martien and Taylor, 2003; Morin *et al.*, 2008; Taylor *et al.*, 2010; Waples and Gaggiotti, 2006). Accurately identifying stocks of large whales is made more difficult by the large abundance and long generation times of most species, both of which tend to reduce genetic differentiation for a given dispersal rate (Morin *et al.*, 2008). These factors also limit the power of non-genetic methods of investigating population structure, such as photo-identification and satellite telemetry. Our results therefore

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[8] The results of Butterworth and Punt (1994) were based on MSYR defined in terms of the mature rather than 1+ population component.

Table 2

Median of abundance at years 100 and 500 for single stock trials. The 5th and 95th percentiles are shown in parentheses.

	TOSSM package		Butterworth and Punt (1994)	
MSYR	Year 100	Year 500	Year 100	Year 500*
1%	0.702 (0.564-0.803)	0.885 (0.627-1.00)	0.624 (0.559-0.663)	0.85
4%	0.966 (0.932-1.00)	0.971 (0.912-1.01)	0.943 (0.843-0.981)	0.85

*Butterworth and Punt (1994) only report median abundance for year 500 in graphical form. Thus, the values reported here are approximate.

emphasise the importance of giving careful consideration to even weak evidence suggesting population structure when developing plausible stock structure scenarios for *IST*s.

The need to identify population structure accurately is particularly acute when MSYR_{1+} is low. All but one of the MSYR_{1+} = 1% trials resulted in very poor (<0.10) conservation performance, and the probability of rebuilding to 0.54*K* was only 0.69 for the one case in which conservation performance was not very poor (Fig. 2). In contrast, the MSYR_{1+} = 4% trials examined proved relatively robust to errors in stock definition; population 1 failed to recover to 0.54*K* only when the *CV* was unrealistically low and in the trial in which population 1 comprised only 10% of the total landscape carrying capacity the *CV* at carrying capacity was 0.17, a low but realistic value.

The impact of errors in stock definition on the performance of the CLA is greater for stocks for which the CV of abundance estimates is low (Fig. 3). This interaction reflects the fact that an error in stock definition is, in essence, an error in estimating the geographic range, and therefore abundance, of the unit that is being affected by removals. The CV is the only input to the CLA that reflects uncertainty associated with the estimates of the abundance of the stock, although the CLA imposes a minimum CV for all abundance estimates, partially to reflect the fact that abundance estimates can contain sources of error not captured by sampling error alone. A high CV implies greater uncertainty regarding the number of animals available for hunt and can therefore partially compensate for abundance estimation errors due to mis-identification of stocks.

The CV also affects total catch, with catch decreasing with increasing CV. Fig. 4 shows a complicated interaction between CV and the relative carrying capacities of the two populations in determining total catch. For the two larger CVs, total catch increases as the size of population 1 decreases. This pattern reflects the fact that population 1 is depleted to 0.3*K* at the beginning of the simulations. Thus, simulations in which population 1 comprises a larger fraction of the overall carrying capacity have lower total abundances in the early years of the simulation, resulting in lower catch. For the lowest CV, however, the higher initial total abundance in simulations in which the relative size of population 1 is small is counteracted by the fact that population 1 continues to decline throughout the entire simulation due to overhunting (Fig. 3). This continued decline results in continual reductions in the catch limit, thus reducing total catch (Fig. 4). This pattern is dramatically reversed when the relative size of population 1 is reduced to only 10%, which results in a more than doubling of total catch. In this scenario, population 1 is extirpated early in the simulation in all replicates. Thus, the landscape is managed 'correctly' for the majority of the simulation – a single (extant) population is managed as a single management unit.

The TOSSM package differs slightly from the model typically used in *IST*s with respect to the way that CV is calculated. In the TOSSM package, the CV is inversely proportional to the total abundance. In contrast, *IST*s (and the trials which were used to test the CLA) generate abundance estimates using CVs that include a constant term and a term that depends on the inverse of total abundance (e.g. IWC, 2004; IWC, 2007). The generation process includes both log-normal and Poisson components. Moreover, *IST*s account for uncertainty caused by errors when estimating the sampling CV from a survey and often the impacts of temporal variation in migration of stocks**.** The TOSSM package is therefore less amenable to the type of case-specific, highly realistic simulations for which the models used in *IST*s are designed. However, the differences between the TOSSM package and the *IST* models would not affect the conclusions of this study.

Our results show that extra caution is necessary to ensure that stocks have been correctly defined in cases where CVs of abundance estimates are low. Similarly, species with low MSYRs warrant special attention with respect to defining stocks, as do those cases in which adjacent populations differ markedly in abundance. It remains to be seen whether existing analytical methods are capable of identifying population structure at the level required for proper stock definition. Even if population structure can be accurately described, defining stocks that adequately protect populations can be very difficult in cases where populations overlap in areas where they are hunted, typically in the migration corridor or on feeding grounds. Managers should thus continue to employ methods to ensure spatially-diffuse hunting patterns (e.g. IWC, 2009) so as to reduce the risk of over-exploiting unrecognised populations, especially when power analysis indicates that available analytical methods would be unable to detect relevant levels of population structure.

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REFERENCES

Aldrin, M., Storvik, B. and Schweder, T. 2006. Standardized catch per unit effort in minke whaling in Norwegian waters, 1952–1983 and 1993–2004. Paper SC/58/RMP6 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies. 23pp. [Paper also available from the Office of this Journal].

Angliss, R. and Wade, P.R. 1997. Guidelines for assessing marine mammal stocks: report of the GAMMS Workshop, 3–5 April, 1996, Seattle, WA [Available at: *www.nmfs.noaa.gov/pr/pdf/sars/gamms_report.pdf*].

Butterworth, D.S. and Punt, A.E. 1994. An investigation of the merits or otherwise of the proposal for an Antarctic-wide whale sanctuary by means of adaptations of the simulation trials used to test the Revised Management Procedure. *Rep. Int. Whal. Commn.* 44: 289–302.

Chen, C., Durand, E., Forbes, F. and Francois, O. 2007. Bayesian clustering algorithms ascertaining spatial population structure: a new computer program and comparison study. *Mol. Ecol. Notes* 7(5): 747–56.

Gardenfors, U., Hilton-Taylor, C., Mace, G. and Rodriguez, J. 2001. The application of IUCN Red List criteria at region levels. *Cons. Biol.* 15: 1,206–12.

IWC. 1991. Report of the Scientific Committee, Annex D. Report of the sub-committee on management procedures. *Rep. int. Whal. Commn.* 41: 90–112C.

IWC. 1992a. Report of the Scientific Committee. *Rep. int. Whal. Commn.* 42: 51–86.

IWC. 1992b. Report of the Scientific Committee, Annex D. Report of the Sub-Committee on Management Procedures. *Rep. int. Whal. Commn* 42: 87–136.

IWC. 1994. Report of the Scientific Committee. Annex H. The Revised Management Procedure (RMP) for Baleen Whales. *Rep. int. Whal. Commn* 44: 145–52.

IWC. 2004. Report of the Scientific Committee. Annex D. Report of the Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 6: 75–184.

IWC. 2007. Report of the Scientific Committee. Annex D. Report of the Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 9: 88–128.

IWC. 2009. Report of the Scientific Committee. Annex D. Report of the Sub-Committee on the Revised Management Procedure (RMP). Appendix 7. Report of the working group on the North Atlantic minke whales RMP *Implementation Review*. *J. Cetacean Res. Manage. (Suppl.)* 11: 132–40.

Latch, E., Dharmarajan, G. and Glaubitz, J. 2006. Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. *Conserv. Genet.* 7: 295–302.

Martien, K.K. and Taylor, B.L. 2003. Limitations of hypothesis-testing in defining management units for continuously distributed species. *J. Cetacean Res. Manage.* 5(3): 213–19.

Martien, K.K. 2006. Progress on TOSSM dataset generation. Paper SC/58/SD2 presented to the IWC Scientific Committee, May 2006, St Kitts and Nevis, West Indies (unpublished). 17pp. [Paper availabel from the Office of this Journal].

Martien, K.K., Gregovich, D., Bravington, M.V., Punt, A.E., Strand, A.E., Tallmon, D.A. and Taylor, B.L. 2009. TOSSM: an R package for assessing performance of genetic analytical methods in a management context. *Mol. Ecol. Res.* 9(6): 1,456–59.

Morin, P.A., Martien, K.K. and Taylor, B.L. 2008. Assessing statistical power of SNPs for population structure and conservation studies. *Mol. Ecol. Res.* 9: 66–73.

Moritz, C. 1994. Defining 'evolutionary significant units' for conservation. *Trends Ecol. Evol.* 9: 373–75.

Palsbøll, P.J., Berube, M. and Allendorf, F.W. 2007. Identification of management units using population genetic data. *Trends Ecol. Evol.* 22(1): 11–16.

Perryman, W.L., Donahue, M.A., Perkins, P.C. and Reilly, S.B. 2002. Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Marine Mammal Science* 18: 121–24.

Punt, A.E. and Donovan, G. 2007. Developing management procedures that are robust to uncertainty: Lessons from the International Whaling Commission. *ICES J. Mar. Sci.* 64: 603–12.

Reilly, S.B. 1984. Observed and published rates of ncrease in gray whales, *Eschrichtius robustus*. *Rep. int. Whal. Commn.* (special issue) 6: 389–99.

Smith, T., Schweder, T., Allison, C., Palka, D., Punt, A.E. and Butterworth, D.S. In press. Effects of combinations of the risk performance of the IWC's commercial whaling management procedure. *J. Cetacean Res. Manage.*

Strand, A.E. 2002. METASIM 1.0: an individual-based environment for simulating population genetics of complex population dynamics. *Mol. Ecol. Notes* 3: 373–76.

Taylor, B.L. 1997. Defining 'population' to meet management objectives for marine mammals. pp.49–65. *In*: Dizon, A.E., Chivers, S.J. and Perrin, W.F. (eds). *Molecular Genetics of Marine Mammals*. The Society for Marine Mammalogy, Lawrence, KS. 388pp.

Taylor, B.L. 2005. Identifying units to conserve. pp.149–64. *In*: Reynolds III, J.E., Perrin, W.F., Reeves, R.R., Montgomery, S. and Regan, T.J. (eds). *Marine Mammal Research: Conservation Beyond Crisis*. The Johns Hopkins University Press, Baltimore, Maryland.

Taylor, B.L., Martien, K.K. and Morin, P.A. 2010. Identifying units to conserve using genetic data. *In*: Boyd, I., Bowen, D. and Iverson, S. (eds). *Marine Mammal Ecology and Conservation: a Handbook of Techniques*. Oxford University Press, Oxford, UK.

Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J. and Hrovat, Y.N. 2007. Lessons from monitoring trends in abundance of marine mammals. *Mar. Mammal Sci.* 23: 157–75.

Waples, R.S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of 'species' under the Endangered Species Act. *Mar. Fish. Rev.* 53(3): 11–22.

Waples, R.S. and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol. Ecol.* 15(6): 1419–39.

Appendix 1

TOSSM DATASET GENERATION

The TOSSM datasets used in this paper were generated following the methodology and parameter values described by Martien (2006). Rmetasim implements density dependence by linearly interpolating between matrices describing life history rates at zero population density (*ZPD*) and at carrying capacity (*K*)[9]. All 4% MSYR datasets were generated using the life history matrices developed by Martien (2006; Table A1) from empirical data for Eastern Pacific grey whales (Perryman *et al.*, 2002; Reilly, 1984). The *ZPD* and *K* matrices developed by Martien (2006) have growth rates of $\lambda = 1.072$ and 1.0003, respectively, and result in an MSYR_{1+} of 3.9%.

Table A1

Life history matrices for used to generate the 4% MSYR datasets.
Matrices describe life history parameters at: (a) zero population density; and (b) carrying capacity.

(a)	juve1	juve2	fert	lact	male	(b)	juve1	juve2	fert	lact	male
juve1	0.730	0	0.889	0	0	juve1	0.768	0	0.278	0	0
juve2	0.210	0	0	0	0	juve2	0.157	0.720	0	0	0
fert	0	0.47	0	0.946	0	fert	0	0.102	0.648	0.946	0
lact	0	0	0.946	0	0	lact	0	0	0.300	0	0
male	0	0.47	0	0	0.954	male	0	0.102	0	0	0.954

*Stage class abbreviations are juve1= juvenile1, juve2= juvenile2, fert=fertile female, lact=lactating female, and male=adult male.

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[9] MSYL does not, therefore, occur at 0.6*K* as is conventional for most of the operating models used to test the CLA.

Generating datasets with an MSYR of 1% required developing a new *ZPD* matrix with a growth rate of $\lambda = 1.02$. We interpolated between the elements of the two matrices developed by Martien (2006; Table A1) to produce a matrix with the desired growth rate (Table A2). When combined with the *K* matrix developed by Martien (2006), this matrix results in an MSYR_{1+} of 1.0%.

Table A2

Life history matrices for used to generate the 1% MSYR datasets. Matrices describe life history parameters at: (a) zero population density; and (b) carrying capacity. The carrying capacity matrix is identical to that used to produce 4% MSYR datasets (Table A1b).

(a)	juve1	juve2	Fert	lact	male
juve1	0.760	0	0.404	1.0	0
juve2	0.168	0.570	0	0	0
fert	0	0.179	0.513	0.946	0
lact	0	0	0.434	0	0
male	0	0.179	0	0	0.954

(b)	juve1	juve2	fert	lact	male
juve1	0.768	0	0.278	0	0
juve2	0.157	0.720	0	0	0
fert	0	0.102	0.648	0.946	0
lact	0	0	0.300	0	0
male	0	0.102	0	0	0.954

Stage class abbreviations are juve1= juvenile1, juve2 = juvenile2, fert=fertile female, lact=lactating female, and male=adult male.

Photo-identification rate and wide-scale movement of common minke whales (*Balaenoptera acutorostrata*) in the coastal waters of Faxaflói and Skjálfandi Bays, Iceland

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ABSTRACT

Information on movement and site fidelity is important for conservation and management. Photo-ID of common minke whales (*Balaenoptera acutorostrata*) was conducted from whalewatching vessels within the coastal waters of Faxaflói (a bay on the southwest coast of Iceland) and Skjálfandi (a bay on the northeast coast) between 2007–10 and 2001–10 respectively, to examine fidelity to the sampling locations and movement between them. Images of 292 individual minke whales were obtained in Faxaflói and 61 in Skjálfandi, with an overall 'annual re-capture proportion' of 23.3% in the former and 16.4% in the latter. Most (about 80%) of the resighted animals in each bay were re-sighted in one year only. The total number of identified whales has increased in both Faxaflói and Skjálfandi Bays since 2007 and 2001 respectively, suggesting the existence of an open population in both bays. One match was found between the two bays, eight years apart; the distance was approximately 600km between southwest and northeast Iceland. This study shows the value of photo-ID studies from platforms of opportunity such as whalewatching vessels. More data are required from broader geographic areas before firm conclusions can be drawn about movements and site fidelity within Icelandic waters.

KEYWORDS: MINKE WHALE; PHOTO-ID; SITE FIDELITY; MOVEMENTS; NORTH ATLANTIC; NORTHERN HEMISPHERE; SURVEY-VESSEL; DISTRIBUTION

INTRODUCTION

The common minke whale (*Balaenoptera acutorostrata*) has a worldwide distribution, with sightings recorded in all oceans (Perrin *et al.*, 2002). In Iceland, it is the most abundant baleen whale (Borchers *et al.*, 2009; Hauksson *et al.*, 2011; Pike *et al.*, 2009a; Pike *et al.*, 2009b; Pike *et al.*, 2011).

Common minke whales are thought to follow the same general balaenopterid life history strategy of seasonal migration between summer feeding grounds and winter breeding grounds (Jonsgård, 1966; Stewart and Leatherwood, 1985; Christensen *et al.*, 1990; Víkingsson and Heide-Jørgensen, 2005). Details of the seasonal movements of these animals to and from Icelandic waters remain unclear. Common minke whale sightings in Faxaflói generally increase around the end of March and peak during the months of July and August (Bertulli, 2010; Salo, 2004). However, at least from 2009 until the 2011 winter (November to March), whalewatching tours organised on the southwest coast found that not all individuals leave the area at the end of the summer (C. Bertulli, pers. obs.).

The summer feeding areas of the bays of Faxaflói (64°24'N, 23°00'W) in the southwest and Skjálfandi (66°05'N, 17°33'W) in the northeast (hereafter Faxaflói and Skjálfandi) were chosen for whalewatching operations from small vessels because of the predictable seasonal occurrence of whales close to shore in relatively high numbers. Common minke whales are more frequently sighted on the southwest coast of Iceland, in Faxaflói, than on the northeast coast, in Skjálfandi (Pike *et al.*, 2009b). Faxaflói is about 50km long and 90km wide (Stefansson and Guðmundsson, 1978; Stéfánsson *et al.*, 1987) and is larger than Skjálfandi, which is about 25km long and extends at its base for 10km (Gíslason, 2004).

The objectives of the present study were to highlight specific findings for common minke whales on photo-ID rate, smaller scale distribution (inter-annual site fidelity) and the potential movement of individuals between Faxaflói and Skjálfandi.

MATERIAL AND METHODS

From April to September, 2007–10, effort, sightings and photo-ID data were collected in the southwestern coastal waters of Faxaflói from a whalewatching operation based in Reykjavík within a maximum of 22km off shore (Fig. 1; Table 1). Similar data from a whalewatching operation based in Husavík were collected from 2003 to 2010 in Skjálfandi from May to October (although no photo-ID data were collected in 2003). In addition, photo-ID images only were collected in 2001 and 2002.

Observations were generally conducted between the hours of 07:00 and 22:00 and distributed across all seasons, although most tours occurred during the summer. The whalewatching companies in both areas conducted morning, afternoon and evening trips lasting approximately three hours each. Cetacean sightings data were collected every day, weather permitting. Fieldwork was carried out in wind speeds of 7 ms^{-1} (13 knots) or less and Beaufort sea state of 0 to 4 (majority below 3). Observations were performed on the roof of the wheelhouse of two vessels (vessels 25–26m in length, wheelhouse 6–8m above sea level) in Faxaflói and

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three within Skjálfandi (vessels 20–25m in length, wheelhouse 2–5m). One to a maximum of four observers, usually the principle investigator and three assistants, were stationed to watch 360° around the survey vessel in Faxaflói. In Skjálfandi, surveys were conducted by one or two investigator teams at a time, with a total of six different investigators being involved on rotation in data collection.

Standardised data forms were used to record the vessel position every 5min (Global Positioning System, *Garmin 60CSx*) and environmental data (Beaufort sea state, swell, and visibility) at 15min intervals. Survey effort was determined by calculating the time spent in actively searching for whales during each survey. Encounter duration was ultimately dependant on the captain's decision to stay with the animals or leave the area (adapted from Gill *et al.*, 2000).

In order to obtain an unbiased estimation of the number of animals with re-identifiable marks in each mark class, whales were photographed without making any distinction of their mark status (Currey *et al.*, 2008; Gormley *et al.*, 2005; Williams *et al.*, 1993). A range of digital cameras were used with zoom lenses ranging from 55–200mm to 70–300mm (Faxaflói) and from 28–135mm to 40–150mm (Skjálfandi). All images were viewed using Adobe *Photoshop CS2/CS3* imaging software. Photos were graded for closeness and sharpness, only photographs accorded as good and average quality were used in the analyses (Bertulli *et al.*, 2012; Van Bressem and Gaspar, 2003). Identification to individuals was undertaken using the classification system developed by Tscherter and Morris (2005). Initial sorting of acceptable quality photographs involved searching for the presence of indentations or 'nicks' on the dorsal fin, usually on the trailing edge; these are known as dorsal fin edge marks or DEMs. The position of these markings on the fin was further compared with the general fin shape and any additional body marks and scars to further reduce the likelihood that two different whales were identified as one. If no nicks were obvious from the photographs, individuals were classified using remaining distinctive fin shapes and body marks where available.

The following analyses were carried out:

(1) estimation of minimum relative abundance based on identified individuals;

(2) estimation of the 'interannual resighting proportion', i.e. the proportion of individual whales identified in more than one year among all years of study; and

(3) the matching of individual whales between the two study areas.

A 're-sighting proportion' is defined as the number of animals re-sighted in both bays divided by the total number of individuals identified in them.

The total distance between bays of the re-sighted minke whale identified in the analysis was determined using the 'ruler' tool provided by *Garmin MapSource* (version 6.14) as the direct route by sea (avoiding land) between Reykjavik and Húsavík.

RESULTS

Common minke whale sightings

During the study period, minke whales were observed on 760 (75.8%) days in both study areas (Table 1), with a total of 1,333 sightings in Faxaflói and 994 in Skjálfandi. Within Faxaflói, the majority of photographed individuals were west of Kollafjörður (a branch of Faxaflói incorporating only the most northeastern part of Kolla bay is named this way), whilst in Skjálfandi, whales were normally captured within the coastal zone of the bay (Fig. 1).

Data relative to monthly and total mean survey effort show that the months with most effort for all years were June, July and August in Faxaflói, and May, June and July in Skjálfandi (Table 1).

Minimum relative abundance and identification rate

A total of 292 individuals were identified in Faxaflói and 61 in Skjálfandi, with just over half from both Faxaflói (54.5%, $n = 159$) and Skjálfandi (55.7%, $n = 34$) identified by the presence of DEMs.

The 'discovery curve' (Fig. 2) using either cumulative numbers of all mark class individuals or only those with DEMs from one year to the next is large and characterised by sharper increases in Faxaflói than in Skjálfandi Bay.

Site fidelity

The estimated annual resighting proportion for Faxaflói between April and September 2007 to 2010 was 23.3% (i.e. 68 animals resighted at least once between years out of the 292 identified there over the whole period). Thus over three-quarters of identified whales were observed only in a single year ($n = 224$, 76.7%). Of those resighted, 53 individuals were observed in two of the years (18.2%), nine were observed in three years (3.1%) and six were observed in four years (2.1%). In Skjálfandi, the annual resighting proportion was 16.4% between 2001 and 2010 (no photo-ID effort in 2003). Again therefore the vast majority (83.6%, $n = 51$) were seen only in a single year, followed by individuals observed in two years (6.6%, $n = 4$) and six in three or more years (9.8%, $n = 6$). See Table 2.

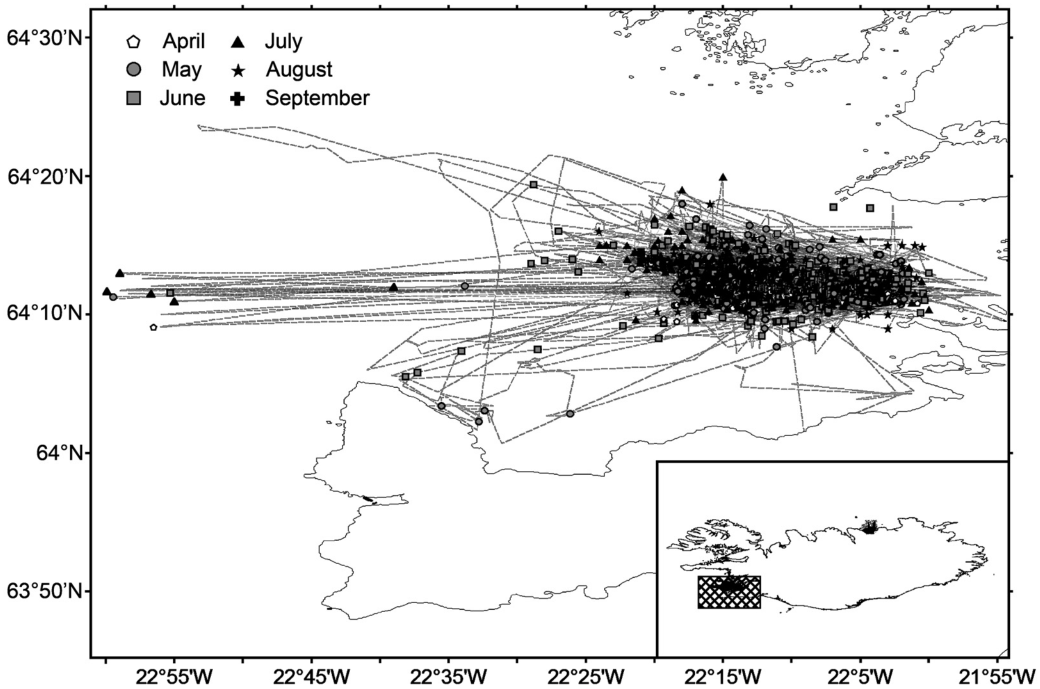
Resightings between Faxaflói and Skjálfandi

Resightings within Faxaflói and Skjálfandi were relatively uncommon and in fact there was only one animal (DEM162 in Faxaflói, DEM24 in Skjálfandi) of the total number of 353 individuals from both catalogues that was sighted in both areas, i.e. 0.3%. This individual was first photographed on 16 July 2002 in Skjálfandi and re-sighted in Faxaflói Bay on 29 April 2010, then photographed again on 10 August 2011 in Skjálfandi, on 5 May 2012 in Faxaflói and on 6 July 2012 in Skjálfandi (the latter showing intra-annual movement between bays). The mark on the trailing edge of the dorsal fin and a large scar on the back were both used to identify this individual in both areas (Fig. 3).

DISCUSSION

In conducting cetacean research, photo-identification is an effective technique (e.g. Hammond *et al.*, 1990; Whitehead *et al.*, 2000). Common minke whales, although considered more difficult than some of the other baleen whale species such as the humpback, blue and right whales, have been successfully studied and photo-identified since 1980 (Anderwald, 2009; Dorsey, 1983; Dorsey *et al.*, 1990; Gill

(a) Faxaflói Bay



(b) Skjálfandi Bay

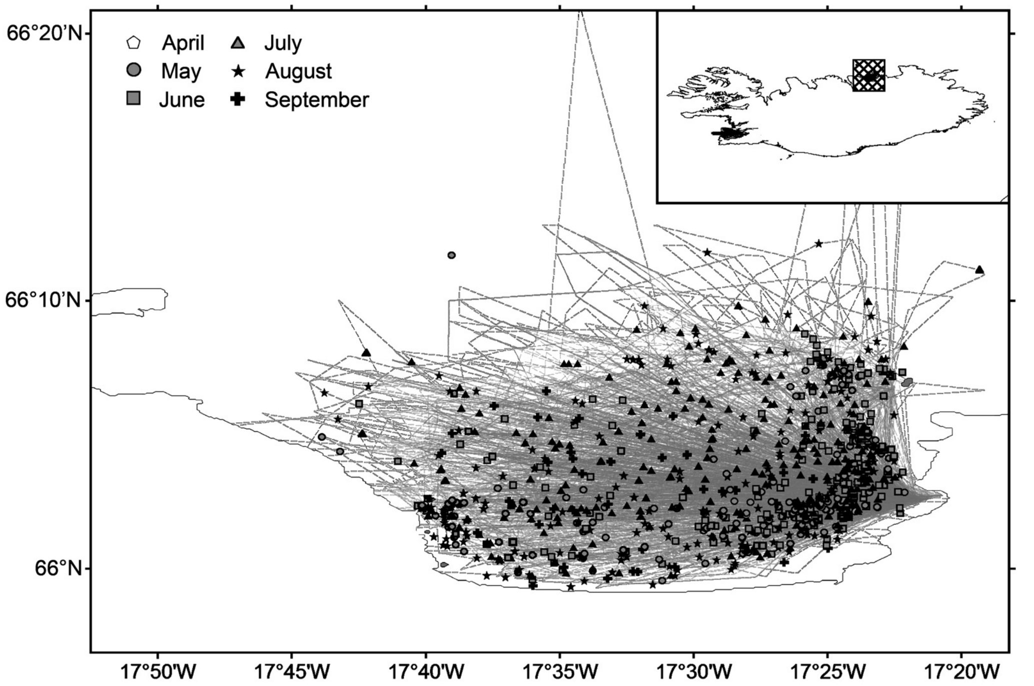


Fig. 1. Monthly location of minke whale photographic sightings from 2007 to 2010 in Faxaflói (Top) and from 2002 to 2010 in Skjálfandi Bay (Bottom). Searching effort using whale-watching vessels is shown by the grey dashed lines.

et al., 2000; Stern *et al.*, 1990; Tscherter and Morris, 2005). The present study is consistent with several previous studies in which the successful identification of individuals was based upon the presence of large and small DEMs. Body scars such as lesions, anthropogenic scars and marks supposedly left by parasites are thought to be less reliable than DEMs in recapturing individuals, except in the San Juan Islands and Monterey Bay, California (Dorsey, 1983; Dorsey *et al.*, 1990; Stern *et al.*, 1990), although they can be used to sustain a possible re-match (Anderwald, 2009; Baumgartner, 2008).

In fact, the percentage of individuals (just over 50%) identified by distinctive large or small DEMs seen in this study off Iceland is similar to values found in the San Juan Islands on the western coast of the USA (40.0%) by Dorsey *et al.* (1990) and around the Isle of Mull in Scotland (50%) by Gill *et al*. (2000). Some individuals photographed in Iceland had the potential to be identifiable due to their distinct dorsal fin shape, as in the Small Isles in Scotland (Anderwald, 2009). However, practical considerations render this feature difficult to use to support reliable re-matches except with excellent photographs from the correct angle;

Table 1

The survey effort for minke whale surveys conducted in (a) Faxaflói Bay between March and November 2007 to 2010 and in (b) Skjálfandi Bay between May and October 2003 to 2010 (no effort or sighting data were available for the years 2001 and 2002).

Study period	Survey effort (days)	Survey effort (trips)	Survey effort (hours)	Observation (days)	Observation (trips)	Observation (hours)
(a) Faxaflói Bay						
2007	77	167	310.56	73	145	284.58
2008	104	203	372.29	72	144	260.35
2009	86	178	350.46	82	157	305.37
2010	84	150	254.01	83	147	243.46
Total	351	699	1,288.20	310	594	1,094.56
(b) Skjálfandi Bay						
2003	48	51	156.03	45	48	142.57
2004	28	28	99.21	25	25	74.43
2005	71	75	192.17	47	49	128.31
2006	79	84	198.48	53	55	136.29
2007	105	105	257.31	59	59	149.27
2008	103	110	280.28	55	59	148.06
2009	103	132	286.11	61	80	191.03
2010	115	181	353.37	105	141	335.03
Total	652	766	1,803.23	450	516	1,306.19

photographs taken from the high platforms of whalewatching boats often resulted in distorted dorsal fin shapes. In the present study, dorsal fin shape without DEMs was used only for 14.7% ($n = 10$) resightings in Faxaflói. It is important to recognise that the value of a morphological characteristic depends on the platform used to approach and photograph the whale. To reduce the occurrence of false positives, only photographs of good quality, capturing the dorsal fin perfectly perpendicular to the body axis are considered and then only for particular types of analysis (e.g. Stevick *et al.*, 2001). Similarly, where individuals can be identified using only their body marks, re-identification will be possible only on photographs of the same side of the animal (animals photographed from only one side may be already in a catalogue photographed from the other side); if such features are to be used, analyses must be undertaken on datasets of only identifications from the same side (e.g. Hammond, 1986; IWC, 1990). The best traits for reliable re-identification of individuals therefore are DEMs. These nicks, notches or indentations can be identified even if only one side of the whale is photographed. Ultimately, however, what is the most appropriate dataset to use is dependent on the nature of the analyses proposed and the assumptions involved in those analyses.

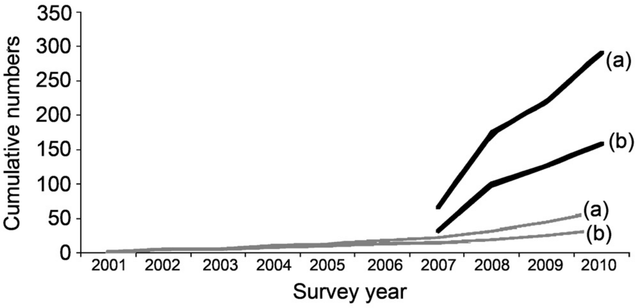


Fig. 2. Identification rate of minke whales along the southwest and northeast coasts of Iceland. The discovery curve is established by plotting the cumulative number of newly identified and catalogued minke whales each year, in (1) Faxaflói Bay from 2007 to 2010 (black line) and (2) in Skjálfandi Bay from 2001 to 2010 (grey line) inclusive. (a) Cumulative number of all classes individuals (b) Cumulative number of marked (DEM) individuals.

Minimum abundance and photographic rate

The number of photo-identified individuals in the present study areas is rising steadily (Fig. 2) which suggests that new whales may be entering these areas although more photographic effort needs to be spent in order to achieve saturation level for the population as is shown by the nature of the non-asymptotic discovery curve (Karczmarski *et al.*, 1999). The rate of discovery of newly identified common minke whales and the shape of the curve could suggest an open population in both bays (Karczmarski *et al.*, 1999; Straley *et al.*, 2009), although more data and analysis on seasonal immigration and emigration as well as sighting frequencies are required to investigate this further.

Table 2

Distribution of annual re-sighting proportions between years for all minke whales identified in (a) Faxaflói and (b) Skjálfandi Bays.

Survey year	No. animals re-sighted	No. years animals were re-sighted
(a) Faxaflói Bay		
2007-2008	8	2
2008-2009	24	2
2009-2010	12	2
2007-2009	1	2
2008-2010	6	2
2007-2010	2	2
2008-2009-2010	3	3
2007-2008-2009	1	3
2007-2009-2010	2	3
2007-2008-2010	3	3
2007-2008-2009-2010	6	4
Total	68	
(b) Skjálfandi Bay		
2006-2008	1	2
2006-2010	1	2
2007-2008	1	2
2008-2009	1	2
2002-2009-2010	1	3
2004-2008-2010	1	3
2008-2009-2010	1	3
2006-2008-2009-2010	1	4
2002-2006-2007-2009-2010	1	5
2005-2007-2008-2009-2010	1	5
Total	10	

Fig. 3. Photograph of a minke whale (DEM24) sighted first in Skjálfandi Bay in July 2002, re-sighted in Faxaflói Bay (DEM162) in April 2010. Photographs by kind permission of Húsavík Whale Museum, Chiara G. Bertulli/Faxaflói Cetacean Research respectively.

At present, a crude minimum estimate of identifiable animals (i.e. those with distinctive characters) for the two study areas is just over 350 over the study period – this does not take into account births/deaths or immigration/emigration, the level of effort, the size of the study and the fact that not all whales are identifiable. With additional data it should be possible to undertake quantitative mark-recapture analyses to obtain abundance estimates of the number of identifiable animals that use the study areas. Information from aerial surveys reveals that the whales' distribution is much larger than the present study areas. For example, the study area within Faxaflói represents only a small part of Faxaflói, which according to previous sighting surveys exhibits a uniform distribution of minke whales and peak abundances of up to seven thousand animals (7,678, 95% Cl: 4,984 to 11,830) in the summer (stratum 1 of table 2 in Borchers *et al.*, 2009). Aerial survey results also confirm our general findings that more common minke whales use Faxaflói than Skjálfandi (Pike *et al.*, 2009b).

Several factors influence the number of individual photo-ID and re-sighting rates. These include the behaviour of individuals and levels of site fidelity, the general occurrence of identifiable animals within a population and changes in methods (Wedekin *et al.*, 2010). For example, the sampling area for both studies has generally been constant but the use of digital cameras since 2005 has made it easier to obtain good photographs which may contribute to the increased number of photo-IDs in Skjálfandi Bay.

Site fidelity

Low inter-annual resighting proportions were observed in both areas (Faxaflói: 23.3%, Skjálfandi: 16.4%) although a higher proportion of identified individuals was re-sighted in three years or more of study in Skjálfandi (9.8%) than in Faxaflói (5.1%). These results differ from observations made in other feeding grounds such as the Isle of Mull (Scotland) where 35% ($n = 30$) of all individuals ($n = 66$) were sighted in more than one year (Gill *et al.*, 2000) or Québec (66%, $n = 115$) if only annual re-sightings of DEMs are considered (Morris and Tscherter, 2005). In Scotland, certain whales were observed returning to the same areas at precisely the same time each year (Gill *et al.*, 2000). Dorsey *et al.* (1990) reported some seasonal residency and site fidelity in parts of the eastern North Pacific.

Determining whether site fidelity is present or not from the present dataset requires knowledge of the temporal and geographical scale of the site fidelity and the representativeness (and relative size) of the identified whales to the full population(s). The opportunistic nature of the study and the use of platforms of opportunity inevitably limits the ability of the study to draw firm conclusions on site fidelity. For example, the area of Faxaflói surveyed represents only a small part of the whole bay, which systematic aerial surveys have revealed to have a relatively uniform distribution of common minke whales with a peak season abundance of up to seven thousand animals (7,678, 95% Cl: 4,984 to 11,830) in the summer (stratum 1 of table 2 in Borchers *et al.*, 2009). The distribution of whales on their feeding grounds is related to the distribution and abundance of their prey.

Photo-ID is an important tool in addressing questions of site fidelity but further information is required before this question can be resolved for common minke whales off Iceland.

Overlap with the Skjálfandi minke whale population

Comparison of the Faxaflói Cetacean Research and the Húsavík photo-ID catalogues, resulted in one rematch: this is the first documented movement (of approximately 600km from southwest to northeast after eight years) of a common minke whale along the Icelandic coastline using photo-ID. No photo-identification studies occurred on the east and west coasts of Iceland during this period. Such surveys are necessary if information on travelling routes within Icelandic waters is to be obtained from photo-identification studies.

The lack of matches between Faxaflói and Skjálfandi between 2001 and 2010 suggests that most identified whales exhibit some degree of site fidelity to these areas but without more extensive and intense effort it is important not to over-interpret the data. In addition there are no photo-ID data prior to the year 2007 in the south or 2001 in the north which again limits the available comparisons. The one match between areas shows that whales can move from southwest to north. Movements between areas within (and outside) Iceland are evident from the distribution and density data from aerial surveys (Pike *et al.*, 2009b). It is also true that present levels of effort would not be able to detect subtle changes in density/abundance between the regions.

Food shortages in the southwest area, notably due to a severe decline in sandeels (*Ammodytes* sp.) since 2005 have been proposed to have affected whales and seabird colonies in the south area (Bogason and Lilliendahl, 2009; Víkingsson and Elvarsson, 2010) and there is evidence of increased water temperatures and salinity in the north and south of Iceland in recent years (Astthórsson *et al.*, 2007). Additional research investigating minke whale spatio-temporal habitat use will assist in the determination of potential underlying environmental drivers. Detailed sightings data within and amongst seasons such as those collected here may form a valuable component of spatial modelling exercises to examine the factors governing common minke whale distribution in Icelandic waters. Of course, this will require information from all around Iceland as well as better information on seasonal and inter-annual density changes such as that being obtained from aerial surveys (Pike *et al.*, 2009b).

This study has shown the importance of using whalewatching vessels to collect information of value to understanding the biology and distribution of common minke whales around Iceland as well as to conservation and management efforts. All companies should be encouraged to participate in such efforts.

The low level of re-sightings in both Faxaflói and Skjálfandi suggests that the present level of whalewatching in those areas is not be focussing excessively on the same individuals which may have possible short- and long-term negative effects on the animals. Occurrence marks of anthropogenic origin (e.g. propeller or net entanglement) have been reported on the skin of common minke whales in a recent photographic study (Bertulli *et al.*, 2012) of skin disorders, parasites and epizoa among common minke whales from Iceland. However, individuals that travel long distances (which may be more the case if there is little site fidelity) may have an increased risk of encountering and becoming entangled in fishing gear or being struck by boats.

This study has shown the value of photo-ID work on common minke whales in Iceland. However, it is clear that in order to better understand the distribution and movements of minke whales in Icelandic coastal waters an expanded geographical and temporal extent is required. Such studies, in conjunction with distribution and abundance surveys and efforts to undertake spatial modelling will contribute towards the knowledge base for the scientific community and for the whalewatching operators in the area and assist in evaluating the effectiveness of existing management actions.

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REFERENCES

Anderwald, P. 2009. Population genetics and behavioural ecology of North Atlantic minke whales (*Balaenoptera acutorostrata*). PhD thesis, University of Durham, UK. 216pp.

Astthórsson, O.S., Gislason, A. and Jonsson, S. 2007. Climate variability and the Icelandic marine ecosystem. *Deep-Sea Res. II* 54: 2456–77.

Baumgartner, N. 2008. Distribution, diving behaviour and identification of North Atlantic minke whale in north east Scotland. Bachelor thesis, University of Rome 'La Sapienza', Italy. 114pp.

Bertulli, C. 2010. Minke whale (*Balaenoptera acutorostrata*) and white-beaked dolphin (*Lagenorhynchus albirostris*) feeding behaviour in Flaxafloi bay, south west Iceland. 239pp. Master's thesis, University of Iceland, Iceland.

Bertulli, C., Cecchetti, A., Van Bressem, M. and Van Waerebeek, K. 2012. A photographic assessment of skin disorders, parasites and epizoa in common minke whales (*Balaenoptera acutorostrata*) and white-beaked dolphins (*Lagenorhynchus albirostris*) from Iceland. *Journal of Marine Animals and their Ecology* 5(2): 29–40.

Bogason, V. and Lilliendahl, K. 2009. Rannsóknir á sandsíli (An initiation of sandeel monitoring in Iceland) *Hafrannsóknir* 145: 36–41.

Borchers, D., Pike, D., Gunnlaugsson, H. and Víkingsson, G. 2009. Minke whale abundance estimation from the NASS 1987 and 2001 aerial cue-counting surveys taking appropriate account of distance estimation errors. *NAAMCO Sci. Publ.* 7: 95–110.

Christensen, I., Haug, T. and Wiig, Ø. 1990. Morphometric comparison of minke whales *Balaenoptera acutorostrata* from different areas of the North Atlantic. *Mar. Mammal Sci.* 6(4): 327–38.

Currey, R., Rowe, L.E., Dawson, S. and Slooten, E. 2008. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. *New Zeal. J. Mar. Fresh* 42: 439–49.

Dorsey, E.M. 1983. Exclusive adjoining ranges in individually identified minke whales (*Balaenoptera acutorostrata*) in Washington state. *Can. J. Zool.* 61: 174–81.

Dorsey, E.M., Stern, J.S., Hoelzel, A.R. and Jacobsen, J. 1990. Minke whales (*Balaenoptera acutorostrata*) from the west coast of North America: individual recognition and small-scale site fidelity. *Rep. int. Whal. Commn* (*special issue*) 12: 357–68.

Gill, A., Fairbairns, B. and Fairbairns, R. 2000. Photo-identification of the minke whale (*Balaenoptera acutorostrata*) around the Isle of Mull, Scotland. Report to the Hebridean Whale and Dolphin Trust. 88pp. [Available from the author].

Gíslason, Á. 2004. Fish farming in Húsavik, Iceland. Arctic charr – Tilapia – Atlantic halibut – Turbot. Report of the Húsavik Academic Center, Iceland. 82pp.

Gormley, A.M., Dawson, S.M., Slooten, E. and Brager, S. 2005. Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Mar. Mammal Sci.* 21(2): 204–16.

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. 1990. *Report of the International Whaling Commission (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.

Hauksson, E., Víkingsson, G.A., Halldorsson, S.D., Ólafsdóttir, D. and Sigurjónsson, J. 2011. Preliminary report on biological parameters for NA minke whales in Icelandic waters. Paper SC/63/O15 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 45pp. [Paper available from the Office of this Journal].

International Whaling Commission. 1990. Report of the Workshop on Individual Recognition and the Estimation of Cetacean Population Parameters, La Jolla, 1–4 May 1988. *Rep. int. Whal. Commn* (*special issue*) 12:3–40.

Jonsgård, Å. 1966. The distribution of Balaenopteridae in the North Atlantic Ocean. pp.114–24. *In*: Norris, K.S. (eds). *Whales, Dolphins, and Porpoises*. University of California Press, Berkeley and Los Angeles. xv+789pp.

Karczmarski, L., Winter, P.E.D., Cockcroft, V.G. and McLachlan, A. 1999. Population analyses of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Algoa Bay, Eastern Cape, South Africa. *Mar. Mammal Sci.* 15(4): 1,115–23.

Morris, C. and Tscherter, U. 2005. Temporal stability of dorsal fin edge marks facilitates long-term identification of minke whales (*Balaenoptera acutorostrata*). Poster presentation, 19th European Cetacean Society Conference, La Rochelle, France

Perrin, W.F., Würsig, B. and Thewissen, G.M. 2002. *Enclyclopedia of Marine Mammals*. Academic Press, San Diego. 1,414pp. [Book review by R.M. Laws in *Marine Mammal Science* 19(3): 599–606].

Pike, D., Paxton, C.G.M., Gunlaugsson, T. and Víkingsson, G. 2009a. Estimates of the abundance of minke whales (*Balaenoptera acutorostrata*) from Faroese and Icelandic NASS shipboard surveys. *NAMMCO Sci. Publ.* 7: 81–93.

Pike, D.G., Gunlaugsson, T., Elvarsson, B. and Víkingsson, G. 2011. Correcting perception bias for Icelandic aerial surveys, 2007 and 2009. 12pp. Paper SC/18/AESP/08, presented to the NAMMCO Scientific Committee. [Available from the author].

Pike, D.G., Paxton, C.G.M., Gunnlaugsson, T. and Víkingsson, G.A. 2009b. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986–2001. *NAMMCO Sci. Pub.* 7: 117–42.

Salo, K. 2004. Distribution of cetaceans in Icelandic waters Master's thesis, University of Southern Denmark, Denmark. 188pp.

Stefansson, U. and Guðmundsson, G. 1978. The freshwater regime of Faxaflói, Southwest Iceland, and its relation to meteorological variables. *Est. Coast. Mar. Sci*. 6: 535–51.

Stefánsson, U., Thórdardóttir, T. and Ólafsson, J. 1987. Comparison of season oxygen cycles and primary production in the Faxafloi region, southwest Iceland. *Deep-Sea-Research* 34(5/6): 725–739.

Stern, J.S., Dorsey, E.M. and Case, V.L. 1990. Photographic catchability of individually identified minke whales (*Balaenoptera acutorostrata*) of the San Juan Islands, Washington and the Monterey Bay Area, California. *Rep. int. Whal. Commn* (*special issue*) 12: 127–33.

Stevick, P.T., Smith, T.D., Bravington, M.V., Palsbøll, P.J. and Hammond, P.S. 2001. Errors in identification of individuals by natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58: 1861–70.

Stewart, B.S. and Leatherwood, S. 1985. Minke whale – (*Balaenoptera acutorostrata*) Lacépède, 1804. pp.91–136. *In*: Ridgway, S.H. and Harrison, R. (eds). *The Sirenians and the Baleen Whales*. Academic Press, London and Orlando. xviii+362pp.

Straley, J.M., Quinn, T.J. and Gabriele, C.M. 2009. Assessment of mark-recapture models to estimate the abundance of a humpback whale feeding aggregation in Southeast Alaska. *J. Biogeography* 36: 427–38.

Tscherter, U. and Morris, C. 2005. Identifying a majority of minke whales (*Balaenoptera acutorostrata*) in the St. Lawrence based on the presence of dorsal fin edge marks. Poster presentation, 19th European Cetacean Society Conference, La Rochelle, France.

Van Bressem, M.F. and Gaspar, R. 2003. Epidemiology of tattoo skin disease in bottlenose dolphins (*Turiops truncatus*) from the Sado Estuary, Portugal. *European Cetacean Society Conference Guide and Abstracts* 17: 56–57. [Paper presented to the 17th Conference of the European Cetacean Society, Las Palmas de Gran Canaria, 9–13 March 2003].

Víkingsson, G.A. and Heide-Jørgensen, M.P. 2005. A note on the movements of minke whales tracked by satellite in Icelandic waters in 2001–2004. Paper SC/57/O9 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 3pp. [Paper available from the Office of this Journal].

Víkingsson, G.A. and Elvarsson, B.Th. 2010. Recent changes in diet composition of minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. Paper SC/17/AS/06 presented to the NAMMCO Scientific Committee Working Group on Assessment, 9–11 March 2010, Copenhagen, Denmark (unpublished). 12pp.

Wedekin, L.L., Neves, M.C., Marcondenes, M.C.C., Baracho, C., Rossi-Santos, M.R. and Engel, M.H. 2010. Site fidelity and movements of humpback whales (*Megaptera novaeangliae*) on the Brazilian breeding ground, southwest Atlantic. *Mar. Mammal. Sci.* 26(4): 787–802.

Whitehead, H., Christal, J. and Tyack, P.L. 2000. Studying cetacean social structure in space and time: innovative techniques. pp.65–87. *In*: Mann, J., Connor, R.C., Tyack, P.L. and Whitehead, H. (eds). *Cetacean Societies. Field Studies of Dolphins and Whales*. The University of Chicago Press, Chicago. 433pp.

Williams, J.A., Dawson, S.M. and Slooten, E. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool.* 71: 2,080–88.

Abundance estimates of southern right whales (*Eubalaena australis*) in Bahía San Antonio, Patagonia, Argentina

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ABSTRACT

The abundance of southern right whales (*Eubalaena australis*) was estimated by the means of aerial line-transect surveys for the area of Bahía San Antonio, a bay located in the north-western region of the San Matías Gulf (40°50'S 64°50'W), Rio Negro, Patagonia Argentina. In total, seven aerial surveys were conducted in the first week of August and September 2009, September, October and November 2010, and August, September 2011. Survey effort equalled a total flight time of 12.4h, during which 200 whales were counted in 119 whale groups. Half of the encounters were solitary animals and 17% were mating groups. Corrected abundance estimates showed the highest amount of whales present in the bay during the month of September, with 85±71, 207±108 and 117±55 animals in 2009, 2010 and 2011 respectively. In adjacent months, less than half the amount of whales seemed to be present. The correction factor $g(0)_{availability}$ resulted 0.392±0.456. Perception bias was not accounted for. These aerial surveys resulted in the first estimates of southern right whale abundance in this north Patagonian bay and indicated a rather abrupt peak during the month of September. This being the peak month for right whale presence is consistent with data from other regions in the Southwest Atlantic, but data obtained in the other months remained scarce and thus results should be interpreted carefully. The complete absence of whales in the area during November 2010 and August 2011 raises further questions on the predictability of the whale's presence in the area. Overall, more consistent aerial surveys should be conducted to accurately determine the annual and interannual evolution of southern right whale abundance in the study area.

KEYWORDS: SOUTHERN RIGHT WHALES; ABUNDANCE ESTIMATE; SURVEY- AERIAL; SOUTHERN HEMISPHERE; SOUTH AMERICA; BREEDING GROUNDS; FEEDING GROUNDS; SITE FIDELITY; DISTRIBUTION

INTRODUCTION

The distribution of southern right whales (*Eubalaena australis*) ranges between 18°S and 50°S (de Oliveira Santos *et al.*, 2001) with the most important known calving areas in the Southwest Atlantic located off Argentina (Península Valdés) and Brazil (Santa Catarina) (Flores *et al.*, 2000; Payne, 1986; Payne *et al.*, 1990; Rowntree *et al.*, 2001). Due to commercial whaling during the 18th and 19th centuries, the population of southern right whales was severely depleted (IWC, 2001), leading to their near extinction. Today, due to the international protection of the species, the worldwide population is growing annually (Best, 1990; Cooke *et al.*, 2001; Payne *et al.*, 1990) including Argentinean waters, with estimated growth of 6.9% (Cooke *et al.*, 2003). This increase has raised various hypotheses about the re-occupation of historical wintering grounds along the Southwest Atlantic coastline (Belgrano *et al.*, 2007; de Oliveira Santos *et al.*, 2001; Failla *et al.*, 2008; Flores *et al.*, 2000; Iñíguez *et al.*, 2003; Piedra *et al.*, 2006).

In Northeast Patagonia, possibly as a result of this apparent increase in occurrence, southern right whales are increasingly being targeted by commercial whale-based tourism activities (Vermeulen *et al.*, 2012). It is important to monitor the presence of this species in this region and obtain accurate information on local tendencies of abundance and group compositions (annually and interannually). Therefore, aerial surveys were conducted in Bahía San Antonio, the foremost touristic area in Northeast Patagonia. In this report, the results of these surveys are presented.

MATERIAL AND METHODS

Data were collected in Bahía San Antonio, a bay located in the north-western region of the San Matías Gulf (40°50'S 64°50'W), Rio Negro, Patagonia Argentina (Fig. 1).

Aerial surveys

Aerial surveys were conducted in the first week of the following months: August–September 2009; September; October–November 2010; and August–September 2011. Both financial resources and climatological conditions were the factors determining the timing and frequency of the surveys. The transects for the aerial surveys were designed using the standard distance sampling methods applied to clusters of animals (Buckland *et al.*, 1993) and the program *DISTANCE* 6.0 (Thomas *et al.*, 2006). The design consisted of 14 North–South (up to 40.9°S) parallel transect lines with a 2.5km separation, covering a total area of 418km^2 (mean CP = 0.78; Fig. 1). Transect length was chosen according to the safety restrictions of the pilot.

Surveys were conducted in good weather conditions and a calm sea state (Beaufort ≤ 3) using a high-wing Cessna 152 with a flat window. Due to the small size of the aircraft, only one researcher could travel on each flight. Observations where therefore made from one side only. Average speed and height of the aircraft was kept constant over the surveys at 90kn (166kmh^{-1}) and 700ft (213m) respectively. All surveys aimed to take place during the period of high tide to minimise the variation in area submerged caused by the large tidal fluctuations characteristic of the study area (up to 9m; Servicio de Hidrografía Naval Argentina).

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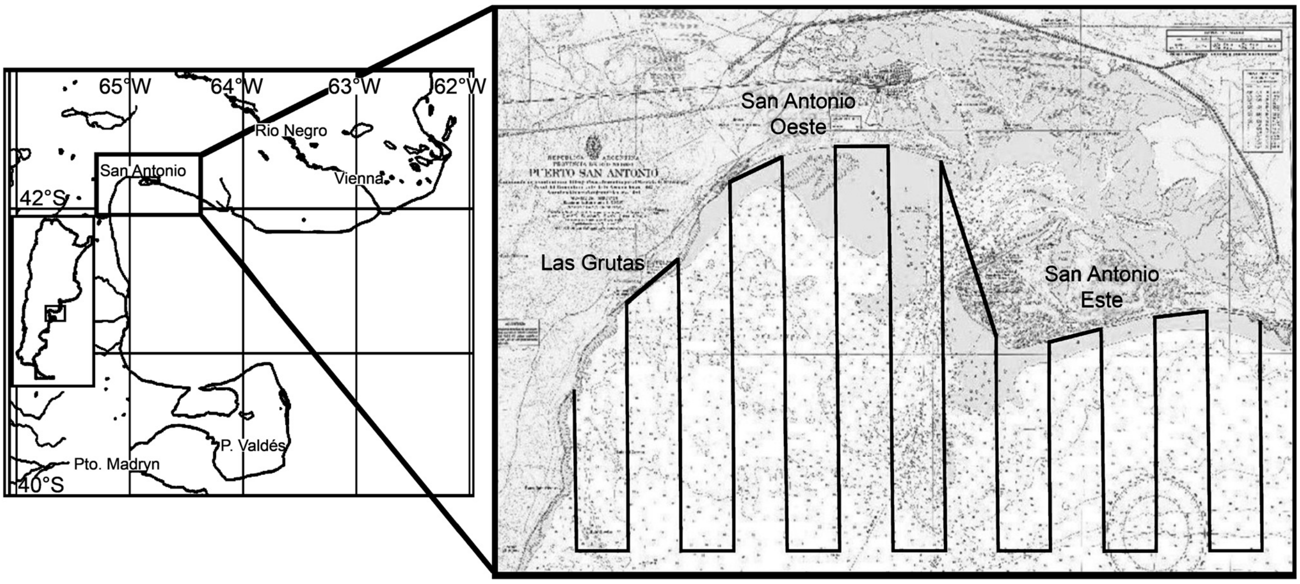

Fig. 1. Study area and transect design for the aerial surveys.

At the start of each survey, weather conditions (wind speed and direction) were noted. When a group of whales was sighted, data were written down on species, location (using a Garmin GPSmap 60csx), time, group size and composition. The downward angle to the group perpendicular to the aircraft's track was then measured using a hand-held clinometer (Suunto PM5/360PC). When possible, the total time the whale was visible to the observer was measured using a chronometer to later aid in the calculation of $g(0)$.

When whales were close enough, the transect line was abandoned to take photo-ID pictures. Afterwards the aircraft returned to the transect line to continue the survey.

Perpendicular distances were trigonometrically calculated using the aircraft's altitude and the declination angle to the sighting. The flat windows of the aircraft did not allow observers to see animals at declination angle between 60°–90°. Therefore a limit was set at 55°, corresponding to a left truncation distance of 150m. Perpendicular distances were also right-truncated at 10% of the observations, as recommended by Buckland *et al.* (1993).

Various models were tested to fit the detection function, including the uniform function, half-normal function and the hazard rate function with cosine, Hermite or simple polynomial adjustments. The model that best fitted the data was selected according to the Akaike Information Criterion (AIC; Akaike, 1973).

Finally, since the detection probability on the trackline, $g(0)_{\text{availability}}$, is not equal to 1 in aerial surveys of whales (availability bias), the probability of detecting a southern right whale was estimated following the approach of Barlow *et al.* (1988):

$$g(0)_{\text{availability}} = (s + t)/(s + d)$$

where s is the average time a southern right whale is at the surface, d is the time the whale is submerged and t is the time the whale is within the visual range of an observer when in the aircraft. The values for s and d were measured from boat-based surveys, whereas the value for t was measured directly from the aircraft when possible. Final abundance estimates were then corrected with this factor.

RESULTS

Effort, group size and composition

Over the study period, seven aerial surveys were conducted, resulting in a total flight time effort of 12.4h. In total, 200 whales were seen in 119 whale groups (2009: $n = 36$ whale groups; 2010: $n = 46$ whale groups; 2011: $n = 37$ whale groups), equally distributed over the study area. Group sizes ranged between 1–5 animals with a mean group size of 1.7 animals (SD = 0.83; median = 1.5). Overall, half of the encounters were solitary animals (50%) whereas 17% were mating groups (SAG) with a mean group size of 2.5 individuals (SD = 0.7). Less than 1% of the encounters were mothers with their calves. For up to 32% of the encounters, the group composition could not accurately be classified. However, the number of whale groups and number of whales seemed to increase from September 2009 to September 2011 as shown in Table 1. The proportions of the different group compositions varied with it. As such, the proportion of solitary animals decreased from 60% ($n = 15$) of the encounters in 2009 to 37% ($n = 14$) in 2011, and the proportion of mating groups (SAG) encountered increased from 4% ($n = 1$) in 2009 to 22% ($n = 8$) in 2011 (Fig. 2). Nevertheless, this variation tested as insignificant ($\chi^2 = 7.73$; df = 2; $p = 0.2$).

Table 1

Summary of the amount of whales (no. whales) and whale groups (no. WG) observed during the aerial surveys of September 2009, 2010 and 2011.

	September	
	No. whales	No. WG
2009	38	25
2010	50	28
2011	69	37
Total	157	90

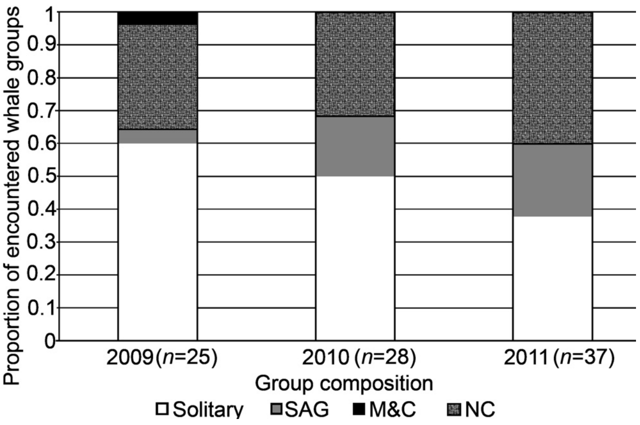

Fig. 2. Proportion of the different group compositions of southern right whales in Bahía San Antonio during the month September of 2009, 2010 and 2011. Solitary = solitary animal; SAG = Surface Active Group (mating group); NC = Not Classified; M&C = Mother and calf.

Abundance

The uniform cosine model was chosen in the view of the minimum AIC to model the detection function of southern right whales in the study area. Pooling all the sighting data together and using the mean group size, this model led to an estimate of the effective strip width (ESW) of 1,587m (%CV = 11.6). The uncorrected density estimates resulted in 0.05 (%CV = 15.1) and 0.08 whales km^{-2} (%CV = 27.8) for August and September 2009 respectively, 0.19 whales km^{-2} (%CV = 44.7) and 0.05 whales km^{-2} (%CV = 43.2) for September and October 2010, and 0.11 whales km^{-2} (%CV = 21.5) for September 2011. During the aerial survey in November 2010 and August 2011 no southern right whales could be observed.

Based on observations from boat-based surveys, the time whales spent at the surface (s) was averaged at 6.13sec ± 3.04sec, while the average time whales were submerged (d) was calculated as 180.4sec ± 84.3sec ($n = 42$). During aerial surveys the time a whale was within the visual range of an observer (t) was measured ($n = 46$), averaging 66.9sec ± 37.5sec. Therefore, the estimates of $g(0)_{\text{availability}} = (s + t)/(s + d)$ resulted in a correction factor of 0.392 ± 0.456. The corrected estimates of whale abundance in the study area over the different surveys are summarised in Table 2.

DISCUSSION

Group size and composition

Data on group composition were similar to previous information obtained from land and boat based surveys (Cammareri and Vermeulen, 2008; 2010; Vermeulen *et al.*, 2012), with the majority of the whales being solitary. The variation in group composition seen over the subsequent September months was insignificant. Continuous research should determine if this tendency remains insignificant over the years, or if this insignificance is a result of, for example, too few data. If the increasing presence of mating groups in Bahía San Antonio is in fact a trend, this could mean that the area is becoming increasingly important for southern right whale mating, which would be important information to be monitored. Continuous research should furthermore investigate a possible shift in the presence of different group compositions within one year. In any case, the overall small group size of the observed mating groups raises doubts on the role of the study area as an important breeding ground at the moment.

The data presented confirm that the study area is neither a calving nor a nursing ground. This is valuable information when considering the local increasing touristic pressure (Vermeulen *et al.*, 2012). Similar data were found for the coastal region of Uruguay (Costa *et al.*, 2007; Jorge *et al.*, 2011), with the two main calving grounds of the species in the Southwest Atlantic located both North (Santa Catarina, Brazil) and South (Peninsula Valdés, Argentina) of the larger area including North Patagonia and Uruguay. As was reported by Jorge *et al.* (2011), southern right whales have a differential habitat use along the Southwest Atlantic Ocean, where only some areas are preferred calving and nursing grounds. Environmental variables such as sea surface temperature, bathymetry and slope have been shown to be significant in determining the southern right whale distribution (Elwen and Best, 2004; Keller *et al.*, 2006; Murison and Gaskin, 1989). As such, southern right whales, and specifically mothers and calves show a clear preference for shallow waters, sheltered from wind and swell (Elwen and Best, 2004; Patenaude and Baker, 2001; Payne, 1986), currents (Rowntree *et al.*, 2001), fronts (Patenaude and Baker, 2001) and possible predators. Although the study area is a shallow enclosed bay (unlike the Uruguayan coast; Riet-Sapriza *et al.*, 2011), preferred by resident bottlenose

Table 2

Abundance estimates for aerial surveys conducted in 2009, 2010 and 2011. *D* uncorrected=uncorrected density of whales in the study area (whales/km^{-2}); *N* uncorrected=estimate of uncorrected number of whales in the study area (no. whales); *N* corrected=estimate of number of whales in study area corrected for detection probability $g(0)_{\text{availability}}$ (no. whales).

		August		September		October		November	
		Estimate	%CV	Estimate	%CV	Estimate	%CV	Estimate	%CV
2009	*D* uncorrected	0.05	15.1	0.08	27.8	–	–	–	–
	N uncorrected	21.6	15.1	33.4	27.8	–	–	–	–
	N corrected	55.2	38.4	85.3	70.9	–	–	–	–
2010	*D* uncorrected	–	–	0.19	42.2	0.05	43.2	0	0
	N uncorrected	–	–	79.4	42.2	20.9	43.2	0	0
	N corrected	–	–	207.4	107.5	53.3	110.2	0	0
2011	*D* uncorrected	0	0	0.11	21.5	–	–	–	–
	N uncorrected	0	0	45.9	21.5	–	–	–	–
	N corrected	0	0	117.1	54.9	–	–	–	–

dolphins (Vermeulen and Cammareri, 2009), the low inclination of the slope, large tidal fluctuations (up to 9m) and overall lack of high cliffs could make the waters of the bay more sensitive for adverse weather conditions and currents, and thus less preferred by mothers with their calves. The study area might, however, be sheltered enough for unaccompanied whales to form groups and engage in social and/or mating behaviour, in which energy saving could also be an advantage (Riet-Sapriza *et al.*, 2011). Overall, no preferred areas within the bay could be observed over the years as all sightings were evenly distributed over the entire study area.

Abundance

The aerial surveys resulted in the first specific estimates of southern right whale abundance in Bahía San Antonio. These results indicated the marked presence of southern right whales in this North Patagonian bay, but the densities remained low when compared to the area around Peninsula Valdés (Crespo *et al.*, 2011).

The estimation of $g(0)_{\text{availability}}$ presented in this article appears to be lower than most of the values found for other large whales (e.g. Andriolo *et al.*, 2006; Barlow and Forney, 2007; Okamura *et al.*, 2010; Skaug *et al.*, 2004). This low value could be caused by the turbidity of the water (Els Vermeulen, pers. comm.), as it has been known to be one of the major sources of availability bias in aquatic surveys (Marsh and Sinclair, 1989) due to the lower amount of time a whale is within the visual range of an observer. However, estimation of $g(0)_{\text{availability}}$ is based on a limited amount of data and should be taken into account prudently. If indeed the estimate of $g(0)_{\text{availability}}$ presented here is an underestimate, the abundance of southern right whales in the study area could be overestimated.

Conversely, the estimation of g(0) from aerial surveys should also include the perception bias (Marsh and Sinclair, 1989), which is a bias due to a proportion of the whales at the surface being missed by the observer. In this study, only one observer was able to travel with the pilot due to limited resources and therefore this bias will be present but could not be taken into account. The inclusion of this bias would most likely result in an increased abundance estimate of southern right whales in the study area. It can thus be concluded that, although these first abundance estimates give a general impression, the specific values should be treated with care as they may be biased due to the failure to meet correctly all the assumptions inherent to line-transect surveying of an aquatic environment.

The results further indicate the occurrence of a sharp peak in whale abundance in the bay in September, with less than half the number of individuals in adjacent months. A peak in September for southern right whale presence has been reported previously for other coastal regions in Argentina (Province Rio Negro: Failla *et al.*, 2008; Province Chubut: Payne, 1986), and other regions in the Southwest Atlantic (de Oliveira Santos *et al.*, 2001; Flores *et al.*, 2000; Parmejane and Groch, 2006; Uruguay: Piedra *et al.*, 2006), but data obtained over the other months remain very scarce and thus results should be interpreted carefully.

The complete absence of whales during the aerial surveys in November 2010 and August 2011 raises questions on the predictability of the occurrence of whales in the area. Furthermore, previous data have also indicated that whales could be seen in the study area as early as April (Cammareri and Vermeulen, 2008). This apparent irregular evolution in whale occurrence over the different months has been reported previously (Cammareri and Vermeulen, 2008), and could be the result of the predominant presence of solitary animals, known to show shorter residence times and to behave in a less predictable way (Jorge *et al.*, 2011). Also, due to several limitations, the area surveyed is relatively small and there is no information available on the presence of southern right whales in the near adjacent regions. Therefore a small change in the distribution pattern of these whales might greatly affect the data gathered in the study area at a particular point in time.

As data are limited, no indication can be given towards the suggested increasing presence of southern right whales in the study area over the years. Once again, aerial surveys should be continued over consecutive years to compare relative abundances and should preferably be more consistent over the different months within one year and covering a larger area of Northeast Patagonia.

Photo-ID

During these first aerial surveys, identification pictures were taken and allowed the identification of seven individual southern right whales. None of these individuals could be re-identified between surveys. These pictures will further be compared with other catalogues of the southwest Atlantic.

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REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp.267–81. *In*: Petran, B.N. and Csaáki, F. (eds). *International Symposium on Information Theory*. Akademia Kiado, Budapest, Hungary. 451pp.

Andriolo, A., Martins, C.C.A., Engel, M.H., Pizzorno, J.L., Mas-Rosa, S., Freitas, A.C., Morete, M.E. and Kinas, P.G. 2006. The first aerial survey to estimate abundance of humpback whales (*Megaptera novaeangliae*) in the breeding ground off Brazil (Breeding Stock A). *J. Cetacean Res. Manage.* 8(3): 307–11.

Barlow, J. and Forney, K. 2007. Abundance and population density of cetaceans in the California Current ecosystem. *Fish. Bull.* 105: 509–26.

Barlow, J., Oliver, C.W., Jackson, T.D. and Taylor, B.L. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. *Fish. Bull.* 86(3): 433–44.

Belgrano, J., Masello, J., Gribaudo, C., Arcucci, D., Krohling, F., Failla, M. and Iñiguez, M. 2007. Sightings of sei whales (*Balaenoptera borealis*) on the south western Atlantic. Paper SC/59/SH13 presented to the IWC Scientific Committee, May 2007, Anchorage, USA. [Paper available from the Office of this Journal] 3pp.

Best, P.B. 1990. Trends in the inshore right whale population off South Africa, 1969–1987. *Mar. Mammal Sci.* 6(2): 93–108.

Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, New York and London. xii+446pp.

Cammareri, A. and Vermeulen, E. 2008. Southern right whales (*Eubalaena australis*): a new touristic attraction in the Natural Protected Area Bahía de San Antonio, Northeast Patagonia? Paper SC/60/BRG2 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 7pp. [Paper available from the Office of this Journal].

Cammareri, A. and Vermeulen, E. 2010. Behavioural response of southern right whales (*Eubalaena australis*) to anthropogenic approaches in Bahía San Antonio, Río Negro, Argentina. Paper SC/62/WW1 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 7pp. [Paper available from the Office of this Journal].

Cooke, J., Rowntree, V. and Payne, R. 2003. Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identification of calving females observed off Península Valdés, Argentina, during 1971–2000. Paper SC/55/O23 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 16pp. [Paper available from the Office of this Journal].

Cooke, J.G., Rowntree, V.J. and Payne, R.S. 2001. Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Península Valdés, Argentina. *J. Cetacean Res. Manage. (special issue)* 2: 125–32.

Costa, P., Piedra, M., Franco, P. and Paez, E. 2007. Distribution and habitat use patterns of southern right whales, *Eubalaena australis*, off Uruguay. *J. Cetacean Res. Manage.* 9(1): 45–51.

Crespo, E.A., Pedraza, S.N., Dans, S.L., Coscarella, M., Svendsen, G. and Degrati, M. 2011. Number of southern right whales *Eubalaena australis* and population trend in the neighbourhood of Peninsula Valdes during the period 1999–2011 by means of aerial and boat surveys. Paper SC/S11/RW4 presented to the Southern Right Whale Assessment Workshop, 13–16 September 2011, Buenos Aires, Argentina (unpublished). 15pp. [Paper available from the Office of this Journal].

de Oliveira Santos, M.C., Siciliano, S., de Souza, S.P. and Altmayer Pizzorno, J.L. 2001. Occurrence of southern right whales (*Eubalaena australis*) along southeastern Brazil. *J. Cetacean Res. Manage. (special issue)* 2: 153–56.

Elwen, S.H. and Best, P.B. 2004. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa II: Within bay distribution. *Mar. Mammal Sci.* 20(3): 583–601.

Failla, M., Vermeulen, E., Carabajal, M., Arruda, J., Godoy, H., Lapa, A., Mora, G., Urrutia, C., Balbiano, A. and Cammareri, A. 2008. Historical records of southern right whales (*Eubalaena australis*) of the province Rio Negro, North Patagonia, Argentina (1991–2008). Paper SC/60/BRG1 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 10pp. [Paper available from the Office of this Journal].

Flores, P.A., Groch, C.K.R. and Palazzo, J.T. 2000. Distribução e tamanho degrupo de baleia franca austral (*Eubalaena australis*) na Centro Sul de Santa Catarina, Brasil. 9° Reunión de Trabajo de Especialistas en Mamíferos Marinos de América del Sur, 3° Congreso de la Sociedad Latinoamericana de Mamíferos Aquáticos– SOLAMAC (Buenos Aires, 31 Octubre – 3 Noviembre de 2000). 54pp.

Iñíguez, M., Belgrano, J., Tomsin, A., de Haro, C., Gribaudo, C. and Tossenberger, V. 2003. Sighting and stranding of southern right whales (*Eubalaena australis*) off Santa Cruz, Patagonia Argentina (1986–2003). Paper SC/55/BRG8 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 5pp. [Paper available from the Office of this Journal].

International Whaling Commission. 2001. Report of the Workshop on the Comprehensive Assessment of Right Whales: A worldwide comparison. *J. Cetacean Res. Manage. (special issue)* 2:1–60.

Jorge, G., Riet-Sapriza, F. and Costa, P. 2011. Status and behaviour of southern right whales (*Eubalaena australis*) in the Uruguayan Atlantic coast. Paper SC/S11/RW8 presented to the Southern Right Whale Assessment Workshop, 13–16 September 2011, Buenos Aires, Argentina (unpublished). 16pp. [Paper available from the Office of this Journal].

Keller, C.A., Ward-Geiger, L.I., Brooks, W.B., Slay, C.K., Taylor, C.R. and Zoodsma, B.J. 2006. North Atlantic right whale distribution in relation to sea-surface temperature in the southeastern United States calving grounds. *Mar. Mammal Sci.* 22(2): 426–45.

Marsh, H. and Sinclair, D.F. 1989. Correcting for visibility bias in strip transect aerial surveys for aquatic fauna. *J. Wildl. Manage.* 53(4): 1017–24.

Murison, L.D. and Gaskin, D.E. 1989. The distribution of right whales and zooplankton in the Bay of Fundy, Canada. *Can. J. Zool.* 67(6): 1,411–20.

Okamura, H., Miyashita, T. and Kitakado, T. 2010. *g*(0) estimates for western North Pacific common minke whales. Paper SC/62/NPM9 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 7pp. [Paper available from the Office of this Journal].

Parmejane, F.B. and Groch, K.R. 2006. Occurrance and distribution of southern right whales (*Eubalaena australis* Demoulins, 1822) in Cabo de Santa Marta, Santa Catarina, southern Brazil and its relation with environmental factors 1 Reunion Internacional Especialistas Mamiferos Marinos (SOMEMA-SOLAMAC) Merida, Mexico 5 al 9 Noiembre 2006.

Patenaude, N.J. and Baker, C.S. 2001. Population status and habitat use of southern right whales in the sub-Antarctic Auckland Islands of New Zealand. *J. Cetacean Res. Manage. (special issue)* 2: 111–16.

Payne, R. 1986. Long term behavioral studies of the southern right whale (*Eubalaena australis*). *Rep. int. Whal. Commn (special issue)* 10: 161–67.

Payne, R., Rowntree, V., Perkins, J.S., Cooke, J.G. and Lankester, K. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. *Rep. int. Whal. Commn (special issue)* 12: 271–78.

Piedra, M., Costa, P. and Franco-Fraguas, P. 2006. Ballena franca *Eubalaena australis* en la costa atlantica Uruguay. *In*: Menafra, R., Rodrigues-Gallego, L., Scarabino, F. and Conde, D.A. (eds). *Bases para la conservacion y el manejo de la costa Uruguaya*. VIDA SILVESTRE, Sociadad Uruguaya para la conservation de la naturaleza [In Spanish].

Riet-Sapriza, F., Jimenez, E., Jorge, G. and Costa, P. 2011. Utilization distribution of southern right whales *Eubalaena australis* off the coast of Uruguay. Paper SC/S11/RW9 presented to the Southern Right Whale Assessment Workshop, 13–16 September 2011, Buenos Aires, Argentina (unpublished). 10pp. [Paper available from the Office of this Journal].

Rowntree, V.J., Payne, R. and Schell, D.M. 2001. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. *J. Cetacean Res. Manage. (special issue)* 2: 133–43.

Skaug, H.J., Øien, N., Schweder, T. and Bothun, G. 2004. Abundance of minke whales (*Balaenoptera acutorostrata*) in the northeastern Atlantic; variability in time and space. *Can. J. Fish. Aquat. Sci.* 61(6): 870–86.

Thomas, L., Laake, J., Strindberg, S., Marques, F., Buckland, S., Borchers, D., Anderson, D., Burnham, K.P., Hedley, S., Pollard, J., Bishop, J.B. and Marques, T.A. 2006. Distance 6.0 Release '1'. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. [Available at: *http://www.ruwpa.st-and.ac.uk/distance/*].

Vermeulen, E. and Cammareri, A. 2009. Residency abundance and social composition of bottlenose dolphins (*Tursiops truncatus*) in Bahia San Antonio, Patagonia, Argentina. *Aquat. Mamm.* 35(3): 379–86.

Vermeulen, E., Cammareri, A. and Holsbeek, L. 2012. Alteration of Southern right whale (*Eubalaena australis*) behaviour by human induced disturbance in Bahia San Antonio, Patagonia, Argentina. *Aquat. Mamm.* 38(1): 56–64.

New insight into migration patterns of western North Pacific humpback whales between the Babuyan Islands, Philippines and the Commander Islands, Russia

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ABSTRACT

The population structure of humpback whales (*Megaptera novaeangliae*) in the North Pacific has received significant attention in recent years through the collaborative Structure of Populations, Levels of Abundance, and Status of Humpback whales in the North Pacific (SPLASH) study. However, the analysis of humpback whales in the western North Pacific Asian population was limited in the SPLASH study, due to small sample size. Much of the Asian population summers off Kamchatka, Russia and spends the winters in breeding grounds in Okinawa and Ogasawara, Japan and the Babuyan Islands in the northern Philippines. Prior studies grouped the Commander Islands feeding ground in Russia, with the eastern Aleutian Islands as part of the central humpback whale stock. This paper uses additional years of photo-ID data from both the Philippines (160 whales from 2000–12) and the Commander Islands (531 whales from 2008–10) to establish a previously unreported migratory connection by matching four animals between the two sites. The new migratory linkage found in the present study suggests that a small portion of humpback whales hypothesised to be migrating to a 'missing' breeding ground in the central North Pacific are actually migrating to the Philippines. However, additional studies on a wider geographical scale are required.

KEYWORDS: HUMPBACK WHALE; ASIA; PACIFIC OCEAN; MOVEMENTS; BREEDING GROUNDS; FEEDING GROUNDS; MIGRATION; DISTRIBUTION; CONSERVATION; SURVEY-VESSEL; PHOTO-ID

INTRODUCTION

The migration patterns and population structure of North Pacific humpback whales (*Megaptera novaeangliae*) are highly complex. Humpback whales often exhibit strong site fidelity to both winter breeding and summer feeding grounds, but many whales do not conform to a single migratory path. Wintering areas in the eastern North Pacific include the mainland coast of Mexico and Central America and the offshore Revillagigedo Islands (Mexico); in the central North Pacific, the main Hawaiian Islands; in the western North Pacific, the Ogasawara and Ryukyu Islands in Japan and around the Babuyan Islands in the northern Philippines (Acebes *et al.*, 2007; Baker *et al.*, 1986; Calambokidis *et al.*, 2000; Calambokidis *et al.*, 2001; Darling and McSweeney, 1985; Nishiwaki, 1959).

While humpback whales were first scientifically documented in the northern Philippines by Yaptinchay (1999), opportunistic sightings have been recorded by local residents since the 1960's (Sumangil, 2000; Tan, 1995). Dedicated small-vessel research surveys in the Philippines began in 2000 and have continued every year since, albeit on varying spatial and temporal scales. Previous photographic comparisons found 12 humpback whales from the Babuyan Islands that matched whales in the breeding grounds off Okinawa and Ogasawara, including one animal that moved between Ogasawara and the Philippines in one season (Acebes *et al.*, 2007; Yamaguchi *et al.*, 2002). Additional matches have been made between Philippine and Japanese breeding grounds, as well as one match to the main Hawaiian Islands (Calambokidis *et al.*, 2008). Earlier connections between Japanese and Hawaiian breeding grounds (Darling and Cerchio, 1993; Salden *et al.*, 1999) and between Japan and eastern Pacific feeding grounds (Calambokidis *et al.*, 2001; Darling *et al.*, 1996) have been reported, although infrequently.

Calambokidis *et al.* (2008) suggested that the predominant feeding ground used by Philippine humpbacks is the area off the Kamchatka Peninsula in Russia, as demonstrated by six photographic matches between the two regions. No matches were found to the adjacent Commander Islands, which were subsequently grouped with the Aleutian Island and Bering Sea populations. Three of seventeen humpback whales from the Commander Islands matched individuals in breeding grounds with one match each to Ogasawara, Hawaii, and the Revillagigedo Archipelago. In contrast, whales using Kamchatka feeding grounds were matched only to Japan and the Philippines (Barlow *et al.*, 2011; Calambokidis *et al.*, 2008). Low sample sizes in both Philippine ($n = 77$) and Russian waters ($n = 17$ from Commander Islands, $n = 102$ from all Russian sites) contributed to uncertainty regarding the migration of humpback whales in the western North Pacific. The purpose of this study was to examine additional years of data from the Babuyan Islands, Philippines (2000–12) and compare photographs with an expanded catalogue of whales from the Commander Islands (whales seen from 2008–10) to investigate the interconnectivity between the two areas.

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METHODS

Small vessel surveys were conducted from 2000–06 off all of the islands in the Babuyan chain (18°53’N, 121°51’E): Camiguin, Fuga, Babuyan Claro, Calayan and Dalupiri (see Acebes *et al.*, 2007). From 2007 onwards, due to logistical constraints, surveys were limited to the western coast of Camiguin Island where the sighting frequency was highest (Fig. 1). All surveys were conducted between February and May, however this varied annually (Table 2). Predetermined tracklines were followed along the western coast of Camiguin Island with track legs running perpendicular and parallel (alternately) to shore. The choice of which trackline to follow was dependent on sea conditions and time of day. When a whale was encountered, the fluke(s) were photographed and recordings were made of behaviour, composition of the group and the presence of other cetacean species.

Photos were graded using an established process (Calambokidis *et al.*, 2008; Calambokidis *et al.*, 2000; Calambokidis *et al.*, 1997). Best fluke shots were scored on a 1–5 scale for quality of proportion visible, vertical angle, lateral angle, focus/sharpness and exposure. Any flukes were removed that scored a three in more than three quality categories, or that received any score of four or higher in any category. Photographic matches were made by at least one of two experienced personnel. All fluke matches were verified by at least three experienced personnel.

Catalogued flukes from the Commander Islands (55°03’N, 166°17’E) came from two separate groups: the Kamchatka Branch of Pacific Institute of Geography (KBPIG) and the State Nature Reserve Komandorski (SNRK) (Fig. 1). Surveys included in the KBPIG catalogue were conducted between June and September from 2008–10 and surveys included in the SNRK catalogue were conducted between September and November in 2009 (Table 3).

RESULTS

There were 160 humpback whales which met the photographic criteria to be included the Philippine catalogue, representing a minimum population number for the breeding area around the Babuyan Islands. For the Commander Islands, after reconciling the SNRK (2008) and KBPIG (2008–10) catalogues, 66 whales were included from the SNRK catalogue and 465 whales were included in the KBPIG catalogue (*n* = 531).

Four photographic matches were made between the Philippine and Commander Island catalogues (Table 1). None of the animals were seen in both areas in the same year and none have been seen in the Philippines since 2006.

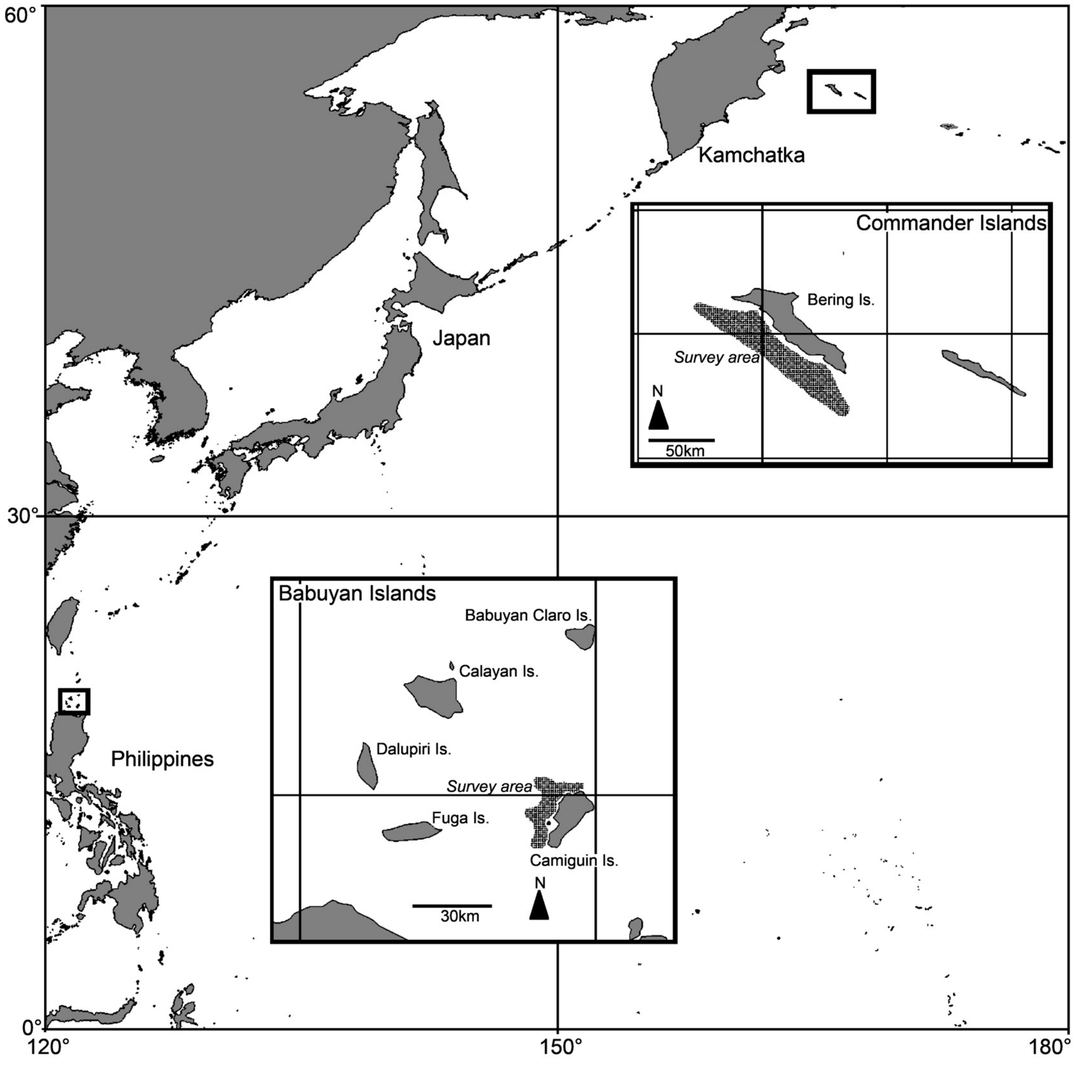

Fig. 1. Humpback whale survey areas in the Babuyan Islands, Philippines and the Commander Islands, Russia.

Table 1

Photographic matches of humpback whales between winter breeding grounds in the Babuyan Islands, Philippines and summer feeding grounds in the Commander Islands, Russia.

SPLASH ID[1]	Philippines ID	Years sighted: Philippines	Commander Islands ID	Year sighted: Commander Is.	Other sightings[1]
N/A	PH008	2001, 2002	066 (SNRK)	2009	–
440014	PH013	2002, 2004	598 (KBPIG)	2010	–
540207	PH063	2003, 2005	254 (KBPIG)	2010	–
440069	PH087	2004, 2006	071 (SNRK)	2009	Ogasawara 2005

[1] From SPLASH structure of populations, levels of abundance, and status of humpbacks (see Calambokidis *et al.*, 2008).

PH008 and PH087 were presumed to be male, as they were seen as escorts in 2002 and 2004, respectively. The sexes of PH013 (Fig. 2) and PH063 are unknown.

Fig. 2. (a) Individual humpback whale (PH013/SPLASH ID 440014) seen in the Babuyan Islands, Philippines breeding ground in the winters of 2002 and 2004. (b) Same individual humpback whale (#598) seen in the Commander Islands, Russia feeding ground in the summer of 2010.

Table 2

Survey effort to collect humpback whale fluke photographs in the Babuyan Islands, Philippines winter breeding ground from 2000 to 2012.

Year	Survey group	Survey season	No. survey days
2000	WWF	Apr.	14
2001	WWF	Mar.–Apr.	43
2002	WWF	Mar.–May	47
2003	WWF	Feb.–May	51
2004	WWF	Mar.–Apr.	33
2005	WWF	Feb.–May	60
2006	WWF	Feb.–Apr.	79
2007	Balyena.org	Mar.–Apr.	30
2008	Balyena.org	Mar.–Apr.	29
2009	Balyena.org	Mar.–Apr.	26
2010	Balyena.org	Mar.	13
2011	Balyena.org	Feb.–Apr.	28
2012	Balyena.org	Mar.–Apr.	32

Table 3

Survey effort to collect humpback whale fluke photographs in the Commander Islands, Russia summer feeding ground from 2008 to 2010.

Year	Survey group	Survey season	No. survey days
2008	KBPIG	Jun.–Sep.	7
2009	SNRK	Sep.–Nov.	10
2009	KBPIG	Jun.–Sep.	7
2010	KBPIG	Jun.–Sep.	41

DISCUSSION

By photographically matching four whales between the Philippines and Commander Islands, these results suggest that the inclusion by Calambokidis *et al.* (2008) of the Commander Islands in a geographical grouping with the Aleutian Islands and Bering Sea populations may not represent the true variability in stock structure within western North Pacific humpback whales. However, the process of assigning individual whales to one specific stock is heavily influenced by uneven sampling effort and may not be representative of the stock structure across the entire North Pacific. Stable isotope analysis has shown that individuals from a particular feeding ground may not migrate to a single breeding area (Witteveen *et al.*, 2009), which is also supported by photographic evidence (Acebes *et al.*, 2007; Calambokidis *et al.*, 2008; Darling and Cerchio, 1993; Salden *et al.*, 1999). Historically, humpback whales feeding off the Commander and Aleutian Islands have a lower match rate to known breeding grounds than whales from other feeding areas, which led to the proposed existence of an 'undiscovered wintering area' in the North Pacific (Calambokidis *et al.*, 2008). It has been hypothesised that the Northwest Hawaiian Islands (NWHI) could represent this missing breeding ground (Johnston *et al.*, 2007; Lammers *et al.*, 2011). Based on 17 whales, Calambokidis *et al.* (2008) found a 17% match rate of Commander Island whales to three geographically distinct breeding grounds spread across the North Pacific, including Ogasawara. The match rate in this study of <1% of Commander Island humpback whales is low. However, this study shows that, along with the previous photographic match to Japan (Calambokidis *et al.*, 2008), at least some portion of the humpback whales feeding around the Commander Islands migrate to Asian breeding grounds, including the Philippines.

The population structure of humpback whales on Asian breeding grounds remains unclear. Photographic matches between Ogasawara and Okinawa in Japan were lower than expected considering the relatively short distance between them (Calambokidis *et al.*, 2008; Calambokidis *et al.*, 2001; Darling and Mori, 1993). Genetic analysis of the SPLASH dataset showed high levels of complexity within the Asian population with significant differences in haplotype frequency between adjacent breeding areas of Okinawa and Ogasawara, as well as between Okinawa and Russia (Baker *et al.*, 2008). However, photographic matches exist between both Japanese breeding grounds and the Philippines, suggesting some interchange between breeding grounds.

The range of humpback whales within the Philippines also remains uncertain, as to date, no dedicated surveys have been conducted off much of northern Luzon. A 2003 survey that found a mother-calf pair off the eastern coast of northern Sierra Madre, Luzon suggests that the breeding ground may extend further south in the archipelago (Acebes *et al.*, 2007). Historical whaling records indicate that humpback whales had a much wider distribution in the Philippines including areas south and east of Mindanao, southwest of Palawan and in the Sulu Sea between 0° and 10°N and 116° and 131°E (Slijper *et al.*, 1964; for map see Acebes, 2009). It is unclear whether this population was a northern extension of Southern Hemisphere humpback range, part of the North Pacific stock, or represented a region of seasonally distinct overlapping habitat use by Southern and Northern Hemisphere whales, such as occurs in Central America (Rasmussen *et al.*, 2011). No recent sightings of humpback whales have been confirmed in Philippine waters south of Luzon or north of the Celebes (Sulawesi) Sea.

Whaling for humpbacks in the 1950s and 1960s in Russian waters (Doroshenko, 2000; Ivashchenko *et al.*) and on Japanese breeding grounds (Nishiwaki, 1959; Rice, 1978) severely depleted western North Pacific stocks of humpback whales. As populations potentially return to historical ranges and recover from whaling, new insight into their distribution and migratory paths are critical to understand stock structure in the western North Pacific. Further studies on Asian humpback whale breeding grounds are necessary to determine how humpback whales in the Philippines fit into the larger population structure in the North Pacific.

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REFERENCES

Acebes, J.M.V., Darling, D.J. and Yamaguchi, M. 2007. Status and distribution of humpback whales (*Megaptera novaeangliae*) in northern Luzon, Philippines. *J. Cetacean Res. Manage.* 9(1): 37–43.

Acebes, J.M.V. 2009. Historical whaling in the Philippines: origins of 'indigenous subsistence whaling', mapping whaling grounds and comparison with current known distribution: a HMAP Asia Project Paper. Working Paper No. 161. Asia Research Centre at Murdoch University, Perth, Western Australia. [Available at: *wwwarc.murdoch.edu.au/publications/wp/wp161.pdf*]. ISSN: 1037-4612.

Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M., Wolman, A.A., Kaufman, G.D., Winn, H.E., Hall, J.D., Reinke, J.M. and Ostman, J. 1986. Migratory movement and population structure of humpback whales, *Megaptera novaeangliae*, in the central and eastern North Pacific. *Mar. Ecol. Prog. Ser.* 31: 105–19.

Baker, C.S., Steel, D., Calambokidis, J., Barlow, J., Burdin, A.M., Clapham, P.J., Falcone, E.A., Ford, J.K.B., Gabriele, C.M., Gozález-Peral, U., LeDuc, R., Mattila, D., Quinn, T.J., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbán-R, J., Vant, M., Wade, P., Weller, D., Witteveen, B.H., Wynne, K. and Yamaguchi, M. 2008. geneSPLASH: An initial, ocean-wide survey of mitochondrial (mt) DNA diversity and population structure among humpback whales in the North Pacific. Final report for Contract 2006-0093-008 to the National Fish and Wildlife Foundation, Washington, DC.

Barlow, J., Calambokidis, J., Falcone, E.A., Baker, C.S., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D.K., Quinn II, T.J., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R., J., Wade, P., Weller, D., Witteveen, B.H. and Yamaguchi, M. 2011. Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. *Mar. Mammal Sci.* 27(4): 793–818.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R, J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J. and Maloney, N. 2008. SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific. Final report for Contract AB133F-03-RP-00078, US Department of Commerce Western Administrative Center, Seattle, Washington. [Available at *http://www.cascadiaresearch.org/SPLASH/SPLASH-contract-report-May08.pdf*].

Calambokidis, J., Steiger, G.H., Rasmussen, K., Urbán R, J., Balcomb, K.C., Ladrón de Guevara P, P., Salinas Z, M., Jacobsen, J.K., Baker, C.S., Herman, L.M., Cerchio, S. and Darling, J. 2000. Migratory destinations of humpback whales that feed off California, Oregon and Washington. *Mar. Ecol. Prog. Ser.* 192: 295–304.

Calambokidis, J., Steiger, G.H., Straley, J., Herman, L.M., Cerchio, S., Salden, D., Urbán R, J., Jacobsen, J.K., von Zeigesar, O., Balcomb, K.C., Gabriele, C.M., Dahlheim, M.E., Uchida, S., Ellis, G., Miyamura, Y., Ladrón de Guevara P, P., Yamaguchi, M., Sato, F., Mizroch, S.A., Schlender, L., Rasmussen, K., Barlow, J. and Quinn II, T.J. 2001. Movements and population structure of humpback whales in the North Pacific. *Mar. Mammal Sci.* 17(4): 769–94.

Calambokidis, J., Steiger, G.H., Straley, J.M., Quinn Ii, T.J., Herman, L.M., Cerchio, S., Salden, D.R., Yamaguchi, M., Sato, F., Urbán R, J., Jacobsen, J., von Ziegesar, O., Balcomb, K.C., Gabriele, C.M., Dahlheim, M.E., Higashi, N., Uchida, S., Ford, J.K.B., Miyamura, Y., Ladrón de Guevara P, P., Mizroch, S., Schlender, A. and Rasmussen, K. 1997. Abundance and population structure of humpback whales in the North Pacific basin. Contract report submitted to NMFS. 72pp. [Available from: *www.nmfs.gov*].

Darling, J.D., Calambokidis, J., Balcomb, K.C., Bloedel, P., Flynn, K., Mochizuki, A., Mori, K., Sato, F., Suganuma, H. and Yamaguchi, M. 1996. Movement of a humpback whale (*Megaptera novaeangliae*) from Japan to British Colombia and return. *Mar. Mammal Sci.* 12(2): 281–87.

Darling, J.D. and Cerchio, S. 1993. Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. *Mar. Mammal Sci.* 9(1): 84–89.

Darling, J.D. and McSweeney, D.J. 1985. Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* 63: 308–14.

Darling, J.D. and Mori, K. 1993. Recent observations of humpback whales (*Megaptera novaeangliae*) in Japanese waters off Ogasawara and Okinawa. *Can. J. Zool.* 71(2): 325–33.

Doroshenko, N.V. 2000. Soviet catches of humpback whales (*Megaptera novaeangliae*) in the North Pacific. pp.48–95. *In*: Yablokov, A.V. and Zemsky, V.A. (eds). *Soviet Whaling Data (1949–1979)*. Center for Russian Environmental Policy, Moscow. 408pp.

Ivashchenko, Y.V., Brownell, R.L.J. and Clapham, P.J. 2013. Soviet whaling in the North Pacific: revised catch totals. *J. Cetacean Res. Manage.* 13(1): 59–71.

Johnston, D., Chapla, M., Williams, L.E. and Mattila, D.K. 2007. Identification of humpback whale *Megaptera novaeangliae* wintering habitat in the northwestern Hawaiian Islands using spatial habitat modelling. *Endangered Species Research* 3: 249–57.

Lammers, M.O., Fisher-Pool, P.I., Au, W.W.L., Meyer, C.G., Wong, K.B. and Brainard, R.E. 2011. Humpback whale *Megaptera novaeangliae* song reveals wintering activity in the Northwestern Hawaiian Islands. *Mar. Ecol. Prog. Ser.* 423: 261–68.

Nishiwaki, M. 1959. Humpback whales in Ryukyuan waters. *Sci. Rep. Whales Res. Inst., Tokyo* 14: 49–87.

Rasmussen, K., Calambokidis, J. and Steiger, G.H. 2011. Distribution and migratory destinations of humpback whales off the Pacific coast of Central America during the boreal winters of 1996–2003. *Mar. Mammal Sci.* DOI: 10.1111/j.1748-7692.2011.00529.x.

Rice, D.W. 1978. The humpback whale in the North Pacific: distribution, exploitation, and numbers. pp.21. *In*: Norris, K.S. and Reeves, R. (eds). *Report on a Workshop on Problems Related to Humpback Whales (Megaptera novaeangliae) in Hawaii*, Report to the Marine Mammal Commission, July 1977, Washington, DC. [Available from NMML Library, *http://nmml.afsc.noaa.gov/library*].

Salden, D.R., Herman, L.M., Yamaguchi, M. and Sato, F. 1999. Multiple visits of individual humpback whales (*Megaptera novaeangliae*) between the Hawaiian and Japanese winter grounds. *Can. J. Zool.* 77: 504–08.

Slijper, E.J., van Utrecht, W.L. and Naaktgeboren, C. 1964. Remarks on the distribution and migration of whales, based on observations from Netherlands ships. *Bijdr. Dierkd.* 34: 3–93.

Sumangil, J.H. 2000. An interview survey of humpback whale (*Megaptera novaeangliae*) sightings in the Babuyan islands, Cagayan, Philippines. A report submitted to the Cetacean Research and Conservation Project Phase Two, WWF-Philippines, September 2000 (unpublished). 19pp. [Available from *jmvacebes@yahoo.com*]

Tan, J.M.L. 1995. *A Field Guide to Whales and Dolphins in the Philippines*. 1st ed. Bookmark, Metro Manila. 125pp.

Witteveen, B.H., Worthy, G.A.J. and Roth, J.D. 2009. Tracing migratory movements of breeding North Pacific humpback whales using stable isotope analysis *Mar. Ecol. Prog. Ser.* 393: 173–83.

Yamaguchi, M., Acebes, J.M. and Miyamura, Y. 2002. The breeding ground distribution of the humpback whales, *Megaptera novaeangliae*, in the western North Pacific and their trans-movements among the Ogasawara Islands, the Ryukyu Islands and the Philippines. Paper presented at the Second Conference on Marine Mammals of Southeast Asia, Dumaguete, Philippines, July 2002 (unpublished). [Available from *mana@bonin-ocean.net*].

Yaptinchay, A.A. 1999. New humpback whale wintering ground in the Philippines. Paper presented to the 13th Biennial Conference on the Biology of Marine Mammals, 28 Nov.–3 Dec, 1999, Maui, Hawaii.

Soviet catches of whales in the North Pacific: revised totals

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ABSTRACT

The USSR conducted a global campaign of illegal whaling beginning in 1948. Catch records for Soviet pelagic operations in the Southern Hemisphere (and the northern Indian Ocean) have been largely corrected, but major gaps have remained for the North Pacific. Here, using newly discovered whaling industry reports, corrected figures for Soviet catches in this ocean are provided. During the period 1948–79, a minimum of 190,183 whales were killed by the USSR in the North Pacific (195,783 if one includes an estimate for sperm whales taken in years for which there are no true data); of these, only 169,638 were reported to the IWC, a difference of 20,568 whales (26,168 including the sperm whale estimate). Figures were falsified for 8 of 12 hunted species, with some catches over-reported to camouflage takes of illegal species. Revised catch totals (caught vs. reported) are as follows: blue whale – 1,621 vs. 858; fin whale – 14,167 vs. 15,445; humpback whale – 7,334 vs. 4,680; sperm whale – 153,686 vs. 132,505; sei whale – 7,698 vs. 11,363; North Pacific right whale – 681 vs. 11; bowhead whale – 145 vs. 0; gray whale – 172 vs. 24. Bryde's, minke, killer and Baird's beaked whale catches were reported correctly. Of all the hunted species, sperm and North Pacific right whales were the most heavily impacted. Major falsifications for sperm whales involved figures for both total catch and sex ratio.

KEYWORDS: WHALING-MODERN; ILLEGAL WHALING; REVISED CATCHES; NORTH PACIFIC; NOTHERN HEMISPHERE; HUMPBACK WHALE; GRAY WHALE; BOWHEAD WHALE; SPERM WHALE; RIGHT WHALE; BLUE WHALE; FIN WHALE; SEI WHALE; BRYDE'S WHALE

INTRODUCTION

Whaling has a long history in the North Pacific. Aboriginal subsistence whaling existed in different areas of this ocean for centuries (Reeves and Smith, 2006). Webb (1988) places the beginning of commercial whaling in the North Pacific at the end of the 1700s, with a major expansion in the 19th century; this was traditional sail-based whaling and concentrated largely on slower species such as sperm (*Physeter macrocephalus*), humpback (*Megaptera novaeangliae*), gray (*Eschrichtius robustus*), North Pacific right (*Eubalaena japonica*) and bowhead (*Balaena mysticetus*) whales. Later, as innovations such as steam catcher boats and explosive harpoons were introduced, faster species such as blue (*Balaenoptera musculus*), sei (*B. borealis*) and fin whales (*B. physalus*) were taken, and by the early 20th century most baleen whales were being regularly hunted in this region.

A number of nations were involved in North Pacific whaling, primarily: Americans, Canadians, UK and Norway. Russian whaling, however, had been virtually non-existent, with the exception of a successful operation conducted by Otto V. Lindholm (a Finn but Russian subject) in the Okhotsk Sea during the period 1864–84, and a brief operation using modern methods operating from Gaydamak near Vladivostok during 1889 by Akim G. Dydymov (Vebermann, 1914).

Modern-type whaling in the eastern North Pacific dates back to 1906 with the opening of the first land-based whaling station in British Columbia (Webb, 1988), while in Japan the first shore station was established in 1896 (Reeves and Smith, 2006). In 1932, the USSR began commercial whaling in the North Pacific using a converted factory ship named *Aleut*, which for 16 years was the only Soviet whaling operation in this ocean (Ivashchenko *et al.*, 2011; Zenkovich, 1954). Soviet whaling expanded after World War II with the restoration, in 1948, of former Japanese land stations in the Kuril Islands. The *Aleut* fleet and catchers from the Kurils stations were operating in the western North Pacific exclusively until 1959; by that time the whale resources in this part of the North Pacific had been heavily depleted and the focus of the Soviet operations moved east, first to the waters around the eastern Aleutian Islands and then into the Gulf of Alaska (GoA), eastern Bering Sea (BS) and areas off the western coast of North America.

In the space of just two years (1962–63), three new large whaling factory ships were added to the Soviet North Pacific whaling operation, with the main focus remaining in the eastern North Pacific[4]. As a result of this expansion, catches dramatically increased from 3,970 whales in 1961, to 12,945[5] in 1964 and continued to increase in subsequent years. Catches of sperm whales (the primary target of Soviet whalers in the North Pacific[6]) increased five-fold from 1962 (3,035) to 1966 (15,205). Such intensive whaling continued in the North Pacific until 1969, with up to four Soviet whaling fleets working in the area simultaneously. Examples

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[3] *Southwest Fisheries Science Center, 1352 Lighthouse Avenue, Pacific Grove, CA 93950, USA.*

[4] At the same time the Kurils stations were closing over a period of 4 years (1961–64) due to a decline in whale abundance in the area.

[5] Unless otherwise noted, all catch figures given in this paper are those derived from the formerly secret reports described in Methods, and are assumed to be an accurate record of the true Soviet catch. These figures are in contrast to the figures officially reported to the IWC which, with the exception of some late years of the Aleut fleet, are known to have been falsified.

[6] In this paper the term 'primary target' means the whale species that was the principal focus of the whaling fleet's search operations during the season, and which therefore usually made up the majority of the catch. For example, blue whales were never the primary target despite being highly prized when available; in contrast, sperm whales and sometimes fin and humpback whales would be the primary target, and the distribution of these species would determine the major search areas of the fleets.

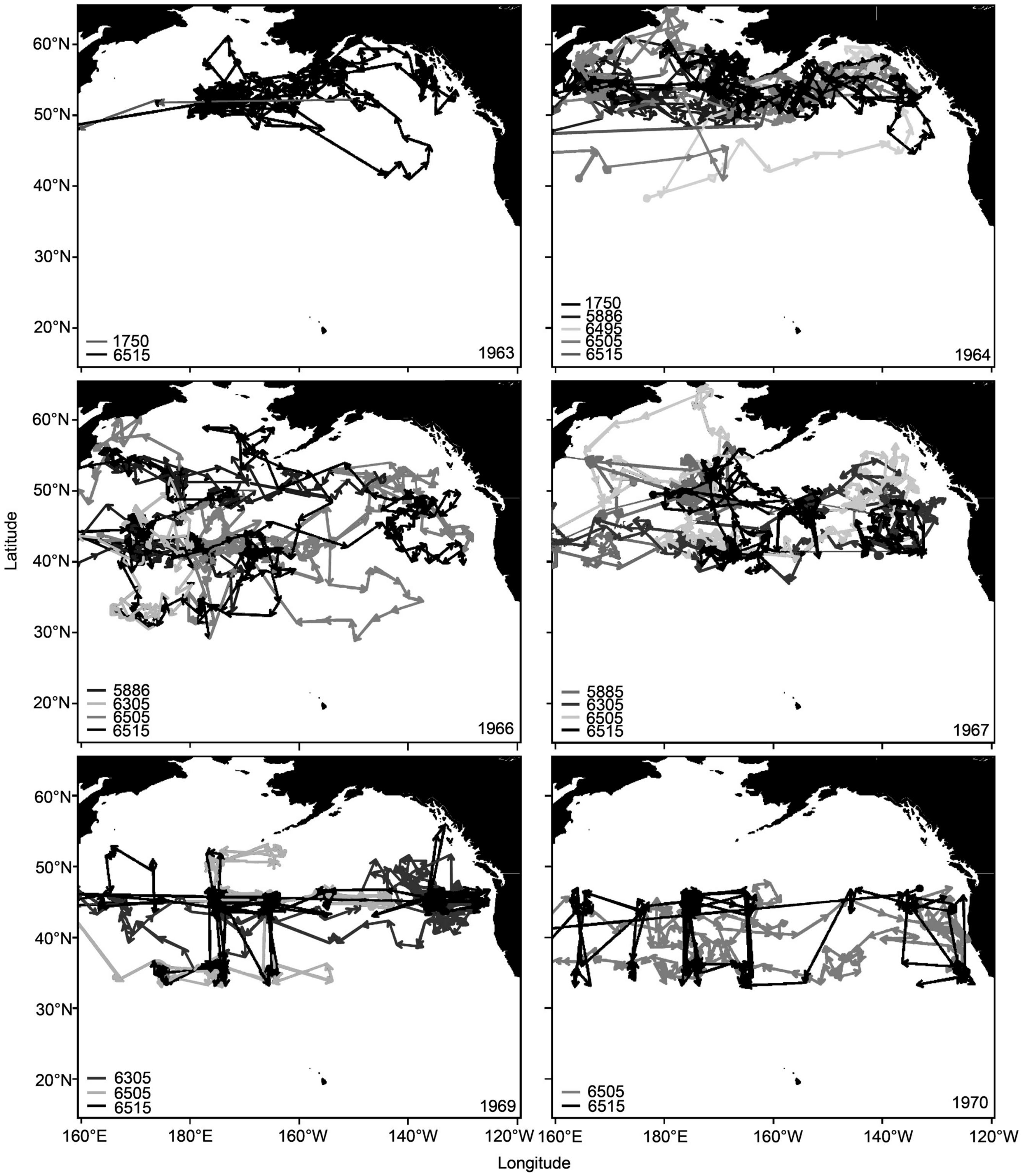

Fig. 1. Examples of search effort (tracks) of Soviet whaling operations in the North Pacific for selected years. Codes for the fleets/stations are as follows: 1750 Kuril land stations; 6515 *Vladivostok*; 6505 *Dalniy Vostok*; 5885 and 5886 *Aleut*; 6495 *Sovetskaya Rossiya*; 6305 *Slava.* Solid circles show the beginning and end of the season. Arrows define the direction of movement of the fleet during the season. The plots (which represent noon positions of the factory ship) show only days when catches were made, since these were the only days for which positions were reported.

of the geographic scope of the Soviet whaling effort is given in Fig. 1.

The high catches, both in the North Pacific and elsewhere in the world, were driven by very specific requirements of the Soviet economic system to meet or exceed annual production targets (see details in Ivashchenko *et al.*, 2011). The need to catch so many whales forced the Soviet whalers to hunt all species and all sizes and the result was an extensive global campaign of illegal whaling that went on, secretly and unchecked, from 1948 until sometime in the 1970s (Berzin, 2008; Clapham and Ivashchenko, 2009; Ivashchenko *et al.*, 2011).

The USSR was a signatory to the International Convention for the Regulation of Whaling (1946) and as such it was

Table 1

List of IWC regulations relating to North Pacific whaling operations.

Years	Regulation	Species covered	Details
1948	Minimum length and age/reproductive status	Blue whale, fin whale, humpback whale, sei whale, sperm whale	70, 60, 35, 40, 38 (35 for land stations) feet, respectively; no lactating females or calves east of 150°W from 0 to 35°N; west of 150°W from 0 to 20°N. Only aboriginal hunting allowed.
	Protected areas	All species	
	Protected species	Right whale, bowhead whale, gray whale	
1953	Protected area	Baleen whale, sperm whale	20°-66°N (to 72°N for sperm whales) in the eastern North Pacific, Bering Sea and all Aleutian Islands.
1964	Method of capture	Gray whale	Forbidden to kill 'except by aborigines or a Contracting Government on behalf of aborigines and only when the meat and products of such whales are to be used exclusively for local consumption by the aborigines'.
1966	Protected species	Blue whale, humpback whale	All areas of the North Pacific north of the Equator.
1967	Limited catches	Fin whale, sei whale	Lowering the catches to bring them to a sustainable level.
1968	Limited catches	Sperm whale	Approximately 8,000-10,000.
1971	National quotas (USSR)	Fin whale, sei whale (with Bryde's whale) and sperm whale	700, 1,527 and 7,716, respectively.
1972	International Observer Scheme	All species	Independent observers placed on all factory ships.
1972	Change in the minimum size limit	Sperm whale	From 35 feet to 30 feet.

required to follow catch restrictions defined in the Schedule of the International Whaling Commission (IWC). Such restrictions typically included areas in which hunting was prohibited, as well as various mandates regarding protected species and the minimum allowable length for catches of 'legal' species; for reference, the major regulations relating to whaling in the North Pacific are summarised in Table 1. This created an obvious conflict with the requirements for increasing catches and production. Accordingly, the reports submitted to the Bureau of International Whaling Statistics (BIWS) from each Soviet whaling fleet were sanitised, with almost all illegally caught whales removed or (in some cases) replaced by falsified numbers for legal species (Ivashchenko *et al.*, 2011). Following the revelation of this illegal whaling by Yablokov (1994), an effort was made by former Soviet whale biologists to correct the catch records using true data that had been kept secret for many years; this has now been largely accomplished for Soviet whaling operations in the Southern Hemisphere[7], but large gaps in the true catch record have remained for the North Pacific.

A complete and accurate catch series is a prerequisite for the IWC's Comprehensive Assessment process which attempts to estimate a whale population's current status relative to its pre-exploitation level (IWC, 1989). Here, using recently discovered, formerly secret reports and other materials from the Soviet whaling industry, a revised catch series for Soviet whaling in the North Pacific Ocean is provided.

METHODS AND MATERIALS

The different Soviet whaling fleets and land stations, together with the periods of time in which they were active, are shown in Table 2. At various times, five factory fleets were operational, as well as five land stations located on four islands in the Kurils.

Catch figures as officially reported by the USSR to BIWS were taken from the IWC's catch database*.

The corrected catch totals given in this paper are based upon various Russian-language sources, consisting of published Soviet literature about catches prior to 1948 and reports from Soviet whaling operations summarised in Table 2. The latter are formerly secret reports and represent the primary source of information. They include:

(1) scientific reports summarising catches by area and time, as well as measurement and biological data, and assessments of the status of species and stocks;

(2) whaling production reports, which summarise the types and quantities of products derived from the caught whales; and

(3) reports from the Soviet government's official whaling inspectors who were present aboard factory ships.

These materials were previously unpublished and largely unavailable until their declassification. They were recently discovered during searches of public archives in Russia (see Ivashchenko *et al.*, 2011 for further details).

However, the range of available reports is not entirely complete, with some types of report missing for specific years and whaling fleets; a list of source material is given in Table 3. Furthermore, the information contained in the reports is not always consistently presented. Some reports have considerable detail on catches (including individual positions and dates), while others give only a gross summary

Table 2

List of all whaling fleets and land stations operated by the Soviet Union in the North Pacific. The number of catchers in operation varied.

Fleet/station name	Years of operation	Areas of operation	No. of catchers
Aleut	1933–67	North Pacific	3–8
Kuril land stations	1948–64	Kuril Islands and areas around (~200 miles)	12–15
Slava	1966–69	North Pacific	10–15
Sovetskaya Rossiya	1962–65, 1973, 1978–79	North Pacific	15–25
Vladivostok	1963–78	North Pacific	10–13
Dalniy Vostok	1963–79	North Pacific	10–13

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[7] In the Southern Hemisphere (primarily the Antarctic), the USSR killed 338,336 whales, of which only 185,778 were reported (Ivashchenko et al., 2011).

*IWC summary catch database, version: October 2010. [Available from: C. Allison, IWC, Cambridge, UK].

Table 3

List of available reports for the Soviet whaling fleets that worked in the North Pacific. Shaded cells represent years when true catch data are not available and the data reported to the International Whaling Commission are considered incomplete.

	Aleut	Kuril Islands	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*
1948			x	x	x	xx
1949			x	x	x	xx
1950			x	x	x	xx
1951			x	x	x	xx
1952	W		x	x	x	xx
1953	W		x	x	x	xx
1954			x	x	x	xx
1955			x	x	x	xx
1956			x	x	x	xx
1957			x	x	x	xx
1958			x	x	x	xx
1959	P	W	x	x	x	xx
1960		W	x	x	x	xx
1961		W	x	x	x	xx
1962	P		S,W	W[1]	x	xx
1963[2]	W		S,W	W	W,F	xx
1964	L		S	S	S	xx
1965[3]		x	S	W,P	W,F	xx
1966[2]		x	W	W	W	
1967		x	xx	S	S,I	
1968	x	x	xx	W,I	S	S
1969	x	x	xx	W	S	S
1970	x	x	xx	S	S	x
1971	x	x	xx	S	S	x
1972	x	x	xx	S	S	x
1973	x	x		S	S	x
1974	x	x	xx	S	S	x
1975	x	x	xx	S	S	x
1976	x	x	xx	S	S	x
1977	x	x	xx	S	S	x
1978	x	x	x	S	S	x
1979	x	x	x	x	S	x

Key: S = scientific report; W = whaling production report; I = inspector's report; P = production reports; L = length measurement journals; F = financial and statistical reports; x = fleet did not exist; xx = fleet not operating in the North Pacific.

Footnotes: [1]Officially the factory ship *Vladivostok* began to work in 1963, but there is a whaling production report for 1962 because in that year some of this fleet's catchers were assigned to the Kuril Islands land stations, *Aleut* or *Sovetskaya Rossiya*; as a result, the takes for these catchers were sometimes double-counted and are not included in the calculated totals. [2]True catch figures for some years for the whaling fleets *Vladivostok* and *Dalniy Vostok* were provided to one of the authors (RLB) by A.A. Berzin, but actual reports were not found to confirm Berzin's data. [3]For 1965, one summary table is available combining into a single figure the total catches for two fleets, *Vladivostok* and *Dalniy Vostok,* but no other details are given (Ivashchenko *et al*., 2007).

of sighted or killed whales during one- or two-month periods and/or over large geographic areas, with no vessel tracks shown. In other words, possession of a particular report does not necessarily mean that there is detailed information about catches for that fleet and whaling season. However, for the purpose of tallying total catches from the North Pacific, the available information is usually sufficient, with the exceptions noted below.

In a few cases, information in whaling production reports directly contradicts catch data given in other types of report for the same whaling fleet and year. This was not the case for the whaling production and scientific reports for the whaling fleet *Sovetskaya Rossiya*, all of which provide the same catch numbers for all whale species. However, a different situation exists for the two Soviet whaling fleets *Vladivostok* and *Dalniy Vostok*, for which the reported catch numbers are sometimes significantly different between the two report types. The difference is especially notable in those years with large catches of right or bowhead whales, where these takes have usually been replaced with names of other species (fin, sei and even humpback whales, the latter being also illegal to take from 1966 on). This appears to have been an attempt to hide catches of protected species in the production reports. This is strange in view of the fact that all such reports were secret. In some cases, there is disagreement not only in the reported numbers but also in the species taken. For example, for the 1967 whaling season the reports from the whaling fleet *Dalniy Vostok* (Anon, 1967; Latishev *et al.*, 1968; Raskatov and Latishev, 1967) describe very different catch results. In the whaling production report the total catch for the year is given as 135 fin, 294 sei, 267 humpback and 4,089 sperm whales (total = 4,785). In contrast, in the scientific and inspectors reports the final numbers are 120 fin whales, 145 sei, 36 humpback,

Table 4

Soviet catches during the period 1932–47 by the *Aleut* whaling fleet, by year and species.

Year/ species	Blue whale	Fin whale	Humpback whale	Sei whale	Gray whale	Right whale	Minke whale	Sperm whale	Killer whale/Baird's beaked whale
1932	–	5	–	3	–	–	–	–	–
1933	5	109	26	–	2	–	–	57	–
1934	2	150	51	1	54	–	1	74	0/6
1935	1	208	143	–	34	1	–	94	3/0
1936	5	210	68	–	102	–	1	113	2/1
1937	0	146	59	1	11	1	0	198	0/0
1938	0	104	43	0	54	0	0	64	0/2
1939	0	238	43	0	29	2	4	156	5/1
1940	2	161	33	0	47	0	0	213	2/2
1941	9	244	7	11	57	0	2	194	4/5
1942	2	203	12	0	101	0	3	215	11/7
1943	0	132	29	0	99	0	0	216	1/1
1944	0	141	0	21	0	3	0	50	0/0
1945	1	131	1	0	30	1	0	206	3/0
1946	2	117	10	0	22	1	0	326	12/6
1947	0	129	10	0	1	0	0	470	0/0
Total	29	2,428	535	40	643	9	11	2,658	43/32

4,495 sperm, 43 blue, 132 right, 124 gray, 1 killer whale (*Orcinus orca*) and 1 Baird's beaked whale (*Berardius bairdii*) (total = 5,097); note that the five latter species are not mentioned at all in the production report.

In other years, simple differences in catch results always involve a lower number of blue and sperm whales (sometimes including other species too) in the whaling production reports. For example, for the 1966 season of the *Dalniy Vostok* fleet, the whaling production report and scientific report give 5 vs. 45 blue and 5,265 vs. 5,752 sperm whales, respectively. Similar figures for the 1967 season of the *Vladivostok* fleet are 1 vs. 51 blue and 3,679 vs. 4,861 sperm whales.

No explanation is given for such differences; it is possible that the numbers in the production reports were an attempt to keep the same average size/weight proportions for sperm whales as those used to calculate the target plan in the first place[8]. There is no obvious explanation for the difference in the number of blue whales killed.

Overall, from discussions with individuals who were present at the time, and familiar with fleet operations[9], it was clear that the true catch figures are those in either the scientific or inspection reports, and accordingly those data have been used in any cases of conflict with figures given in production reports. However, for those years when only whaling production reports are available (see Table 3), the figures given there have been used.

As no true catch data are available for several fleets/years in which sperm whales were the primary target, it has been necessary to apply a correction factor in order to estimate the true catch of this species. The correction factor was based upon known differences between the officially reported and actual catches for years and fleets for which complete data were available; specific details of these calculations are given below in the section on sperm whales. For all other species there does not appear to be any need to apply correction factors.

We have not accounted here for lost whales, which would include animals that were struck but escaped, lost during towing, killed and flagged but not subsequently recovered or whales used as fenders and not processed. No details regarding lost whales were found in the reports; however, former whalers indicated that the number of lost whales was very small, as it was critical to bring as many whales as possible to the factory ship to meet production quotas.

RESULTS AND DISCUSSION

The analysis presented here deals largely with Soviet catches (both legal and illegal) from 1948 to 1979; however, previously published catches of the *Aleut* whaling fleet from 1932 to 1947 are given for reference in Table 4. During the period 1948–79, a minimum of 190,183 whales were killed by the USSR in the North Pacific (Table 5). The USSR

Table 5

Total catches of whales in the North Pacific by the USSR, 1948–79, by species.

Species	Actual catch	Reported catch	Difference
Blue whale	1,621	858	+763 (189%)
Fin whale	14,167	15,445	–1,278 (92%)
Humpback whale	7,334	4,680	+2,654 (157%)
Sperm whale	153,686*	132,505	+21,181 (116%)
Sei whale	7,698	11,363	–3,665 (68%)
Gray whale	149	1	+148 (-)
North Pacific right whale	681	11	+670 (6,191%)
Bowhead whale	145	0	+145 (-)
Baird's beaked whale	146	148	–2 (99%)
Killer whale	401	401	0 (100%)
Bryde's whale	3,466	3,517	–51 (99%)
Minke whale	689	686	+3 (101%)
Total	190,183*	169,615	+20,568 (112%)

*If an estimate is added for catches in years for which no data exist (see details in the sperm whale section), the total sperm whale catch is estimated at 159,286, and the overall total for Soviet catches in the North Pacific would be 195,783 whales.

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[8] In the Soviet planning system, catches were translated into raw output weight based upon the average data from previous seasons for different species (using a table that converted length to weight). In all production reports, discussion regarding the achievement of production targets notes that the average weight of sperm whales taken reflects a high proportion of under-sized (illegal) animals.

[9] Details of the interviewees, and an overview of Soviet illegal whaling operations in general, are given in Ivashchenko et al. (2011).

reported 169,638 whales to the IWC and many of these reports involved falsifications of species, sex and length; consequently, it is not correct to state that 169,638 (or 89%) of the 190,183 killed whales were accurately reported.

As detailed below, the average differences between actual and reported catch figures for sperm whales were used to estimate catch totals in those years for which reports are not available; this correction would bring the total catch for all species to 195,783. Thus, the nominal difference between reported and actual catches was 20,568 whales (or 26,168 including the sperm whale estimate); but as noted above this difference is not strictly meaningful because of other falsifications in the official reports.

The difference between actual and reported catches is much lower than in the Antarctic, in part because the intensive period of whaling in the North Pacific was shorter, with fewer fleets and resources involved. Revised catch totals are given in Table 6 (blue whales), Table 7 (fin whales), Table 8 (humpback whales), Table 9 (sei whales) and Table 10 (sperm whales). Further details are given, by species, below.

Some gaps and uncertainties remain in the North Pacific catch record. As noted above, true catch data are missing for some years (1963 for *Dalniy Vostok*; 1969 for *Vladivostok;* and 1966/67 for *Slava*). The effect of these omissions on catch figures is likely to be only minor for all species except sperm whales, which are known to have been the primary target of whaling operations during the years concerned. Further details are given below.

Overall, unless additional data are recovered the figures reported here probably represent the best assessment of the total Soviet catch for the period 1948 to 1979, with the caveat that the numbers given for sperm whales are likely to be underestimates of the true catches (see below).

Most species of whales from the North Pacific were misreported to some degree, but right, bowhead and sperm whales were the main species for which catch data were falsified. Of these, the first two species were officially completely protected, while for sperm whales a large part of the Soviet catch consisted of undersized females. None of the right and bowhead whale catches were reported; instead, fictional fin, humpback and sei whale takes were created in the catch reports to cover up the products from these whales. Reported catches of sperm whales represented only a part of the true total for this species; additionally, the true sex ratio of the catch was significantly altered. For example, the scientific report for the 1975 season (Ivashchenko *et al.*, 2007) notes that in the two years (1970/71) before the IWC's International Observer Scheme was implemented, the true Soviet sperm whale catches were 9,011 females and 5,725 males; however, the catch was reported to BIWS as 1,789 females and 12,290 males.

Table 6

Soviet catches of blue whales in the North Pacific, 1948–78. Numbers in parentheses are the officially reported catches. Shaded cells represent years for which true catch data (from either scientific reports or whaling inspectors' reports) are not available; in these cases, the data reported to the International Whaling Commission have been used even though these are considered incomplete.

	Aleut	Kuril Islands	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*	Total (reported)
1948	3	0					3 (3)
1949	3	0					3 (3)
1950	5	2					7 (7)
1951	7	9					16 (16)
1952	7	17					24 (24)
1953	11	10					21 (21)
1954	12	23					35 (35)
1955	4	27					31 (31)
1956	7	45					52 (52)
1957	9	44					53 (53)
1958	0	14					14 (14)
1959	22	19					41 (41)
1960	0	14					14 (14)
1961	2	15					17 (17)
1962	19	11	37				67 (30)
1963	14	1	108	299	88		510 (348)
1964	17	0	79	25	67		188 (77)
1965	10		43	163			216 (72)
1966	0			15	45	0	60 (0)
1967	0			51	43	0	94 (0)
1968				3	28	25	56 (0)
1969				2	15	33	73 (0)
1970				7	12		19 (0)
1971				4	3		7 (0)
1972				0	0		0 (0)
1973			0	0	0		0 (0)
1974				0	0		0 (0)
1975				0	0		0 (0)
1976				0	0		0 (0)
1977				0	0		0 (0)
1978			0	0	0		0 (0)
Total	**152**	**251**	**267**	**592**	**301**	**58**	**1,621 (878)**

Table 7

Soviet catches of fin whales in the North Pacific, 1948–79. Numbers in parentheses are the officially reported catches. Shaded cells represent years for which true catch data (from either scientific reports or whaling inspectors' reports) are not available; in these cases, the data reported to the International Whaling Commission have been used even though these are considered incomplete.

	Aleut	Kuril Islands	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*	Total (reported)
1948	229	26					255 (255)
1949	64	53					117 (117)
1950	92	106					198 (198)
1951	90	157					247 (247)
1952	234	241					475 (475)
1953	145	179					324 (324)
1954	238	266					504 (504)
1955	79	219					298 (298)
1956	65	241					306 (306)
1957	81	173					254 (254)
1958	39	328					367 (367)
1959	132	223					355 (355)
1960	128	265					393 (393)
1961	83	156					239 (239)
1962	437	77	65				579 (514)
1963	140	90	512	795	432		1,969 (1,150)
1964	62	76	417	1,200	1,168		2,923 (2,576)
1965	128		318	642			1,088 (1,492)
1966	196			273	110	154	733 (1,347)
1967	439			82	120	177	818 (1,188)
1968				182	297	80	559 (1,064)
1969				258	48	113	419 (593)
1970				17	103		120 (412)
1971				12	14		26 (187)
1972				29	228		257 (250)
1973			1	0	137		138 (138)
1974				16	157		173 (173)
1975				0	33		33 (33)
1976				0	0		0 (0)
1977				0	0		0 (0)
1978				0	0		0 (0)
1979			0		0		0 (0)
Total	**3,101**	**2,876**	**1,313**	**3,506**	**2,847**	**524**	**14,167 (15,445)**

THE *ALEUT* FLEET AND KURIL ISLANDS

Some uncertainties remain with regard to catches by the Kuril Islands land stations and the *Aleut* fleet, and there is little information with which to assess the validity of the catch data reported by these operations to BIWS. A total of five land stations situated on four of the Kuril Islands were operating for different periods of time. Islands and station names were as follows: Iturup Island – *Kasatka* and *Yasniy*; Simushir Island – *Skalistiy*; Shikotan Island – *Ostrovnoy;* and Paramushir Island – *Podgorniy.*

No scientific reports are available for these stations, or from *Aleut*. However, a few whaling production reports have the same numbers as those in the IWC database, except for one journal from *Aleut* which gives whale length measurements for 1964 (Anon, 1964) (see below).

There is little reason to believe that significant falsifications of the catch were made at the Kuril land stations, since they were operating at a time when whales were locally abundant and catches of all locally occurring species except right and gray whales were legal. An individual who worked at one of these stations in 1955 related that whalers sometimes increased the reported length of undersized sperm whales to equal or exceed the legal size, or reported a few small animals as one large whale (G. Derviz, pers. comm., October 2008); it is not clear how frequent these falsifications were, but they do not seem to have been extensive. It has therefore been assumed that the reported catches for the Kuril land stations are largely accurate and that they omitted only a small number of right whales taken during their years of operation (Anon, 1960; 1961); there was also a catch of ten right whales taken for research purposes in 1955, but these were reported (Klumov, 1962).

A similar situation existed for the *Aleut* whaling fleet in at least its early years. *Aleut* had more flexibility than the land stations in terms of whaling areas and species taken, but also possessed a relatively low capacity due to the small number of old-type catchers in its fleet and this small factory ship's inability to process large numbers of whales (A.P. Avtukhov, pers. comm., May 2010). Our assumption, based upon the general agreement between production reports and the numbers reported to BIWS, is that *Aleut*'s catches were falsified or under-reported before 1959 only for protected species (such as right and perhaps gray whales), and involved only small numbers of animals. The situation for the later years of operation (1960–67) is somewhat more complicated.

A brief review of *Aleut*'s history is helpful here. Up until 1959, *Aleut* did not have the capability to travel far from land because of logistical issues relating to (among other things) the availability of fresh water on board; consequently, the factory ship remained close to land off Kamchatka,

Table 8

Soviet catches of humpback whales in the North Pacific, 1948–79. Numbers in parentheses are the officially reported catches. Shaded cells represent years for which true catch data (from either scientific reports or whaling inspectors' reports) are not available; in these cases, the data reported to the International Whaling Commission have been used even though these are considered incomplete.

	Aleut	Kuril Islands	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*	Total (reported)
1948	8	5					13 (13)
1949	0	7					7 (7)
1950	4	18					22 (22)
1951	1	8					9 (9)
1952	17	9					26 (26)
1953	11	6					17 (17)
1954	21	8					29 (29)
1955	8	23					31 (31)
1956	31	10					41 (41)
1957	50	2					52 (52)
1958	10	4					14 (14)
1959	74	5					79 (79)
1960	57	3					60 (60)
1961	335	19					354 (354)
1962	1,213	2	608				1,823 (1,215)
1963	772	5	505	1,122	226		2,630 (2,247)
1964	168	0	144	660	437		1,409 (242)
1965	82		148	240			470 (243)
1966	0			70	7	0	77 (0)
1967	0			70	36	0	106 (0)
1968				5	24	17	46 (0)
1969				0	1	4	5 (0)
1970				0	13		13 (0)
1971				1	0		1 (0)
1972				0	0		0 (0)
1973				0	0		0 (0)
1974				0	0		0 (0)
1975				0	0		0 (0)
1976				0	0		0 (0)
1977				0	0		0 (0)
1978			0	0	0		0 (0)
1979			0	0	0		0 (0)
Total	**2,862**	**134**	**1,405**	**2,168**	**744**	**21**	**7,334 (4,680)**

Chukotka, the Commander Islands or the Kurils. A refit in 1959 (including installation of a modernised fresh water supply system) allowed the fleet to cover new whaling areas farther from land and increase the catch of sperm whales (and other species) by moving farther east in the North Pacific. Productivity was enhanced in 1961 by the temporary addition to the *Aleut* fleet of new catcher vessels which had been built to service the not-yet-completed new factory ship *Sovetskaya Rossiya*.[10] Accordingly, from 1960 to 1962, *Aleut*'s catches of sperm, fin and humpback whales increased; since all three species were at the time legally catchable, there would have been no reason to falsify reports to BIWS.

In 1962, using catchers from another new factory fleet, the *Vladivostok*, *Aleut* took 1,200 humpback whales. High catches of humpback and sperm whales followed in 1963 (this time with help from catchers built for the new *Dalniy Vostok*), but by 1964 whale abundance in the eastern North Pacific had dropped and there was increased competition from not only the large new Soviet factory fleets, but also from Japan. As a result, the smaller, slower *Aleut* had to seek out other areas, and in order to meet its production quotas during this time *Aleut* began to take more sperm whales and probably an increased proportion of females and undersized animals.

Although it is likely that some under-reporting began around 1964 (only one report gives some details), the level of falsification for sperm whale catch numbers by the *Aleut* fleet is considered low. One journal reported data on whale length measurements from the 1964 season, and provided numbers that for some but not all species are higher than those officially reported: blue whales 17 vs. 8 reported; fin 57 vs. 90; humpback 168 vs. 35; sei 66 vs. 86; and sperm whales 1,662 vs. 1,369. In the report of whale length measurements, 441 of the 1,662 sperm whales are listed as female. While it is known that only 168 of the 441 females were reported to the IWC, there is no way of assessing the overall composition of the 293 under-reported whales (i.e. whether they were lactating females, calves, or under-sized animals of either sex). It is likely that some under-reporting occurred in the *Aleut's* final few years of operation (1964–67) due to the rising competition and other factors mentioned above. Except for the one journal, there is no information to assess the extent of under- and mis-reporting. However, in reality the limitations of this old fleet would likely not allow catches much larger than those officially reported to BIWS; our best guess is that the difference in catch numbers lies in the low hundreds. Consequently, for the catches summarised

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[10] Typically, catchers would be built before a new factory ship was completed. The larger floating factories such as Sovetskaya Rossiya had up to 25 catchers each, and some of these could be put into operation as they were produced.

Table 9

Soviet catches of sei whales in the North Pacific, 1948–79. Numbers in parentheses are the officially reported catches. Shaded cells represent years for which true catch data (from either scientific reports or whaling inspectors' reports) are not available; in these cases, the data reported to the International Whaling Commission have been used even though these are considered incomplete.

	Aleut	Kuril Islands	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*	Total (reported)
1948	3	36					39 (39)
1949	21	60					81 (81)
1950	7	51					58 (58)
1951	16	52					68 (68)
1952	13	188					201 (201)
1953	26	86					112 (112)
1954	22	126					148 (148)
1955	28	128					156 (156)
1956	16	171					187 (187)
1957	36	108					144 (144)
1958	19	336					355 (355)
1959	93	131					224 (224)
1960	59	140					199 (199)
1961	57	52					109 (109)
1962	303	79	92				474 (382)
1963	47	16	112	168	256		599 (530)
1964	66	35	288	144	121		654 (630)
1965	86		203	417			706 (695)
1966	268			177	78	306	829 (1,545)
1967	379			115	145	347	986 (1,994)
1968				37	154	119	310 (1,105)
1969				409	88	220	717 (1,091)
1970				46	47		93 (782)
1971				23	10		33 (299)
1972				23	32		55 (71)
1973			7	0	88		95 (95)
1974				3	39		42 (42)
1975				0	24		24 (24)
1976				0	0		0 (0)
1977				0	0		0 (0)
1978			0	0	0		0 (0)
1979			0		0		0 (0)
Total	**1,565**	**1,795**	**702**	**1,562**	**1,082**	**992**	**7,698 (11,363)**

here, officially reported data from the *Aleut* fleet were used on the assumption that if there were unreported takes, these would be too low to significantly increase the total. In addition, it has been assumed that there was no falsification of the sex ratio in *Aleut*'s sperm whale catch; however, given the unavailability of scientific reports for this fleet for certain years, there is no way of assessing the validity of this assumption.

Catch data by species

Blue whale

Blue whale catches (Table 6) were limited, and the species was never a primary target for Soviet whalers in the North Pacific. The total catch of blue whales for the period 1948–79 was 1,621, vs. 858 reported to BIWS (= 763 under-reported). The 1,621 animals represent less than 0.9% of the total Soviet catch of 190,183 whales (see Table 5). An additional 29 blue whales were caught before 1948. Most of the blue whale catches were made in the eastern North Pacific, with high catches in just three years: 510, 188, and 216 whales for 1963–65, respectively.

Fin whale

Fin whales were one of the main target species among baleen whales but still made up a relatively small portion (a little more than 7%) of the total Soviet catches in the North Pacific (Table 7). The total catch of fin whales for 1948–79 was 14,167, vs. 15,445 reported to BIWS (= 1,278 over-reported). An additional 2,428 fin whales were caught before 1948. Fin whales were used to cover up illegal takes of blue, bowhead and right whales, resulting in the over-reporting noted here.

Humpback whale

The Humpback whale was not an important whaling species until 1961, when the Soviet whaling fleets began exploring the Aleutian Islands and then the pelagic eastern North Pacific (Table 8). Catches then increased significantly and were very high for a few years. By 1965 the stocks were already recognised as being heavily depleted and the IWC introduced complete protection for the North Pacific populations in 1966. However, Soviet catches continued, further depleting what was left of the previously large populations in the GOA, BS and Aleutians areas. The total catch for 1948–79 was 7,334, vs. 4,680 reported to BIWS (= 2,654 under-reported); the 7,334 whales represent 3.9% of the total Soviet catch. An additional 535 humpback whales were caught before 1948. Falsification of the catches began even before the species was under protection and it is not clear why this early falsification occurred. One possible explanation is that a sharp increase in the catch numbers may have resulted in criticism by other IWC members. The result of these catches was that by 1970 humpback whales were relatively scarce in most areas of the North Pacific.

For the 1963 season there is considerable variation regarding total humpback whale catches for the *Dalniy Vostok* whaling fleet. Three different sources give three different numbers: 323 were officially reported to the IWC; Doroshenko (2000) lists 226 as the total humpback catch for the *Dalniy Vostok* fleet; finally, a *Dalniy Vostok* whaling production report (Anon, 1963b) gives a figure of 546. The IWC data are known to be incorrect and are not considered further here; however, that leaves a choice between 226 and 546 whales.

It is known that the factory ship *Dalniy Vostok* left her home port in Vladivostok only in the middle of June and prior to that time her catchers worked with the factory fleets *Sovetskaya Rossiya*, *Vladivostok* and *Aleut*, as well as with the Kuril Islands land stations. For the production report one can assume that 320 humpback whales were killed by the catchers assigned to *Dalniy Vostok*, but processed elsewhere before the factory ship of this fleet left port. The production report still counts these whales as hunted by the fleet, while the scientific report would have counted only those whales that were processed on the decks of the factory ship to which the catchers were actually assigned (in this case, *Dalniy Vostok* from the end of June through November). Whaling production reports from other fleets give the number of humpback whales caught by the *Dalniy Vostok* catchers as 75 for the *Sovetskaya Rossiya* fleet and 161 for *Aleut* and *Vladivostok* (Anon, 1963a; 1963b). However, adding up all these numbers (including the scientific report catches) gives a total that is still 84 animals short of the production report's figure of 546 whales.

Another reason for listing a larger number of humpback whales could be to cover up the production from illegal catches of right whales that year. Since it is not possible to determine the origin of the humpback whale catch figure in the whaling production report, this number was not used in the calculation of the total North Pacific catch. In the catch tables for the 1963 season for the other fleets, catches from the scientific reports were used; to be consistent with that, the final number of the *Dalniy Vostok* catches of humpback whales in 1963 was taken as 226.

Sei whale

A secondary choice for Soviet whalers, sei whales were nevertheless subject to high catches in some years. In addition, 'fake' sei whale catches were reported to cover up illegal takes of other species. The total catch for 1948–79 was 7,698 vs. 11,363 reported to the IWC (= 3,665 over-reported) (Table 9). Only 40 sei whales were caught before 1948. Since there are a few years for which scientific reports are not available, and when the reported sei whale catches were relatively high (1966, 1967 and 1969), it is possible that these numbers were over-reported. However, without the true data it is not possible to assess the level of falsification and the total catch number given here (7,698) is probably higher than the actual catch for this species. It is also impossible to assess whether any of the sei whales taken in lower latitudes were actually Bryde's whale (*Balaenoptera edeni*). The combination of high Soviet takes and extensive Japanese pelagic catches caused serious depletion of sei whale populations in the North Pacific.

Right and bowhead whales

The Soviet right and bowhead whale catches are not discussed in depth here; however, many new details are now available on numbers, distribution and composition of catches and these are described in Ivashchenko and Clapham (2012). The total estimated Soviet catch of right whales in the North Pacific is 681[11], of which only 11 were officially reported (ten taken off the Kurils under a permit for scientific research, and one reported as a 'mistake' in the eastern North Pacific in 1964; see Brownell *et al.*, 2001). Of 681 animals, 529 were killed in the eastern North Pacific (the Gulf of Alaska and the south-eastern Bering Sea).

Overall, the catches of right whales occurred over a period of a few years. In 1958–61 the *Aleut* fleet and Kuril land stations were taking 1–2 animals a year (for a total of 10 whales); however, beginning in 1962 the catches quickly increased. In 1962, 23 right whales were killed (with 21 taken by *Sovetskaya Rossiya*); in 1963 the catch was 275 whales (112 taken by *Sovetskaya Rossiya* and the remainder by *Vladivostok* and *Dalniy Vostok*); in 1964 the catch was 200 whales (22 by *Sovetskaya Rossiya*, 178 by *Vladivostok* and *Dalniy Vostok*). In 1965 and 1966 the total catches for all fleets decreased to 20 and 3 right whales, respectively. However, in 1967 whalers of the *Dalniy Vostok* fleet found an aggregation of right whales in the Okhotsk Sea and a total of 134 whales were killed that year (126 in the Okhotsk Sea and 8 others in different parts of the North Pacific by *Dalniy Vostok* and *Vladivostok*). Possibly a few of the right whales were taken in 1968 in the Okhotsk Sea by *Vladivostok*, with the last known right whales killed in 1971 around the Kuril Islands. The majority of animals taken in 1963/64 were large, mature whales occurring over an extensive area of the Gulf of Alaska in deep offshore waters, with the overall distribution similar to that of 19th century American whaling catches plotted by Townsend (1935) (Ivashchenko and Clapham, 2012). In the western North Pacific, catches of 152 right whales were distributed around the Kuril Islands (on both sides) and along the eastern coast of Sakhalin Island. The latter involved 132 right whales killed in the Okhotsk Sea in 1967/68.

The total catch of bowhead whales in the North Pacific was at least 145, all of them taken in the Okhotsk Sea (primarily in the Shantar Archipelago and Shelikov Bay) in 1967; at least 18 of these whales were killed by the *Aleut* fleet. An additional 127 bowheads were killed by the *Vladivostok* fleet in 1968 (Ivashchenko and Clapham, 2012). None of these catches were reported.

Gray whale

The total catch of gray whales during 1948–79 was 149 animals, of which only 1 was reported. An additional 643 gray whales were killed before 1948. In 1967, 124 of the 149 gray whales were killed by Soviet catchers in the Bering Sea (Doroshenko, 2000).

A scientific and scout vessel named *Druzhniy* (which was also a catcher) and another Soviet catcher (of the type used from the Kuril Islands land stations [A.A. Berzin,

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[11] This total includes all known catches of right whales and an additional 10 whales taken in the period 1958–62 by the Aleut whaling fleet or by Kuril land stations; these latter animals are listed in the whaling production reports as 'other' or 'dau hval' (which means 'dead whale' in Norwegian). Given that all other species were listed and identified separately in the reports concerned, we inferred that these 10 animals represented illegal takes of right whales.

Table 10

Soviet catches of sperm whales in the North Pacific, 1948–79. The last column is an estimate of the actual catch for years in which true data are not available (see text). Numbers in parentheses are the officially reported catches. Shaded cells represent years for which true catch data (from either scientific reports or whaling inspectors' reports) are not available; in these cases, the data reported to the International Whaling Commission have been used even though these are considered incomplete.

	Aleut	Kuril Islands	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*	Total (reported)	Correction
1948	574	390					964 (964)	
1949	774	986					1,760 (1,760)	
1950	588	1,469					2,057 (2,057)	
1951	765	1,474					2,239 (2,239)	
1952	731	1,641					2,372 (2,372)	
1953	865	1,521					2,386 (2,386)	
1954	816	1,192					2,008 (2,008)	
1955	996	1,494					2,490 (2,490)	
1956	998	1,693					2,691 (2,691)	
1957	1,174	1,821					2,995 (2,995)	
1958	1,430	2,185					3,615 (3,615)	
1959	1,560	1,878					3,438 (3,438)	
1960	2,228	1,487					3,715 (3,715)	
1961	1,917	1,401					3,318 (3,318)	
1962	1,011	1,347	677				3,035 (3,304)	
1963	1,093	659	693	1,898	2,298		6,641 (5,783)	800
1964	1,662	452	1,133	2,135	2,171		7,553 (5,886)	
1965	1,572	0	1,452	0	9,932		12,956 (8,196)	
1966	1,522	0	0	6,391	5,752	1,540	15,205 (9,477)	1,600
1967	432	0	0	4,861	4,495	2,620	12,408 (9,431)	1,600
1968			0	1,548	4,853	5,139	11,540 (9,542)	
1969				3,152	2,933	5,016	11,101 (8,211)	1,600
1970				4,113	4,982		9,095 (8,585)	
1971				2,715	2,926		5,641 (5,525)	
1972				854	788		1,642 (1,736)	
1973			501	23	1,544		2,068 (2,068)	
1974				2,265	1,700		3,965 (3,965)	
1975				2,056	1,683		3,739 (3,748)	
1976				2,076	1,595		3,671 (3,671)	
1977				1,991	1,275		3,266 (3,266)	
1978			325	871	968		2,164 (2,164)	
1979			748	0	1,200		1,948 (1,948)	
Total	**22,708**	**23,090**	**5,529**	**36,949**	**51,095**	**14,315**	**153,686* (132,505)**	**5,600**

*This number represents a minimum catch for sperm whales; if a correction factor is added, the total removal will be 159,286 whales.

pers. comm., 28 November 1993 to RLB]) were observed and photographed about 75 miles out (64˚00'N, 168˚40'W) by an aircraft en route from Savoonga, St. Lawrence Island to Nome, Alaska on 27 June 1967 with a few gray whales in the vicinity (James G. Mills, pers. comm. 6 December 1967 to RLB; and see Mills' photo of the *Druzhniy* in Berzin, 2008, Plate 29). The harpoon line from the *Druzhniy* was out, but there was no sign of a whale at the end of it. Furthermore, Mills reported that his pilot observed three smaller vessels and one larger one in the distance. These vessels were reported to the Northeast Cape Air Force Station on St. Lawrence Island. A US Air Force aircraft flew over the area and identified a Soviet factory ship with whale carcasses on deck, but they could not identify them to species. Based on records submitted to the IWC by the Soviets, the closest Soviet factory ship was supposedly almost 800 miles away at the time. However, in light of the observations by Mills and the US aircraft, it is possible that gray whales were killed in this location and the official report of the factory ship's location 800 miles away was false.[12]

In addition to the above commercial catches of gray whales, 4,166 aboriginal catches were made between 1948 and 1979 (Yablokov and Bogoslovskaya, 1984). Between 1948 and 1957, these catches averaged 42 whales annually, but from 1958 to 1979 the average annual take was 170. This suggests a change in catching methods; starting in 1969, the whale catcher *Zvezdny* was used to take gray whales for the Chukotka natives because most local hunting with small boats had ceased (Ivashin and Mineev, 1981).

Sperm whale

Sperm whales were the primary target of Soviet whaling operations in the North Pacific. Here, two catch totals are given (Table 10); a minimum known and a second figure that includes a correction factor for unknown takes (explained further below). The total catch for the period 1948–79 was 153,686 (minimum) or 159,286 (estimated), vs. 132,505 reported to BIWS (= 21,181 or 26,781 under-reported). An additional 2,658 sperm whales were caught before 1948. The catches of sperm whales increased substantially with the introduction of new whaling fleets into the area and from 1966 made up 80–85% of the total Soviet catch of all species. As a result, a large part of the total number of sperm whales after 1962 was taken in the central and eastern North

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[12] Although this incident suggests that factory ship positions were sometimes falsified, overall the noon positions of factory ships reported to the IWC are consistent with locations given in the Soviet scientific and production reports that were available to us for this study.

Pacific. Starting in 1966, the catch consisted of a large number of females, and falsified data were submitted regarding both numbers and sex ratio. In 1966 the *Dalniy Vostok* fleet reported taking 3,327 sperm whales, including 153 females; in reality the catch was 5,752 sperm whales, of which 3,660 were females. In the same year, the *Vladivostok* fleet reported 3,088 sperm whales, but actually caught 6,391, including 4,679 females.

This type of under-reporting of totals, and mis-reporting of sex ratio, continued until 1972. In creating the impression that males were under heavy pressure, these falsified data prompted the IWC to change the minimum legal length for sperm whales in June 1972 (down to 30 feet) in order to encourage the taking of more females (IWC, 1974). Tragically, this exacerbated an already dire situation for females, which (unknown to the IWC) were already under extreme whaling pressure from the Soviets as well as from Japanese operations, which also falsified sex ratio data (Berzin, 2008; Kasuya, 1999).

The submitted data on sex and length of sperm whales were falsified by changing a few small females or juveniles into a single adult male for the resulting report. Given that the USSR is believed to have usually accurately reported the noon positions of their factory ships, it is somewhat surprising that no one ever questioned how so many males could have been taken when the fleets were spending much of their time in lower latitudes.

No true catch data are currently available for the following: 1963 for *Dalniy Vostok*; 1969 for *Vladivostok*; and 1966/67 for *Slava*. For years with known true and falsified data the average difference between them was 1,600 sperm whales (range: 454–3,303). Accordingly, to estimate the catches for the unknown years, 1,600 whales were added to the reported total for the years 1966/67 (*Slava*) and 1969 (*Vladivostok*). However, half of this number (800) was rather arbitrarily used for *Dalniy Vostok* in 1963 because it was the first season for this fleet and the factory ship left its home port later in the season, presumably resulting in a lower catch than in subsequent years. These correction factors are certainly not ideal, but they represent the simplest solution to the problem given the available data; the true differences for the missing years are unlikely to be much greater or smaller than our crude estimate.

Given these assumptions, the total estimate of under-reported sperm whales for the seasons and fleets in question is 5,600 animals. This puts the corrected total Soviet catch of sperm whales in the North Pacific during 1948–79 at 159,286 whales.

Brownell *et al.* (2000) analysed the true data on sperm whale catches available at that time, and concluded that until 1973 some Soviet whaling fleets were taking 1.8 times more sperm whales than reported. This correction factor was derived from true catch data that were then available from two factory fleets, *Dalniy Vostok* and *Vladivostok*; the factor was then applied to three other factory fleets for which true data were unavailable. However, there are two problems with this estimate. Firstly, in tables 3, 4 and 5 of Brownell *et al.* (2000) the 'true' catch of sperm whales is reported incorrectly; specifically, for some years the number of females is added to the total catch (which already included the females), resulting in almost double the number of whales used in the calculations. Secondly, the difference between true and reported sperm whale catch totals for *Dalniy Vostok* and *Vladivostok* was greater than for at least two of the three other factory fleets, so any correction factor derived from these two fleets would overestimate the true catch for the other three. Consequently, the Brownell *et al.* (2000) estimate of about 180,000 sperm whales taken by Soviet fleets in the North Pacific is excessive; as noted above, we estimate the true total catch at 159,286.

It is true that in some years the difference between reported and actual sperm whale catches was high (2,400–3,303 whales); however, it is worth noting that in the later years (1969–72) the difference between the reported and actual total catches was not as significant (454–1,240 whales) but that the sex ratio of the catch was falsified to a great extent. Overall, it is difficult to apply a single correction factor to the Soviet catches due to the variable operational conditions under which the fleets were working during that period of time.

Other species: not falsified

The following four species were also occasionally taken by Soviet whalers in the North Pacific. Catch totals are given for the period 1946 to 1979 unless otherwise noted.

(1) Minke whales (*Balaenoptera acutorostrata*): this species was never an important target for Soviet whalers. A total of 86 minke whales were caught, vs. 83 reported. Only 12 minke whales were killed before 1948.

(2) Baird's beaked whales (*Berardius bairdii*): 146 caught vs. 148 reported. In some reports catches were listed as bottlenose whales. Confusion between the species (i.e. *Berardius* spp. vs. *Hyperoodon* spp.) seems to have been common until it was clarified that the range of bottlenose whales does not include the North Pacific (Tomilin, 1967).

(3) Bryde's whale (*Balaenoptera edeni*): 4,069 caught vs. 4,120 reported.

(4) Killer whale (*Orcinus orca*): 401 whales caught, all of which were reported. Before 1948 an additional 31 killer whales were taken.

CONCLUSIONS

In terms of total numbers, illegal whaling by the USSR after World War II was not as extensive in the North Pacific as in the Southern Hemisphere, where the difference between reported versus actual catches was approximately 152,558 whales. However, its consequences for some populations (e.g. North Pacific right whales and sperm whales) were potentially devastating. Furthermore, the difference between reported and actual catches was still substantial, being at least 20,568 whales (or 26,168, including a correction factor for sperm whales). The figures reported here represent the best accounting to date, and cannot be further refined unless new material becomes available. A few gaps and uncertainties remain, which means that the true catch totals are probably still somewhat underestimated. These would include further unreported catches of blue, right, bowhead and gray whales, as noted above; a lack of scientific reports for the *Aleut* whaling fleet; and a few missing years for other fleets as detailed in Table 3. Despite these issues, for the reasons given above the true catch totals are unlikely to be substantially greater than those given here.

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REFERENCES

Anon. 1960. Promisloviy otchet 2-oy Dalnevostochnoy Kitoboinoy flotili za 1960 god. [Whaling production report of the 2nd Far Eastern Whaling fleet for 1960]. Vladivostok, 208pp [In Russian] (Unpublished).

Anon. 1961. Promisloviy otchet 2-oy Dalnevostochnoy Kitoboinoy flotili za 1961 god. [Whaling production report of the 2nd Far Eastern Whaling fleet for 1961]. Vladivostok, 58pp. [In Russian] (Unpublished).

Anon. 1963a. Otchet o proizvodstvennoy deyatel'nosty kitoboynoy flotili Sovetskaya Rossiya za promisel 1963 goda. [Report of the production activities of the whaling fleet Sovetskaya Rossiya for 1963]. Upravlenie proizvodstvennikh flotiliy 'Dal'moreprodukt', Vladivostok, 121pp. [In Russian] (Unpublished)

Anon. 1963b. Promisloviy otchet flotiliy Aleut, Vladivostok, Dalniy Vostok za promisel 1963 goda. [Whaling production report of whaling fleets in Aleut, Vladivostok, Dalniy Vostok during the 1963 season]. Upravlenie proizvodstvennikh flotiliy 'Dal'moreprodukt', Vladivostok, 208pp. [In Russian] (Unpublished)

Anon. 1964. Zhurnal ucheta zamera kitov 1964g. . [Journal of length measurements of whales 1964] Upravlenie proizvodstvennikh flotiliy 'Dal'moreprodukt', Vladivostok, 64pp. [In Russian] (Unpublished).

Anon. 1967. Promisloviy otchet kitoboynoy flotilii Dalniy Vostok za promisel 1967 goda. [Whaling production report of the whaling fleet Dalniy Vostok during the 1967 season]. Upravlenie Kitoboinikh Flotiliy, Vladistok, 64pp. [In Russian] (Unpublished).

Berzin, A.A. 2008. The truth about Soviet whaling. *Mar. Fish. Rev.* 70(2): 4–59.

Brownell, R.L., Jr., Clapham, P.J., Miyashita, T. and Kasuya, T. 2001. Conservation status of North Pacific right whales. *J. Cetacean Res. Manage.* (*special issue*) 2: 269–86.

Brownell, R.L., Yablokov, A. and Zemsky, V. 2000. USSR pelagic catches of North Pacific sperm whales, 1949–1979: conservation implications. pp.123–30. *In*: Yablokov, A. and Zemsky, V. (eds). *Soviet Whaling Data*, Moscow: Center for Russian Environmental Policy, Marine Mammal Council.

Clapham, P. and Ivashchenko, Y. 2009. A whale of a deception. *Mar. Fish. Rev.* 71: 44–52.

Doroshenko, N.V. 2000. Soviet catches of humpback whales (*Megaptera novaeangliae*) in the North Pacific. pp.48–95. *In*: Yablokov, A.V. and Zemsky, V.A. (eds). *Soviet Whaling Data (1949–1979)*. Center for Russian Environmental Policy, Moscow. 408pp.

Ivashchenko, Y. and Clapham, P.J. 2012. Soviet catches of bowhead (*Balaena mysticetus*) and right whales (*Eubalaena japonica*) in the North Pacific and Okhotsk Sea. *Endanger. Species. Res.* 18: 201–17.

Ivashchenko, Y.V., Clapham, P. and Brownell, R.L., Jr. (Eds). 2007. Scientific reports of Soviet whaling expeditions in the North Pacific, 1955–1978. NOAA Tech. Memo. NMFS-AFSC-175. 36pp. [Transl. by Y. V. Ivashchenko].

Ivashchenko, Y., Clapham, P. and Brownell, R.L., Jr., 2011. Soviet illegal whaling: The devil and the details. *Mar. Fish. Rev.* 73(3): 1–19.

Ivashin, M.V. and Mineev, V.N. 1981. The history of gray whale harvesting off Chukotka. *Rep. int. Whal. Commn* 31: 503–05.

IWC. 1974. Chairman's Report of the Twenty-Fourth Meeting. *Rep. int. Whal. Commn* 24:20–36.

IWC. 1989. Report of the Special Meeting of the Scientific Committee on Planning for a Comprehensive Assessment of Whale Stocks, Cambridge, UK, 7–11 April 1986. *Rep. int. Whal. Commn* (*special issue*) 11: 3–13.

Kasuya, T. 1999. Examination of the reliability of catch statistics in the Japanese coastal sperm whale fishery. *J. Cetacean Res. Manage.* 1(1): 109–22.

Klumov, S.K. 1962. Gladkie (Yaponskie) kity Tikhogo Okeana [The right whales in the Pacific Ocean]. *Tr. Inst. Okeanol. Akad. Nauk SSSR* 58: 202–97. [In Russian].

Latishev, V.M., Doroshenko, N.V., Erdakov, L.N., Veinger, G.M., Bardin, V.F. and Latisheva, I.M. 1968. Sostoyanie zapasov kitov v severnoy chasty Tikhogo okeana. [Condition of whale resources in the North Pacific]. TRINO, Vladivostok, 76pp. [In Russian] (Unpublished).

Raskatov, E.A. and Latishev, V.M. 1967. Otchet gosudarstvennikh inspectorov po kitoboynomu promisluza promisloviy sezon 1967 goda na kitoboynoy flotilii *Dalniy Vostok.* [Report of state whaling inspectors during the 1967 season of the whaling fleet *Dalniy Vostok*]. Vladivostock, 76pp. [In Russian] (Unpublished).

Reeves, R. and Smith, T.D. 2006. A taxonomy of world whaling operations and era. pp.82–101. *In*: Estes, J.A., DeMaster, D., Doak, D.F., Williams, T.M. and Brownell Jr, R.L. (eds). *Whales, Whaling and Ocean Ecosystems*. University of California Press, Berkeley, CA, USA.

Tomilin, A.G. 1967. Cetacea. *In*: Heptner, V.G. (eds). *Mammals of the USSR and Adjacent Countries. Mammals of Eastern Europe and Adjacent Countries*. Israel Program for Scientific Translations, Jerusalem. [Translated from Russian. Published first in Russian; Moscow, 1957. IPST Cat. No. 1124]. *xxi* + 717pp.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica (NY)* 19(1–2): 1–50+6 maps.

Vebermann, E. 1914. Kitoboiniy promisel v Rossii. Chast 1: Istoriya promisla. [The whale fishery in Russia. Part 1: A history of the whale fishery]. Izvestiya Moskovskogo Komercheskogo Instituta, Moscow. 321pp + 44plts. [In Russian].

Webb, R.L. 1988. *On the Northwest, Commercial Whaling in the Pacific Northwest 1790–1967*. University British Columbia Press, Vancouver. xxi+425pp.

Yablokov, A.V. 1994. Validity of Soviet whaling data. *Nature, Lond.* 367(6,459): 108.

Yablokov, A.V. and Bogoslovskaya, L.S. 1984. A review of Russian research on the biology and commercial whaling of the gray whale. pp.465–85. *In*: Jones, M.L., Swartz, S.L. and Leatherwood, S. (eds). *The Gray Whale* Eschrichtius robustus. Academic Press Inc., Orlando, Florida. xxiv+600pp.

Zenkovich, B.A. 1954. Vokrug sveta za kitami. [Around the world after whales]. Government Publishers of Geographical Literature, Moscow, 408pp. [In Russian].

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Trends in collisions between vessels and North Pacific humpback whales (*Megaptera novaeangliae*) in Hawaiian waters (1975–2011)

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ABSTRACT

Injury from collisions with vessels is a growing threat worldwide for many species of whales. Thirty seven years of historical records were examined for evidence of vessel collisions with humpback whales in the main Hawaiian Islands. Between 1975 and 2011, 68 collisions between vessels and whales were reported including 59 witnessed collisions and 9 observed whale injuries that were consistent with a recent vessel collision. No collisions were immediately lethal. The waters between Maui, Molokai, Lanai and Kahoolawe, which are known to have one of the highest concentrations of humpback whales in the Hawaiian Islands, had the highest incidence of collisions. Over 63% of the collisions involved calves and subadults, suggesting a greater susceptibility towards collisions among younger animals. The rate of collisions increased significantly over the final twelve breeding seasons of the study and was greater than predicted by the estimated annual increase in the whale population, suggesting that the rising number of reported collisions cannot be explained solely by the annual increase in whale abundance. Although the total number of registered vessels and shipping traffic in Hawaii remained relatively constant between 2000 and 2010, there was a significant increase in the number of vessels between 7.9m and 19.8m in length. Vessels within this size range were also the most commonly involved in collisions during the study period, accounting for approximately two thirds of recorded incidents. It is concluded that from 1975–2011, there was a significant increase in reports of non-lethal collisions between vessels and humpback whales, especially calves and subadults, in the main Hawaiian Islands that likely reflects a combination of factors including the recovery of the population of North Pacific humpback whales, increases in traffic of particular vessel types, and increased reporting practices by operators of vessels.

KEYWORDS: HUMPBACK WHALE; SHIP STRIKES; STATISTICS; TRENDS; PACIFIC OCEAN; NORTHERN HEMISPHERE

INTRODUCTION

As populations of mysticete whales recover from intensive commercial hunting during the first half of the 20th century (see review in Clapham and Baker, 2009), they face a host of new anthropogenic threats. These include habitat degradation, entanglement (e.g. in fishing gear), underwater noise and collisions with vessels (Fleming and Jackson, 2011). There is mounting evidence that collisions between whales and vessels are increasing globally (Carrillo and Ritter, 2010; De Stephanis and Urquiola, 2006; Douglas *et al.*, 2008; Laist *et al.*, 2001; Panigada *et al.*, 2006). As whale and human populations continue to grow, encounters at sea between whales and vessels are becoming more frequent, sometimes with disastrous consequences for the whales, humans or both. This is notably true in areas where both human and whale concentrations are high, such as coastal urban areas in the proximity of whale feeding or breeding grounds (Carrillo and Ritter, 2010; De Stephanis and Urquiola, 2006; Panigada *et al.*, 2006; Ritter, 2010). One such location is the Hawaiian archipelago where thousands of humpback whales (*Megaptera novaeangliae*) congregate seasonally between December and April (e.g. Calambokidis *et al.*, 2008) and where in excess of eight million people reside or visit annually. This paper investigates trends in collisions between vessels and humpback whales in Hawaiian waters over a 37-year period.

The Hawaiian Islands are the principal breeding grounds for North Pacific humpback whales (Calambokidis *et al.*, 2008; Calambokidis *et al.*, 2001; Fleming and Jackson, 2011). Each year, thousands of North Pacific humpback whales migrate to Hawaiian waters, where they take up temporary residence (Craig *et al.*, 2003; Craig *et al.*, 2001). Barlow *et al.* (2011) provided a 2006 estimate of 21,808 humpback whales in the North Pacific population based on a three-year North Pacific-wide mark and recapture survey known as SPLASH (Structure of Populations, Levels of Abundance, and Status of Humpbacks). Calambokidis *et al.* (2008), using the same SPLASH data, estimated a 6% annual increase in the population of humpback whales in the North Pacific. Also, as of 2006, approximately 10,103 (55%) of the North Pacific population of humpback whales (excluding newborn calves) were estimated to visit the Hawaiian Islands (Calambokidis *et al.*, 2008).

While on their breeding grounds, humpback whales (other than newborn calves) fast and behaviour is largely related to mating and calving. Calves make up 7–9% of the Hawaii population (Mobley *et al.*, 2001). The mean age that humpback whales attain sexual maturity has been estimated at five years of age (Chittleborough, 1965; Clapham, 1992), but recent evidence suggests that it may be closer to ten in the North Pacific (Best, 2011; Gabriele *et al.*, 2007). In addition to sexually mature adults, immature whales of both sexes also migrate to Hawaii from higher latitude feeding grounds (e.g. Craig *et al.*, 2003).

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Despite their growing numbers, humpback whales are still considered an endangered species. Twentieth century commercial whaling reduced the North Pacific population to between 1,000 and 1,400 (Gambell, 1976; Johnson and Wolman, 1985; Rice, 1978). The IWC banned commercial whaling for North Pacific humpback whales in 1965. However, recent reports reveal that Soviet whaling for humpback whales actually continued until 1971 (Doroshenko, 2000). Currently, humpback whales in Hawaii (and other US waters) are protected and managed under US Federal laws including the Endangered Species Act and the Marine Mammal Protection Act, and a variety of state laws. In 1992, the US Congress designated portions of the waters of the main Hawaiian Islands as a marine sanctuary for humpback whales (Subtitle C of Public Law 102–587, the Oceans Act of 1992). In 1997, the Governor of the State of Hawaii provided approval for designated State waters to be included in the Hawaiian Islands Humpback Whale National Marine Sanctuary. Under US Federal Law, vessels other than those with a Federal Permit to conduct research or film humpback whales must remain at least 100 yards from individual humpback whales. Despite these conservation efforts and regulations, collisions between vessels and humpback whales still occur.

Several reports have been published that reviewed records of vessel collisions with humpback whales in the United States and globally (e.g. Douglas *et al.*, 2008; Jensen and Silber, 2003; Laist *et al.*, 2001; Wiley *et al.*, 1994). Wiley *et al.* (1994) examined records of humpback whale strandings along the US Atlantic coast between 1985 and 1992. They reported that 30% (6 of 20) of stranded individuals had injuries caused by vessels. Laist *et al.* (2001) conducted a study on collisions between vessels and whales worldwide, which included humpback whales. Although records revealed that vessel strikes on fin whales (*Balaenoptera physalus*) were most common, collisions with humpback whales (along with right whales (*Eubalaena glacialis*), gray whales (*Eschrichtius robustus*), and sperm whales (*Physeter macrocephalus*)) were considered relatively common.

As an island state, Hawaii is highly dependent on vessel traffic for commerce, transportation and as a major source of revenue for the local economy through the sightseeing, diving, fishing and whalewatching industries. Concurrent with the recovery of the population of North Pacific humpback whales and the growing number of humpback whales wintering in Hawaiian waters, there is growing concern about the potential for collisions (National Marine Fisheries Service, 1991). Presently, however, there is little quantitative evidence to evaluate the severity of the issue from both a conservation and safety perspective. This study provides the first empirical measure of the incidence of collisions between humpback whales and vessels in Hawaiian waters. The available historical information on the number and location of collisions over the 37-year period between 1975 and 2011 are summarised. Where available, data on vessel type and speed, as well as the age-class of whales involved in collisions are collated. The rate of collisions relative to the annual increase in whale abundance is investigated. Finally, available vessel statistics are examined to infer corollary relationships with collision trends.

METHODS

The historical occurrence of collisions between vessels and whales in Hawaiian waters was investigated by searching print media archives, government records and the scientific literature for accounts of past incidents. Print media sources included: *The Honolulu Advertiser*, *The Star Bulletin*, *West Hawaii Today*, *The Maui News*, *The Hawaii Herald Tribune*, *Hawaii Fishing News* and *The Garden Isle*. Some of these sources did not come into existence until after 1975, so their databases were searched beginning with the first archives. The government records that were examined included the ‘Whale Incident Log’ maintained by the National Oceanic and Atmospheric Administration’s (NOAA) Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS), stranding and incident records from the National Marine Fisheries Service’s Pacific Islands Regional Office and information gathered via personal communication with NOAA’s Office of Law Enforcement and the management staff of the HIHWNMS. Statistics on the abundance and location of registered vessels in the State of Hawaii, as well as rates of overseas and inter-island commercial ship traffic between 2000 and 2010, were obtained from *State of Hawaii Data Book* records available online from the Department of Business, Economic Development and Tourism (*http://hawaii.gov/dbedt/info/economic/databook/*).

RESULTS

Numbers of reported collisions and types of injuries

A ‘collision’ was defined as any physical contact occurring between a vessel and a humpback whale. No reports of collisions were found prior to 1979. From 1979–2011, there were 68 confirmed reports of collisions including 59 witnessed collisions (Table 1)[6] and 9 suspected collisions (i.e. a recent whale injury was observed consistent with a collision with a vessel but the actual collision was not reported) (Table 2). Forty-five witnessed collisions were reported as a vessel striking a whale, 12 were reported as a whale striking a vessel, and 2 were reported as both a vessel striking a whale and a whale striking a vessel (Table 1).

There were no reports of immediate whale fatalities from observed collisions. However, a dead-stranded calf found with deep, propeller-inflicted lacerations is suspected to have died from its wounds. Where injuries could be determined, the most common were lacerations for both witnessed collisions and suspected collisions. Some of these were clearly wounds from contact with a vessel’s propeller (i.e. the cuts were uniform, evenly spaced, and consistent with other observations on confirmed propeller wounds). Only one confirmed case of blunt trauma was observed, with two others likely (see Tables 1 and 2).

Characteristics of vessels involved in collisions

The type of vessel was reported in 56 witnessed collisions. The majority of collisions (61%, n = 34) involved tour

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[6] At least two additional incidents occurring in the late 1980s/early 1990s were reported by a humpback whale researcher on Maui in a ‘Star Bulletin’ article on 1 April 2002. In each case, a whale reportedly bumped the inflatable research vessel as it was operating in neutral gear. No injuries or damages were reported.

Table 1

Witnessed collisions between whales and vessels in Hawaiian waters 1979–2011.

Year	Month/day	Island	Age class	Initiator (W/V)	Injury type	V type	V length (m)	V max speed
1979	NR	Maui	NR	W	U	Research	NR	NR
1981	Feb. 02	Hawaii	Adult	W	U	Tour	NR	7
1987	Jan. 01	Hawaii	NR	V	L	Dive	9.1	15
1988	Mar. 26	Maui	Adult	V	U	NR	7.3	26
1990	Mar. 01	Hawaii	Adult	V	U	Fishing	5.8	NR
1995	Feb. 22	Maui	Adult*	V	L	Tour	19.8	NR
1996	Jan. 16	Maui	Adult	V	U	Tour	25	8
1998	Jan. 01	Maui	NR	V	U	Tour	25	NR
1998	Mar. 30	Oahu	Adult	V	BT	Mil/Gov	91.4	8
2000	Feb. 04	Oahu	NR	V	U	Fishing	6.1	8
2001	Feb. 01	Maui	U	V	L	Tour	NR	18
2001	Feb. 15	Kauai	Juvenile	W	U	Tour	12.2	NR
2002	Mar. 01	Maui	Adult	W	U	NR	NR	0
2002	Mar. 15	Maui	Adult	W	L	Tour	19.8	NR
2002	Mar. 27	Maui	Calf	V	U	NR	NR	NR
2003	Feb. 10	Maui	Juvenile	V	U	Tour	19.8	NR
2003	Feb. 16	Kauai	NR	V	U	Cargo	91.4	NR
2003	Mar. 07	Maui	NR	V	U	Tour	NR	17
2003	Dec. 25	Oahu	Adult	V	U	Tour	32.9	NR
2004	Jan. 05	Maui	NR	V	U	Fishing	5.5	NR
2004	Feb. 08	Maui	Calf	V	U	Pleas/Priv	6.7	NR
2005	Feb. 06	Lanai	Calf	V	U	Ferry	45.4	17.4
2005	Feb. 21	Oahu	NR	V	U	Fishing	NR	NR
2005	Feb. 25	Oahu	NR	V	U	Sailboat	NR	NR
2006	Jan. 04	Maui	NR	V	U	Tour	NR	13
2006	Jan. 17	Kauai	NR	V	U	Tour	18.3	15
2006	Feb. 13	Maui	NR	V	U	Mil/Gov	7.6	10
2006	Mar. 09	Maui	Calf	V	L	Tour	19.8	15
2006	Mar. 25	Maui	U**	V	U	Tour	9.8	22
2006	Dec. 28	Kauai	NR	V	U	Tour	NR	15
2007	Feb. 07	Maui	U	V	L	Ferry	19.8	20
2007	Mar. 08	Maui	Juvenile	W	U	Tour	9.1	0
2007	Apr. 01	Kauai	Juvenile	V	U	Tour	19.8	10
2007	Apr. 13	Lanai	Calf	V	L	Tour	15.5	18
2008	Jan. 10	Hawaii	Adult	V	U	Tour	9.1	13
2008	Jan. 27	Oahu	Calf	V	U	Tour	13.41	6
2008	Feb. 05	Maui	Juvenile	V	U	Research	10.36	8
2008	Feb. 27	Oahu	Adult	W	U	Mil/Gov	NR	NR
2008	Feb. 28	Maui	Juvenile	V	L	Tour	19.81	12.5
2008	Mar. 04	Hawaii	Calf	V	L	Tour	8.84	13
2008	Mar. 05	Maui	Adult*	V	U	Tour	19.81	NR
2008	Mar. 21	Hawaii	Adult	W	U	Tour	NR	NR
2008	Mar. 27	Lanai	Calf	V	U	Tour	9.14	19
2009	Feb. 05	Maui	Adult	V	L	Ferry	19.8	NR
2009	Feb. 21	Maui	Calf	V	U	Tour	15.24	8
2009	Feb. 27	Maui	Adult	W	U	Research	8.53	1
2009	Mar. 01	Maui	Calf	W	U	Tour	19.81	0
2009	Mar. 22	Hawaii	Juvenile	V	U	Tour	7.32	20
2009	Mar. 23	Maui	Calf	V and W	U	Other	4.57	10
2009	Mar. 27	Maui	Adult	W	U	Research	10.36	5
2009	Mar. 29	Maui	Juvenile	V and W	U	Other	4.57	NR
2009	Dec. 08	Maui	Juvenile	V	U	Tour	9.14	25
2010	Jan. 08	Maui	Juvenile	V	U	Tour	19.81	13
2010	Feb. 14	Hawaii	Adult	V	U	Tour	9.75	10
2010	Feb. 23	Hawaii	Calf	V	U	Tour	19.81	10
2011	Feb. 15	Maui	Calf	V	U	Tour	19.81	15
2011	Feb. 16	Maui	Mother and Calf	V	L	Fishing	9.45	NR
2011	Feb. 21	Oahu	Juvenile	V	U	Mil/Gov	7.62	26
2011	Mar. 08	Maui	Adult	W	U	Tour	16.76	4

*Mother-calf pair (mother struck). **Mother-calf pair (unknown whether one or both whales struck). Mi = military vessel, Gov = government vessel, Pleas = pleasure boat, Priv = private boat. L = laceration, BT = blunt trauma, NR = not reported, U = unknown, W = whale, V = vessel.

vessels (e.g. whalewatching, diving, snorkelling; Fig. 1). Vessel length was determined in 47 witnessed collisions (Mean = 17.78m, SD = 17.59m, Range = 4.57m–91.4m). 87 percent of collisions involved vessels whose lengths were ≤ 21.2m (Fig. 2). The speeds of vessels involved in collisions were reported in 39 incidents. Mean reported maximum vessel speed at the time of the collision was 12.33 kts (SD = 6.96 kts, Range = 0–26.1 kts) (Fig. 3). The majority of vessels involved in a collision (51%) had maximum reported speeds of between 10 and 19 knots.

Location and timing of collisions

Witnessed collisions were not distributed equally among island regions (Fig. 4; χ^2 (3) = 45.3, $p < 0.001$). The majority

Table 2

Suspected collisions between whales and vessels in Hawaiian waters 1979–2011.

Year	Month/day	Island	Age class	Injury type
1994	Feb. 10	Maui	NR	L
1996	Jan. 18	Oahu	Calf	L
1996	Jan. 22	Maui	Calf	L
1999	Mar. 25	Maui	Calf	L
2005	Feb. 28	Maui	Calf	L
2006	Mar. 15	Maui	Calf	U
2006	Dec. 29	Maui	Calf	L
2008	16. Apr	Maui	Calf	L
2010	Feb. 28	Hawaii	Calf	U

L = laceration, U = unknown.

($n = 37$) of collisions were in the Maui Nui Region (i.e. the channels between Maui, Lanai, Kahoolawe, and Molokai) while the fewest number ($n = 5$) occurred off Kauai. Fig. 5 shows the percentage of witnessed collisions occurring per month. The two months with the highest incidents of collisions were February and March.

Age class of whales involved in collisions

The age class of a humpback whale involved in a vessel collision (witnessed and suspected combined) was reported in 52 cases. Calves and juveniles combined had a greater incidence of reported vessel collisions (63.5%) than did adults (36.5%) (χ^2 (1) = 3.77, p = 0.05), (Fig. 6). In the Maui Nui region, of 29 collisions in which the age class of the whale was reported, 62% involved either a calf or a juvenile.

Temporal trends in collisions

Fig. 7 shows the number of reported collisions (witnessed and suspected combined) per year across six 6-year binned calving seasons from 1976–2011. There was a 20-fold significant increase in the annual incidence of reported collisions over this period ($r^2 = 0.74$, $f\,(1,4) = 11.22$, $p = 0.03$). To examine if the rate of collisions relative to whale abundance remained constant over time, a mean whale abundance estimate for each 6-year binned calving season was calculated by taking the 2006 whale abundance estimate for the Hawaiian Islands of 10,103 whales provided by Calambokidis *et al.* (2008) and extrapolating using an estimated annual increase in whale abundance of 6% (Calambokidis *et al.*, 2008) and an estimated 9% of the Hawaii population of humpback whales being composed of calves (Mobley *et al.*, 2001). There was a significant increase in the number of collisions per mean number of whales across binned periods ($r^2 = 0.69$, $f(1,4) = 8.69$, $p = 0.04$). Thus, the rate of whale collisions relative to whale abundance did not remain constant across years but instead increased. Furthermore, when we controlled statistically for the estimated annual increase in whale abundance, the increasing number of collisions per year remained significant (standardised regression coefficient $\beta = -1.09$, $t = -5.35$, $p = 0.01$). In summary, the increase in number of collisions over time could not be attributed solely to greater estimated whale abundance. This increase in collisions was also present when considering only the most recent 12-year period (2000–11). There was a significant increase in the mean number of collisions adjusted for estimated annual whale abundance between the periods from 2000–05 (mean = 2.92×10^{-4}) and 2006–11 (mean = 5.18×10^{-4}) ($t(10) = 2.64$, p = 0.025).

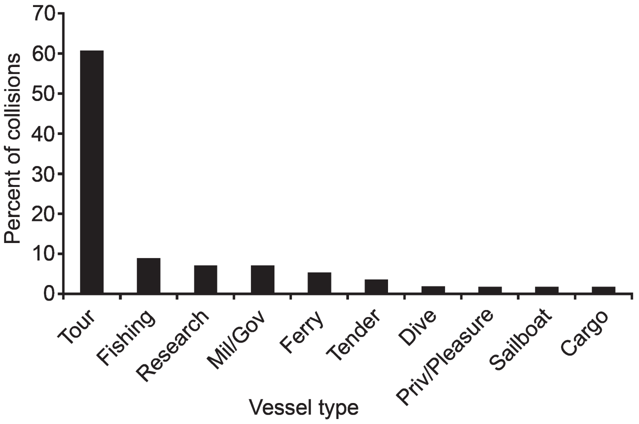

Fig. 1. Percentage of witnesssed collisions between humpback whales and vessels in Hawaiian waters from 1975–2011 as a function of vessel type ($n = 56$ reports).

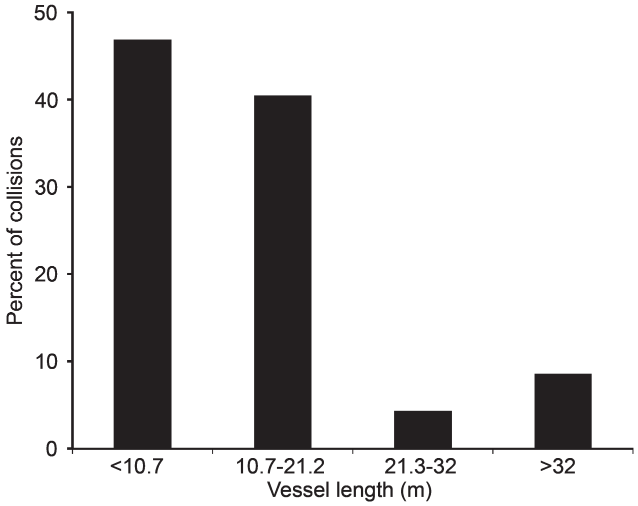

Fig. 2. Percentage of witnessed collisions between humpback whales and vessels in Hawaiian waters from 1975–2011 involving vessels of various lengths ($n = 47$ reports).

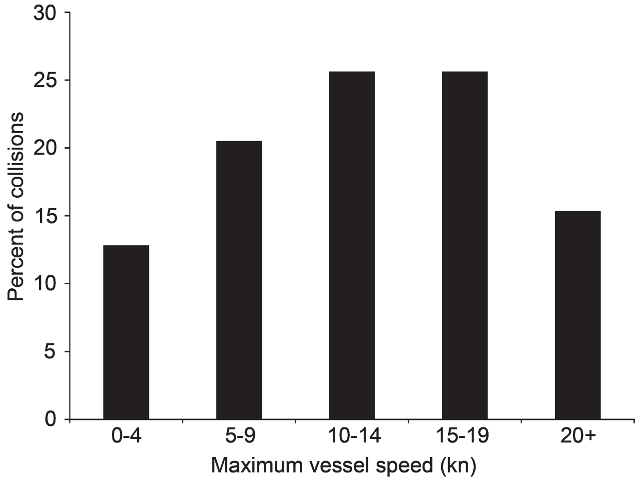

Fig. 3. Percentage of witnessed collisions between humpback whales and vessels in Hawaiian waters from 1975–2011 involving vessels traveling at various maximum speeds ($n = 39$ reports).

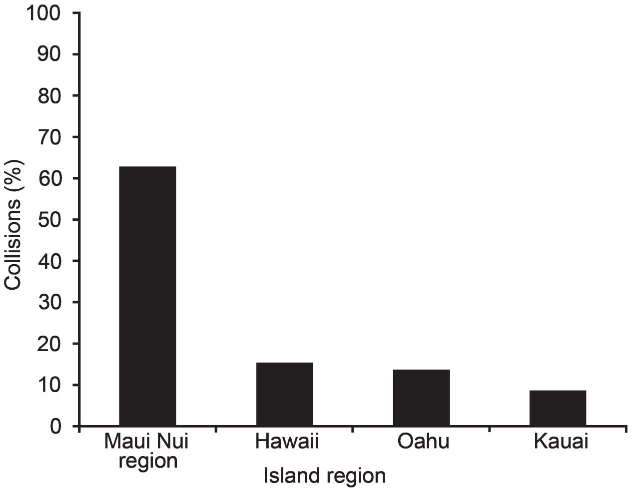

Fig. 4. Percentage of witnessed collisions between humpback whales and vessels in Hawaiian waters from 1975–2011 off each island region (n = 58 reports).

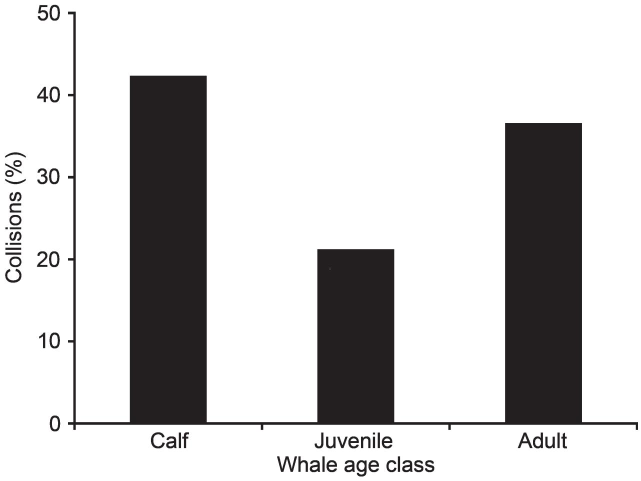

Fig. 6. Percentage of humpback whales of reported age classes involved in vessel collisions (witnessed and suspected combined) in Hawaiian waters 1975–2011 (n = 52 reports).

State of Hawaii vessel registrations and shipping traffic between 2000–2010

Table 3 shows the data for annual vessel registrations by size class and by island, as well as ship arrivals at Honolulu harbour from overseas and inter-island traffic. Only Hawaii Island experienced a significant increase in the mean number of vessel registrations from 2000–2005 (Mean = 2512.33, SD = 135.84) versus 2006–10 (Mean = 2,676.60, SD = 119.92) (one-tailed *t* test, t((9) = 2.10, $p < 0.05$). The other island regions experienced no significant increase in mean vessel registrations from 2000–2005 versus 2006–10. Overseas shipping traffic showed a significant decrease from 2000–05 (Mean = 1213.33 arrivals, SD = 81.26 arrivals) versus 2006–10 (Mean arrivals = 983.40 arrivals, SD = 68.29 arrivals) ($t(9) = 5.01$, $p < 0.001$) while inter-island traffic remained unchanged.

Fig. 8 shows annual trends in vessel registrations in Hawaiian waters from 2000–10 for vessels of various lengths with the abundance of each year normalised to the maximum for the 11-year period. A regression analysis revealed only two significant positive linear correlations between year and normalised vessel abundance: for vessels 7.9–12.2m (r^2 = 0.85, $f(1,9) = 52.30$, $p < 0.001$; and for vessels 12.2–19.8m (r^2 = 0.65, F (1,9) = 17.01, p = 0.003). The difference between the mean abundance of vessels of different size from 2000–05 versus 2006–10 was also tested. A one-tailed t test revealed that the only significant increases in abundance between the two periods were for vessels 7.9–12.2m ($t(9) = 4.31$, p < 0.01) and 12.2–19.8m ($t(9) = 2.17$, $p < 0.05$).

DISCUSSION

Historical trends

Although the number of whale/vessel collisions varies from year to year, there is compelling evidence that the rate of incidents is on the rise in Hawaiian waters. Perhaps most telling are the data showing an increase during the two most recent six-year periods (2000–05 and 2006–11). Because this comparison excludes data from earlier years when more incidents may have gone unobserved and/or unreported (e.g. due to a lack of formal reporting mechanisms or possibly a reluctance of some vessel operators to report incidents), it

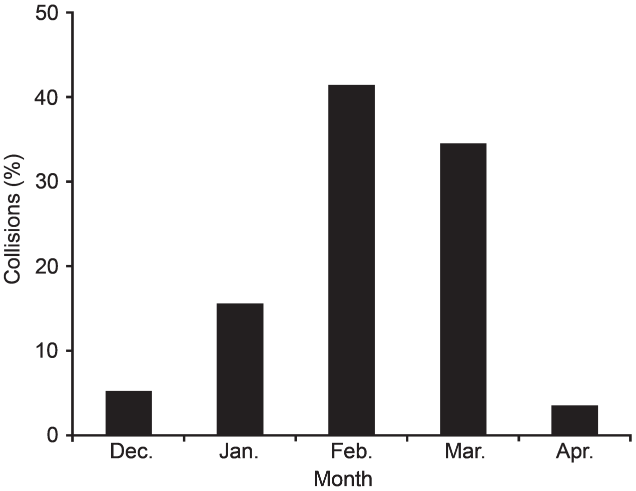

Fig. 5. Percentage of witnessed collisions between humpback whales and vessels in Hawaiian waters from 1975–2011 occurring per month (n = 58 reports).

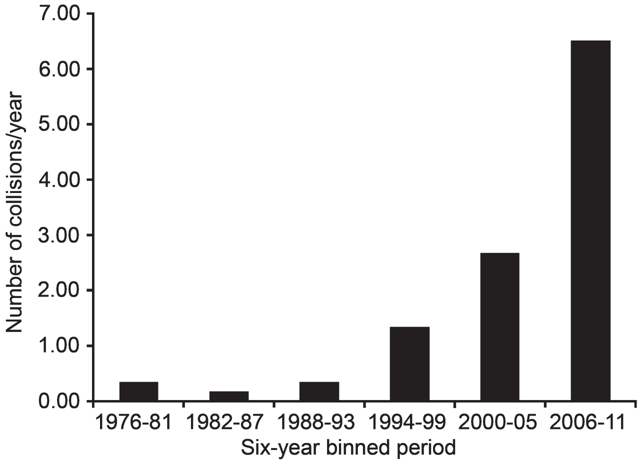

Fig. 7. The number of reported collisions between humpback whales and vessels in Hawaiian waters (witnessed and suspected combined) per year across six 6-year binned calving seasons from 1976–2011.

Table 3

Annual vessel registrations by size class and by island and ship arrivals at Honolulu harbour from overseas and from inter-island traffic between 2000 and 2010.

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Length (m)											
< 4.9	5,680	5,370	5949	5,827	6,533	5,940	5,770	5,695	6,424	5,842	5,343
4.9 < 7.9	7,476	7,248	7698	7,918	8,772	7,367	7,420	7,443	8,138	7,762	7,455
7.9 < 12.2	1,537	1,483	1596	1,632	1,616	1,695	1,701	1,736	1,914	1,860	1,804
12.2 < 19.9	169	166	187	193	191	251	209	211	256	231	229
> 19.9	12	6	15	17	18	49	9	9	12	14	16
Total	14,874	14,273	15445	15,587	17,130	15,302	15,109	15,094	16,744	15,709	14,847
Location											
Hawaii	2,420	2,328	2519	2,521	2,731	2,555	2,650	2,632	2,876	2,671	2,554
Kauai	1,728	1,647	1748	1,604	1,713	1,585	1,580	1,539	1,718	1,647	1,564
Maui Nui	1,882	1,777	2146	2,017	2,410	2,121	2,041	2,042	2,326	2,170	2,007
Oahu	8,829	8,543	9032	9,445	9,251	8,016	8,791	8,881	9,824	9,221	8,722
NS	N/A	N/A	N/A	N/A	1,025	1,025	47	N/A	N/A	N/A	N/A
Honolulu arrivals											
Overseas	1,292	1,295	1270	1,169	1,133	1,121	1,061	1,027	1,002	931	896
Inter-island	2,215	2,280	2663	2,521	2,418	2,580	2,972	3,157	2,964	2,512	2,264

is probably a more accurate assessment of the trend in collisions.

Approximately 75% of reported collisions occurred during either February or March, which coincides with the seasonal peak of whale abundance in Hawaii (see Baker and Herman, 1984; also summarised in Mobley *et al.*, 1999). This indicates that a relationship exists between whale density and the frequency of collisions. However, it was found that on an annual basis the higher number of reported collisions could not be solely accounted for by the estimated annual increase in whale abundance in Hawaii. This suggests that either higher vessel traffic and/or the behaviour of vessels around whales also play a role in the rate of collisions. Although the total number of registered vessels and shipping traffic in Hawaii remained relatively constant between 2000 and 2010, there was a significant increase in the number of vessels between 7.9m and 19.8m in length. In other words, there was a correspondence between the number of vessels of this size class operating in Hawaii and the rate of collisions with whales. Coincidentally, vessels within this size range were also the most commonly implicated in collisions during the study period, accounting for approximately two thirds of recorded incidents.

The majority of reported incidents occurred in waters in the Maui Nui region, a relatively shallow (< 200m depth) area with one of the densest aggregations of humpback whales in the Hawaiian Islands. This is also an area of high vessel concentration, especially during whalewatching months. The majority of incidences over the past five years in which the vessel type was specified involved commercial whalewatching vessels. This could simply reflect a greater likelihood that a collision with a whalewatching vessel carrying passengers will be reported. Alternatively, it may indicate that tour vessels that regularly operate in whale-dense areas or in the proximity of whales, and specifically seek out whales for close approach and observation, may be more prone to collisions.

Collision characteristics

Laist *et al.* (2001) noted that vessel collisions with whales generally result in two types of injuries; propeller wounds and blunt trauma. Both types were evident in our database,

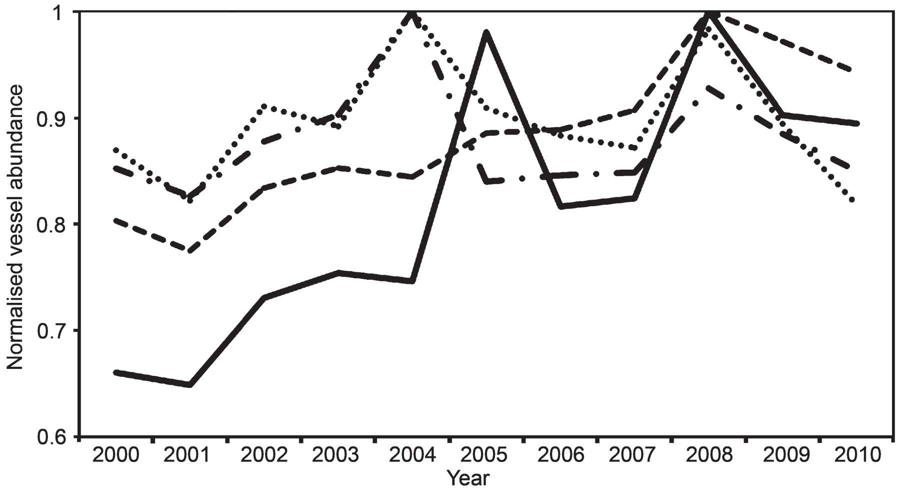

Fig. 8. Annual trends in vessel registrations in Hawaiian waters from 2000–10 for vessels of various lengths with the abundance of each year normalised to the maximum for the 11-year period.

though lacerations were much more prevalent. Only one instance of a suspected vessel collision-related mortality was recorded; a dead-stranded calf with deep propeller wounds on the island of Oahu. However, in several other incidences where deep wounds were observed on living calves, as well as the adult observed with blunt trauma, the whale's survival was considered dubious.

The data compiled by Laist *et al.* (2001) indicated that calves and juveniles on the feeding grounds or along a migration route were highly vulnerable to collisions with vessels. A parallel situation is seen for the Hawaiian wintering grounds. For humpback whales in Hawaiian waters, over half of the incidents in which the age class of the whale was specified involved either a calf or a juvenile. This may not be surprising as calves spend more time at the surface to breathe than adults, will often surface without the mother if the pod is stationary, are less visible than adults, and are relatively naïve to interactions with vessels (Glockner and Venus, 1983). Silber *et al.* (2010) showed that whales submerged by only one or two times a vessel's draft, which is typical for calves, experience a pronounced propeller suction effect, drawing them toward the hull, and thereby increasing the probability of a propeller strike.

Vessel speed does appear to play a role in collisions in Hawaiian waters. The majority of incidents (where maximum speed was reported) were with vessels having top speeds of 10–19 knots. This trend is consistent with findings by Gende *et al.* (2011) who examined the role of vessel speed in whale/ship encounters and found that the relationship between whale distance and ships changes at 11.8 knots (6.1 m s^{-1}), with whales encountering ships at significantly closer range, on average, when the ship's speed is above 11.8 knots. Vanderlaan and Taggart (2007) similarly found that the probability of a lethal injury to North Atlantic right whales (*Eubalaena glacialis*) is greater than 0.5 at collision speeds above 11.8 knots, while Silber *et al.* (2010) also found that factors affecting the severity of injury are tied to vessel speed. These lines of evidence suggest that above speeds of approximately 12 knots whales may have more difficulty avoiding a close encounter with a vessel and that collisions above this speed have a greater likelihood of injury or death.

The extent of injuries suffered from collisions by whales is a difficult variable to quantify. Laist *et al.* (2001) indicated that trauma suffered from collisions among stranded whales is often not apparent unless a thorough necropsy is performed and the integrity of the bones is examined by flensing through the blubber. Lacerations resulting from propeller cuts are the more obvious form of injury observable, but perhaps not necessarily the most common type. Blunt trauma such as fractures and internal bleeding are more difficult to establish and probably go unnoticed more often. Therefore, although several of the reports described suggested that no injuries were sustained, these assessments were likely biased by the inability to observe blunt trauma injuries.

Finally, no cases of whale carcasses pinned to the bow of ships were reported in Hawaii during the period examined. This is in contrast to the findings of Laist *et al.* (2001) for whom such cases comprised a significant component of the database. In Hawaii, it appears the majority of vessels involved in collisions are small to medium sized boats less than 21.2m in length. The lack of incidents reported involving large ships is somewhat curious, but perhaps indicates that presently established shipping lanes are not a major problem in this regard. However, a more thorough assessment of this assumption is clearly warranted, as alternate explanations such as under-reporting are also possible.

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REFERENCES

Baker, C.S. and Herman, L.M. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Can. J. Zool.* 62: 1,922–37.

Barlow, J., Calambokidis, J., Falcone, E.A., Baker, C.S., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D.K., Quinn II, T.J., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R., J., Wade, P., Weller, D., Witteveen, B.H. and Yamaguchi, M. 2011. Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. *Mar. Mammal Sci.* 27(4): 793–818.

Best, P.B. 2011. A note on the age at sexual maturity of humpback whales. *J. Cetacean Res. Manage. (special issue 3)*: 71–73.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R, J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J. and Maloney, N. 2008. SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific. Final report for Contract AB133F-03-RP-00078, US Department of Commerce Western Administrative Center, Seattle, Washington. [Available at *http://www.cascadiaresearch.org/SPLASH/SPLASH-contract-report-May08.pdf*].

Calambokidis, J., Steiger, G.H., Straley, J., Herman, L.M., Cerchio, S., Salden, D., Urbán R, J., Jacobsen, J.K., von Zeigesar, O., Balcomb, K.C., Gabriele, C.M., Dahlheim, M.E., Uchida, S., Ellis, G., Miyamura, Y., Ladrón de Guevara P, P., Yamaguchi, M., Sato, F., Mizroch, S.A., Schlender, L., Rasmussen, K., Barlow, J. and Quinn II, T.J. 2001. Movements and population structure of humpback whales in the North Pacific. *Mar. Mammal Sci.* 17(4): 769–94.

Carrillo, M. and Ritter, F. 2010. Increasing numbers of ship strikes in the Canary Islands: proposals for immediate action to reduce risk of vessel-whale collisions. *J. Cetacean Res. Manage.* 11(2): 131–38.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshwater Res.* 16(1): 33–128.

Clapham, P.J. 1992. Age at attainment of sexual maturity in humpback whales, *Megaptera novaeangliae*. *Can. J. Zool.* 70(7): 1,470–72.

Clapham, P.J. and Baker, C.S. 2009. Whaling, Modern. pp.1,239–43. *In*: Perrin, W.F., Wursig, B. and Thewissen, G.M. (eds). *Encyclopedia of Marine Mammals*. Academic Press, New York.

Craig, A.S., Herman, L.M., Gabriele, C.M. and Pack, A.A. 2003. Migratory timing of humpback whales, *Megaptera novaeangliae*, in the Central

North Pacific varies with age, sex and reproductive status. *Behaviour* 140: 981–1,001.

Craig, A.S., Herman, L.M. and Pack, A.A. 2001. Estimating residence times of humpback whales in Hawaii. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary Office, Office of National Marine Sanctuaries, National Ocean and Atmospheric Administration, U.S. Department of Commerce and Department of Land and Natural Resources, State of Hawaii. 22pp. [Available from the HIHWNMS office]

De Stephanis, R. and Urquiola, E. 2006. Collisions between ships and cetaceans in Spain. Paper SC/58/BC5 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 6pp. [Paper available from the Office of this Journal].

Doroshenko, N.V. 2000. Soviet catches of humpback whales (*Megaptera novaeangliae*) in the North Pacific. pp.48–95. *In*: Yablokov, A.V. and Zemsky, V.A. (eds). *Soviet Whaling Data (1949–1979)*. Center for Russian Environmental Policy, Moscow. 408pp.

Douglas, A.B., Calambokidis, J., Raverty, S., Jeffries, S.J., Lambourn, D.M. and Norman, S.A. 2008. Incidence of ship strikes of large whales in Washington State. *J. Mar. Biol. Assoc. UK* 88(6): 1,121–32.

Fleming, A.H. and Jackson, J. 2011. Global review of humpback whales, *Megaptera novaeangliae*. NOAA-TM-NMFS-SWFSC-474. 207pp.

Gabriele, C.M., Straley, J.M. and Neilson, J.L. 2007. Age at first calving of female humpback whales in southeastern Alaska. *Mar. Mammal Sci.* 23(1): 226–39.

Gambell, R. 1976. World whale stocks. *Mammal Rev.* 6(1): 41–53.

Gende, S.M., Hendrix, A.N., Harris, K.R., Eichenlaub, B., Nielsen, J. and Pyare, S. 2011. A Bayesian approach for understanding the role of ship speed in whale-ship encounters. *Ecol. Appl.* 21(6): 2,232–40.

Glockner, D.A. and Venus, S.C. 1983. Identification, growth rate, and behavior of humpback whale (*Megaptera novaeangliae*) cows and calves in the waters off Maui, Hawaii, 1977–1979. pp.223–58. *In*: Payne, R. (eds). *Communication and Behavior of Whales*. AAAS Selected Symposium 76. Westview Press, Colorado. xii+643pp.

Jensen, A.S. and Silber, G.K. 2003. Large whale ship strike database. *NOAA Tech. Mem.*: 37pp. NMFS-OPR. 37pp. [Available at: *http://www.nmfs.noaa.gov/pr/overview/publicat.html*]

Johnson, J., H. and Wolman, A.A. 1985. The humpback whale. *Mar. Fish. Rev.* 46: 30–37.

Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S. and Podesta, M. 2001. Collisions between ships and whales. *Mar. Mammal Sci.* 17(1): 35–75.

Mobley, J.J.R., Bauer, G.B. and Herman, L.M. 1999. Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Aquat. Mamm.* 25(2): 63–72.

Mobley, J.M., Spitz, S., Grotenfeld, R., Forestell, P., Frankel, A.S. and Bauer, G.B. 2001. Abundance of humpback whales in Hawaiian waters: results of 1993–2000 aerial surveys. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary, Kihei, HI 96753. 16pp.

National Marine Fisheries Service. 1991. Final recovery plan for the humpback whale (*Megaptera novaengliae*). Prepared by the Humpback Whale Recovery Team for the National Marine Fisheries Service, Silver Spring, Maryland. 105pp. [Available from: *http://www.nmfs.noaa.gov/pr/pdfs/recovery/whale.humpback.pdf]*.

Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A. and Weinrich, M. 2006. Mediterranean fin whales at risk from fatal ship strikes. *Mar. Poll. Bull.* 52: 1287–98.

Rice, D.W. 1978. The humpback whale in the North Pacific: distribution, exploitation, and numbers. pp. 29–44. *In*: Norris, K.S. and Reeves, R. (eds). *Report on a Workshop on Problems Related to Humpback Whales* (Megaptera novaeangliae) *in Hawaii*, Report to the Marine Mammal Commission, July 1977, Washington, DC. NTISPB 280-794. [Available from NMML Library, *http://nmml.afsc.noaa.gov/library]*.

Ritter, F. 2010. Quantification of ferry traffic in the Canary Islands (Spain) and its implications for collisions with cetaceans. *J. Cetacean Res. Manage.* 11(2): 139–46.

Silber, G.K., Slutsky, J. and Bettridge, S. 2010. Hydrodynamics of a ship/whale collision. *J. Exp. Mar. Biol. Ecol.* 391: 10–19.

Vanderlaan, A. and Taggart, C.T. 2007. Vessel collisions with whales: the probability of lethal injury based on vessel speed. *Mar. Mammal Sci.* 23(1): 144–56.

Wiley, D.N., Asmutis, R.A., Pitchford, T.D. and Gannon, D.P. 1994. Stranding and mortality of humpback whales, *Megaptera novaeangliae*, in the mid-Atlantic and southeast United States, 1985–1992. *Fish. Bull. S. Afr.* 93: 196–205.

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Testing the *Gray Whale* Strike Limit Algorithm (*SLA*): allowing environmental variability to influence population dynamics

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ABSTRACT

The performance of the *Gray Whale SLA* is evaluated based on an operating model conditioned on available information for the eastern North Pacific stock of gray whales including: survey estimates of 1+ abundance; calf counts; strandings data; and the extent of sea-ice in the feeding grounds in the Bering Sea in the early season. Multiple scenarios are considered in the analyses to explore the impact of different sources of environmental variation, including scenarios in which future environmental forcing and episodic events are driven by the relationships between reproductive success and survival to sea ice. A variety of sources of uncertainty are considered, including parameter uncertainty, the uncertainty about the relationship between the extent of sea-ice and population dynamics, and observation error. The impact of these sources of uncertainty on the performance of the *Gray Whale SLA* is small. For all scenarios considered in the simulations, application of the *SLA* results in the stock being at or near carrying capacity at the end of a 92 year projection period for which sea-ice cover forecasts are available, while still satisfying the needs of aboriginal whalers.

KEYWORDS: BIRTH RATE; CLIMATE CHANGE; ICE; MANAGEMENT PROCEDURE; MODELLING; MORTALITY RATE; WHALING–ABORIGINAL; GRAY WHALE

INTRODUCTION

The IWC has established a procedure (an '*Implementation*') to provide scientific advice on catch limits for different whale stocks (e.g. IWC, 2012). The eastern North Pacific (ENP) population of gray whales is currently subject to aboriginal hunting, with recommended strike limits based on the *Gray Whale Strike Limit Algorithm* (*Gray Whale SLA*) under the Aboriginal Subsistence Whaling Management Procedure (AWMP) of the IWC (IWC, 2003). *Implementation Reviews* are scheduled under the AWMP every five years. The goal of *Implementation Reviews* is to evaluate new information that has become available since the last *Implementation Review* (or the original *Implementation*), *inter alia* to determine whether the current state of nature is outside the realm of plausibility envisioned during the simulation testing of the original *SLA*. If this is the case, additional simulation trials may be conducted to assess whether the anticipated performance of the *SLA* adopted remains reasonable, and if not, what changes to the *SLA* are needed.

New or updated sources of information pertaining to the population dynamics of ENP gray whales have become available in recent years, including: (1) new abundance estimates (Rugh *et. al.,* 2008); (2) new estimates of calf production during 1994–2008 from the northbound migration at Point Piedras Blancas, California (Perryman *et al.*, 2002; Perryman, unpublished data); and (3) the number of stranded animals on the coasts of California, Oregon and Washington states, for which a combined annual count is available for 1975–2006 (Brownell *et al.*, 2007). The last data source potentially contains information on the magnitude of the mortality event during 1999/2000 (Gulland *et al.*, 2005). In addition to these data sets, it has been hypothesised that observed variability in the calf counts is a function of the amount of sea-ice covering the feeding grounds in the Bering Sea in the early season (Perryman *et al.*, 2002).

Accordingly, in this paper the performance of the *Gray Whale SLA* is tested given scenarios when future population dynamics are subject to environmental forcing and episodic events, using an operating model that integrates these sources of new information and the hypothesis of environmental forcing on the population dynamics (Brandon and Punt, 2009). A forecast of relevant sea-ice conditions based on global climate model output (Overland and Wang, 2007) is used to modify the future stochastic birth and survival rates generated when testing the *SLA*, given the estimated relationships of calf production and strandings data to observed variations in recent sea-ice. This technique involves the incorporation of climate-model-based forecasts into the operating model. The same basic framework is also being used to test the performance of alternative management approaches in other fisheries (e.g. Gulf of Alaska and Eastern Bering Sea walleye pollock, *Theragra chalcogramma*; A'mar *et al.*, 2009; Ianelli *et al.*, 2011).

Standard summary statistics are provided for the trials investigated here, and these are compared to results from the *Evaluation Trials* provided by Punt and Breiwick (2008) to the extent possible. The analyses presented here should help to ensure that the anticipated performance of the current *Gray Whale SLA* remains satisfactory (or else provide insight into potential weaknesses), given the new information that has become available since the phase of testing and adoption reported in IWC (2005a).

METHODS

Operating model

The population dynamics model developed by Brandon and Punt (2009) (corresponding to their 'Full' scenario) was used as the operating model. This model is sex- and age-based,

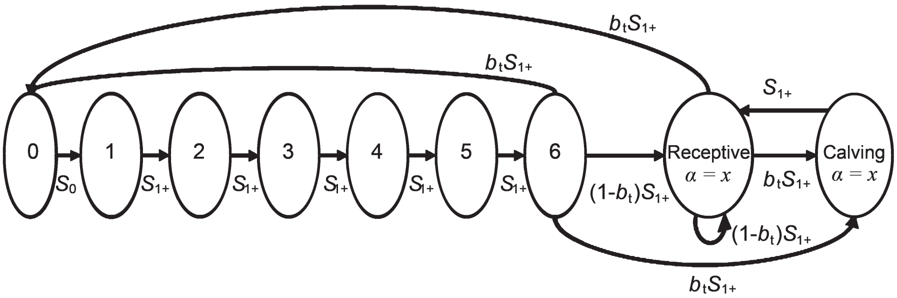

Fig. 1. Life cycle graph of the model used to track the number of females in each reproductive stage though time. This life cycle refers to the underlying deterministic model, with transition probabilities shown as functions of life history parameters. However, it should be noted that the birth and survival rates were modified to be stochastic in the all analyses except for 'H0'. The arrow from immature to calf arises because some immatures may mature and give birth (i.e. become pregnant at first estrous) during the projection interval from time t to t+1.

with an annual time-step. The dynamics include stochastic birth and survival rates, and explicitly consider the transition between receptive and calving stages for mature females (Fig. 1). For consistency, the notation of Brandon and Punt (2009) is adopted below.

Density dependence was assumed to act through the birth rate according to a Pella-Tomlinson function of 1+ depletion:

$$b_t = max\left\{0,\ b_{eq} + (b_{max} - b_{eq})\left[1 - \left(\frac{N_{1+,t}}{K_{1+}}\right)^z\right]\right\}N_{1+,t} \quad (1)$$

where b_{max} is the maximum birth rate (in the limit of zero population size); K_1 is the carrying capacity in terms of the 1+ component of the population (all animals aged 1 year and older)[1]; b_{eq} is the equilibrium birth rate at carrying capacity; z is the degree of density-dependent compensation (assumed to equal 2.39, which implies maximum sustainable yield at a population size approximately 60% of K_1, the conventional value for MSYL assumed for whale populations, e.g. IWC, 2005a); and $N_{1+,t}$ is the size of the 1+ component of the population (both sexes combined) at the start of year t.

Selectivity was assumed to be knife-edged and uniform for ages 5+, catches were assumed to be taken at the start of the year, before natural mortality, and the population trajectories were initialised in 1930, under the assumption of a stable-age-distribution given some level of hunting mortality in 1930 (as in Brandon and Punt, 2009). Process error after 1930 ensures that the age-structure by the time data are available is non-equilibrium.

Deviations from expected birth and survival rates were allowed to be functions of sea-ice variability in the Bering Sea. Thus, the operating model is an adaptation of the hypothesis that the variability in calf production the following year may be related to the amount of sea-ice in the Bering Sea early during the feeding season (Perryman *et al.*, 2002). Birth rates were assumed to vary annually about the deterministic value given by Equation (1). Since this rate must lie between zero and one, its realisation in any one year was calculated using a logistic transformation:

$$b_t^* = \left[1 + \exp(-(\Phi^{-1}\left(b_t\right)\sqrt{2.76 + \sigma_\varepsilon^2} + \varepsilon_t + \varepsilon_{\text{add}}))\right]^{-1} \quad (2)$$

Where Φ^{-1} is the inverse standard normal cumulative distribution function; ε_t is the process error deviation for year t, $\varepsilon_t \sim N(0;\sigma_\varepsilon^2)$, σ_ε is a measure of the extent of variability in process error and; allows for additional process error in the birth (and survival) rate during years with extraordinary dynamics, such as 1999 and 2000 (in other years before 2009, this parameter was set equal to zero; see below for how future catastrophic events are generated). This formulation of stochastic birth rates (e.g. the 2.76 factor) ensures that the expected birth rate in a given year equals the deterministic value from Equation (1) (see Appendix A of Brandon and Punt, 2009). The form of Equation (2) (and (3)) is such that 'positive' catastrophic events can lead to very high survival and birth rates (where the maximum birth rate is bounded by 0.99). However, it should be noted that Equation (2) only applies to receptive females and that a high birth rate in one year will result in a decrease in receptive females and hence a lower pregnancy rate the following year (Fig. 1).

Survival rates were also allowed to vary annually with the same process error deviations as birth rates to reflect the assumption that survival and birth rate covary. The effects of process error on survival and birth rate are assumed to be the same in the absence of data to distinguish these sources of process error. It was assumed that process error in survival rates were independent of sex and perfectly correlated between ages in a given year, so that:

$$S_{a,t}^* = \left[1 + \exp(-(\Phi^{-1}\left(S_a\right)\sqrt{2.76 + \sigma_\varepsilon^2} + \varepsilon_t + \varepsilon_{\text{add}}))\right]^{-1} \quad (3)$$

where $S_{a,t}^*$ is the realised age-specific survival rate during year t; and S_a is the expected survival rate from age a to age a+1.

Conditioning

The operating model was conditioned on available data, including: (1) estimates of population size during 1967–2006 (covering the years of surveys) from the southbound migration at Granite Canyon, California (Rugh *et al.*, 2005; 2008); (2) estimates of calf production during 1994–2008[2] from the northbound migration at Point Piedras Blancas,

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[1] Strictly, K_{1+} is only the carrying capacity in the deterministic case (no fluctuations in birth rate and no catastrophic events). It should be interpreted here as a parameter which relates to stochastic carrying capacity. The latter could be defined as the average long-term population size in the absence of catches.

[2] The two early estimates of calf production during 1980–1981 (Poole, 1984) were not used in these analyses.

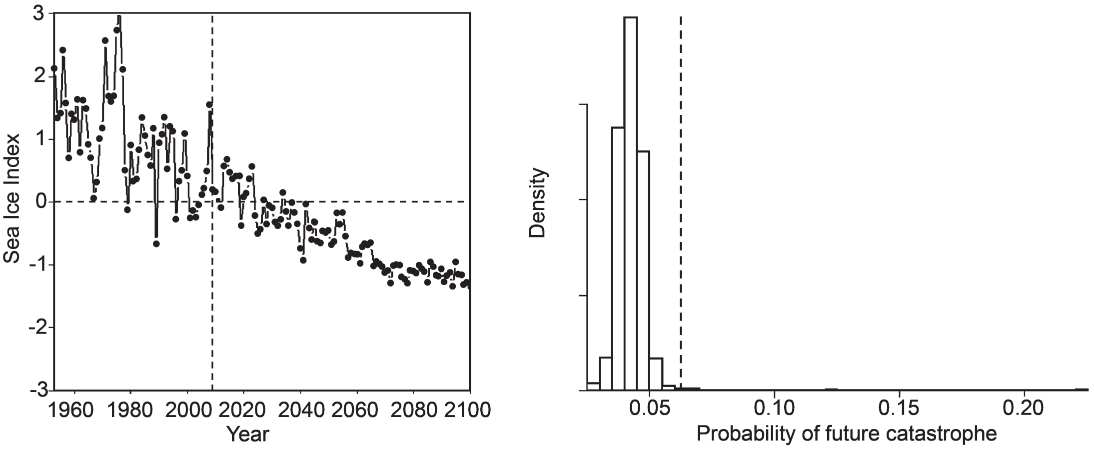

Fig. 2. Left panel: The standardised index for the March–April average sea-ice area covering the Bering Sea. The vertical dashed line denotes 2009 and the start of that portion of the time series which is based on the ensemble global climate model mean predictions provided by Overland and Wang (2007). Prior to 2009, the time series is based on the HadSST observations of sea-ice (Rayner *et al*., 2003). The horizontal dashed line at zero is shown for reference; positive values indicate years with greater than average sea-ice over the entire time period and *vice versa*. Right panel: The distribution for the probability of a future catastrophe in any one year. This distribution is conditioned on the number of years for which the depletion of each trajectory is greater 0.40 during 1930–2008, divided by 2 (the number of years with observed catastrophes, corresponding to 1999 and 2000) (Brandon and Punt, 2009). The dashed vertical line denotes the probability as calculated from the strandings index (Brownell, *et al*., 2007).

California (Perryman *et al*., 2002; Perryman, unpublished data); (3) the number of stranded animals on the coasts of California, Oregon and Washington states, for which a combined annual count is available for 1975–2006 (Brownell *et al*., 2007)[3]; and (4) estimated sea-ice area cover in the Bering Sea, averaged over March and April during 1953–2008, as calculated by the Hadley Center for their sea ice and sea surface temperature data set version 1 ('HadSST') (Rayner *et al*., 2003) (see Fig. 2, left panel). The conditioning process involves fitting the operating model to the data and estimating posterior distributions from the basis for probabilistic projections of future population dynamics.

The deviations of birth and survival rates about the deterministic relationship each year were allowed to be related to an environmental index I_t (the amount of sea-ice covering the Bering Sea) during the conditioning. It was assumed that I_t was measured subject to observation error (or there was some error in the relationship between the process error deviations and the environmental index). Consequently, I_t was a state variable, like the model prediction of population size. Hence, the measurements of the environmental index were treated as data and were consequently included as a component of the likelihood function when the model was fit. The expected environmental index in a given year was assumed to be related to process error residuals for that year, such that the observed index was normally distributed about its expectation:

$$I_t^{obs} = \beta \varepsilon_t + \gamma_t \tag{4}$$

where I_t^{obs} is the observed value of the environmental index in year t; β is a scaling parameter for the influence of the environment on the process error residuals; γ_t the difference between the observed and model-predicted amount of sea ice in year t, such that $\gamma_t \sim N(0;\sigma_I^2)$; and σ_I is the standard deviation of the residual error for the environmental index:

$$\sigma_I = |\beta| \sigma_I^* \tag{5}$$

This formulation takes a fixed input value for (assumed to be 0.30 for these analyses, corresponding to the 'Full' model of Brandon and Punt, 2009) and scales the expected standard deviation of the fits to the environmental index by the estimated absolute value for β.

Future projections

Once the operating model was conditioned on the available data, it was possible to project simulated population trajectories into the future. Each forward projection was initialised in 2009, based on the estimated status of the simulated population and the parameter values (e.g. K_{1+}, $b_{\max}$ etc…) for a given trajectory from the joint Bayesian posterior distribution. The posterior was constructed using the MCMC algorithm during the conditioning phase (Brandon and Punt, 2009).

Future values for the sea-ice index were based on an ensemble mean forecast of sea-ice in the Bering Sea (March–April average) (Overland and Wang, 2007). The trials were based on a 92-year time horizon ($T = 92$), because the time series of forecasted sea-ice was only available until 2098. In a given year, the process error deviations about the expected birth and survival rates were a function of forecasted sea-ice according to:

$$\varepsilon_t = \left(I_t^{obs} / \beta \right) - \gamma_t \tag{6}$$

where I_t^{obs} is the forecasted value of the sea-ice index for year t (Fig. 2, left panel); and $\gamma_t \sim N(0;\sigma_I^2)$

Future abundance estimates were assumed to become available every 10 years. Observation error was assumed to be log-normal:

$$N_{1+,t}^{\text{obs}} = N_{1+,t} e^{\phi_t} \tag{7}$$

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[3] Data on strandings are collected in other locations (e.g. Mexico and Alaska), but the stranding network effort in California, Oregon and Washington has been more consistent over time.

where $I^{obs}_{1+,t}$ is the survey estimate of 1+ abundance for year t; $N_{1+,t}$ is the 'true' 1+ abundance at the start of year t; $\phi_t \sim N(0;\sigma^2)$; where $\sigma = \sqrt{\overline{CV}^2_{\text{est}} + CV^2_{\text{addA}}}$; CV_{addA} is the extent of additional error about the abundance estimates (sampled from the joint posterior), and; $\overline{CV}_{est}$ is the expected (sampling) standard deviation of the logarithm of $N^{obs}_{1+,t}$:

$$\overline{CV}_{est} = \sqrt{\tfrac{1}{Y}\sum_{y=1}^{Y} CV_{\text{y}}^2} \qquad (8)$$

where y indexes years for which there are survey data up to 2008; CV_y is the sampling CV associated with the abundance estimate for year y; and Y is the total number of years with past surveys. The estimates of abundance and $\overline{CV}_{est}$ (as distinct from σ) were passed to the *SLA*. No attempt was made to account for further estimation error in the abundance estimates (i.e. mean school size estimation error calculations were ignored).

Need[4]

The annual need Q_t for year t was calculated according to the 'need envelope':

$$Q_t = Q_{2009} + \frac{t-2009}{91}\left(Q_{2098} - Q_{2009}\right) \qquad (9)$$

where Q_{2009} (= 150) is the present need; and Q_{2098} is the final need (in year 2098). The level of need supplied to the *SLA* was the total (block) need for the 5-year period for which the strike limits were to be set. Two values were assumed for final need (in year 2098), corresponding to the 'base case' (Q_{2098} = 340) and 'high need' (Q_{2098} = 530) trial levels used in previous testing of the *SLA* (IWC, 2003).

Trials

The set of trials is listed in Table 1. In addition to the two levels of final need, six scenarios were explored with respect to p^*, the future probability (if any) of catastrophic (otherwise known as 'episodic') events, and the nature of stochastic (or deterministic) population dynamics.

(1) (H0) Deterministic population dynamics with no future catastrophic events[5];

(2) (H1) Environmental stochasticity (as a function of sea-ice) with no future catastrophic events;

(3) (H2) Environmental stochasticity (as a function of sea-ice), with probability of future catastrophic events conditioned on the stranding index (0.0625, the proportion of years for which an episodic event was observed, divided by the total number of years in the strandings index (2yr/32yr) (Brownell *et al.*, 2007));

(4) (H3) Environmental stochasticity (as a function of sea-ice) with the probability of future catastrophic events conditioned on the percentage of times they occurred during the fitting process when 1+ depletion was greater than 0.40 (Eqn. 9; Fig. 2 right);

(5) (H4) As for H3, but the environmental stochasticity was independent of the sea-ice index, i.e. simply $\varepsilon_t \sim N(0,\sigma_\varepsilon^2)$; and

(6) (H5) As for H4 but with no future catastrophes.

A depletion level of 0.40 during the conditioning phase was used for calculating the probability of future episodic events for scenarios H3 and H4 because the population almost always recovers to 40% of carrying capacity by when the catastrophes occur. The probability of future catastrophes p^* conditioned on the percentage of times they occurred during the fitting process when 1+ depletion was greater than 0.40 was then:

$$p^* = 2\left[\left(\sum_{t=1930}^{2008} I(N_{1+,t}/K > 0.4)\right)^{-1}\right] \qquad (10)$$

where $I()$ is the indicator function. Hence, a future year was determined to be either normal ($\varepsilon_{\text{add}} = 0$) or catastrophic by drawing a random variate from a Bernoulli distribution with probability p^* for these scenarios if the 1+ depletion was greater than 0.40. Future catastrophic years were modelled through the inclusion of the estimated ε_{add} parameter into Eqn. 2 and 3 for birth and survival rates during those years (Fig. 2, right).

No attempt was made to model correlation between years with catastrophes, i.e. the probability of a catastrophe occurring did not depend on the whether or not there was one the previous year.

Performance statistics

The performance statistics were calculated based on future block quotas returned from the standalone version of the 'GUP2' *SLA* (IWC, 2005b; Punt and Breiwick, 2008). All performance statistics were computed in terms of the age 1+ component of the population following the standard methods and notation of the AWMP (IWC, 2003). Specifically, four performance statistics were calculated:

(1) (D1) Final depletion: $N_{1+,2098}/K_{1+}$;

(2) (D8) Rescaled final population size: $N_{1+,2098}/N^*_{1+,2098}$, where $N_{1+,2098}$ is the 1+ population size in 2098, under a scenario of zero future catches;

(3) (D10) Relative increase: $N_{1+,2098}/N_{1+,2009}$; and

(4) (N9) Average need satisfaction: $\dfrac{1}{T}\sum\limits_{t=2009}^{2098}\dfrac{C_t}{Q_t}$

where T is the number of years in the projection period; and C_t is the catch during year t, which is determined by the *SLA* through the 5-year block quota system.

RESULTS

1,601 simulations were run for each scenario, corresponding to the number of samples from the posterior provided by Brandon and Punt (2009). In general, the *Gray Whale SLA* was able to satisfy need and maintain a population size near carrying capacity for all of scenarios examined in these analyses. For example, all of the scenarios with base need had an average need satisfaction of 100% and the lowest median final 1+ depletion was 0.874 (Table 2). Not

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[4] This is the number of whales a country or the Commission specifies is required to satisfy cultural and subsistence 'needs' before taking the conservation situation into account

[5] The two deterministic trials are most comparable with the base case operating models in IWC (2004).

Table 1

The scenarios considered. The trials are denoted by an 'H' followed with the trial number and then 'BN' or 'HN' for base or high final need. Descriptions are given for each scenario in terms of the stochastic or deterministic nature of the population dynamics and the probability of future catastrophes.

Trial	Description	σ_ε	Final need	Probability of future catastrophe	Future stochasticity
H0:BN	Deterministic + no future catastrophes	N/A	340	0	None (deterministic)
H1:BN	Environmental stochasticity + no future catastrophes	0.5	340	0	Environmental
H2:BN	Environmental stochasticity + *p*(future catastrophe) = 0.0625	0.5	340	0.0625	Environmental
H3:BN	Environmental stochasticity + *p*(future catastrophe) = *p**	0.5	340	*p** (Eqn. 10)	Environmental
H4:BN	Stochasticity (no sea-ice) + *p*(future catastrophe) = *p**	0.5	340	*p** (Eqn. 10)	Environmental (no sea-ice)
H5:BN	Stochasticity (no sea-ice) + no future catastrophes	0.5	340	0	Environmental (no sea-ice)
H0:HN	Deterministic + no future catastrophes	N/A	530	0	None (deterministic)
H1:HN	Environmental stochasticity + no future catastrophes	0.5	530	0	Environmental
H2:HN	Environmental stochasticity + *p*(future catastrophe) = 0.0625	0.5	530	0.0625	Environmental
H3:HN	Environmental stochasticity + *p*(future catastrophe) = *p**	0.5	530	*p** (Eqn. 10)	Environmental
H4:HN	Stochasticity (no sea-ice) + *p*(future catastrophe) = *p**	0.5	530	*p** (Eqn. 10)	Environmental (no sea-ice)
H5:HN	Stochasticity (no sea-ice) + no future catastrophes	0.5	530	0	Environmental (no sea-ice)

surprisingly, those scenarios based on higher final need resulted in lower final depletion levels and lower average need satisfaction. However, the differences were not large (e.g. the lowest median 1+ depletion for the high need scenarios was 0.817). Moreover, none of the scenarios resulted in a lower 5th percentile for the final 1+ depletion less than 0.60. The relative increase statistic (D10) was close to 1 for all scenarios. The increase in population size is somewhat constrained because even under decreases in ice cover, Eqn. 1 still imposes an upper bound on abundance.

The distribution of probabilities of future catastrophes for the 'H3' and 'H4' scenarios is shown in Fig. 2 (right panel). The probability of future catastrophe ranged between 0.025 and 0.222 for those scenarios, with a median of 0.043, which was less than that when conditioned on the stranding index. However, the average difference between these two approaches was relatively small, as evidenced by the nearly identical results for these two assumptions (Table 2; Fig. 3).

The predicted area of sea-ice on the Bering Sea feeding grounds is forecast to decrease dramatically, with less than 50% of the average observed area of sea-ice in March–April during future decades (Fig. 2, left panel; Overland and Wang, 2007). The scenarios H1, H2, and H3 with population dynamics that are a function of this sea-ice index resulted in the most optimistic outcomes (Table 2), with some final depletion levels slightly greater than 1.0. On the other hand, the two scenarios that modelled generic environmental stochasticity independent of sea-ice (H4 and H5) resulted in the most pessimistic final depletion levels of any of the scenarios investigated (Table 2). Likewise, the trend in process error deviations was very different between these two sets of scenarios. Those scenarios which modelled

Table 2

The medians, and upper and lower 5th percentiles of the performance statistics for each scenario. See text for the definitions for each of the performance statistics.

		D1: Final 1+ depletion			D8: Rescaled 1+ depletion			D10: 1+ relative increase			N9: Avg. need satisfaction		
Trial	Description	5%	Median	95%	5%	Median	95%	5%	Median	95%	5%	Median	95%
H0:BN	Deterministic + no future catastrophes	0.908	0.933	0.950	0.875	0.918	0.948	0.947	0.986	1.095	1.000	1.000	1.000
H1:BN	Environmental stochasticity + no future catastrophes	0.940	0.981	1.030	0.910	0.965	1.019	0.973	1.041	1.179	1.000	1.000	1.000
H2:BN	Environmental stochasticity + p(future catastrophe) = 0.0625	0.914	0.974	1.026	0.886	0.959	1.016	0.954	1.032	1.158	1.000	1.000	1.000
H3:BN	Environmental stochasticity + p(future catastrophe) = *p**	0.922	0.976	1.027	0.896	0.961	1.017	0.960	1.034	1.167	1.000	1.000	1.000
H4:BN	Stochasticity (no sea-ice) + *p*(future catastrophe) = *p**	0.745	0.874	0.953	0.731	0.861	0.945	0.807	0.932	1.050	1.000	1.000	1.000
H5:BN	Stochasticity (no sea-ice) + no future catastrophes	0.802	0.897	0.960	0.775	0.883	0.954	0.846	0.952	1.066	1.000	1.000	1.000
H0:HN	Deterministic + no future catastrophes	0.855	0.899	0.927	0.833	0.884	0.921	0.913	0.950	1.038	0.971	0.980	0.988
H1:HN	Environmental stochasticity + no future catastrophes	0.913	0.963	1.017	0.889	0.946	1.006	0.951	1.022	1.156	0.974	0.981	0.988
H2:HN	Environmental stochasticity + *p*(future catastrophe) = 0.0625	0.880	0.954	1.011	0.858	0.937	1.001	0.927	1.011	1.132	0.973	0.981	0.988
H3:HN	Environmental stochasticity + *p*(future catastrophe) = *p**	0.894	0.957	1.013	0.868	0.941	1.002	0.932	1.015	1.138	0.973	0.981	0.988
H4:HN	Stochasticity (no sea-ice) + *p*(future catastrophe) = *p**	0.657	0.817	0.917	0.649	0.805	0.909	0.725	0.873	0.989	0.959	0.979	0.987
H5:HN	Stochasticity (no sea-ice) + no future catastrophes	0.722	0.847	0.927	0.707	0.834	0.921	0.776	0.901	1.013	0.964	0.980	0.988

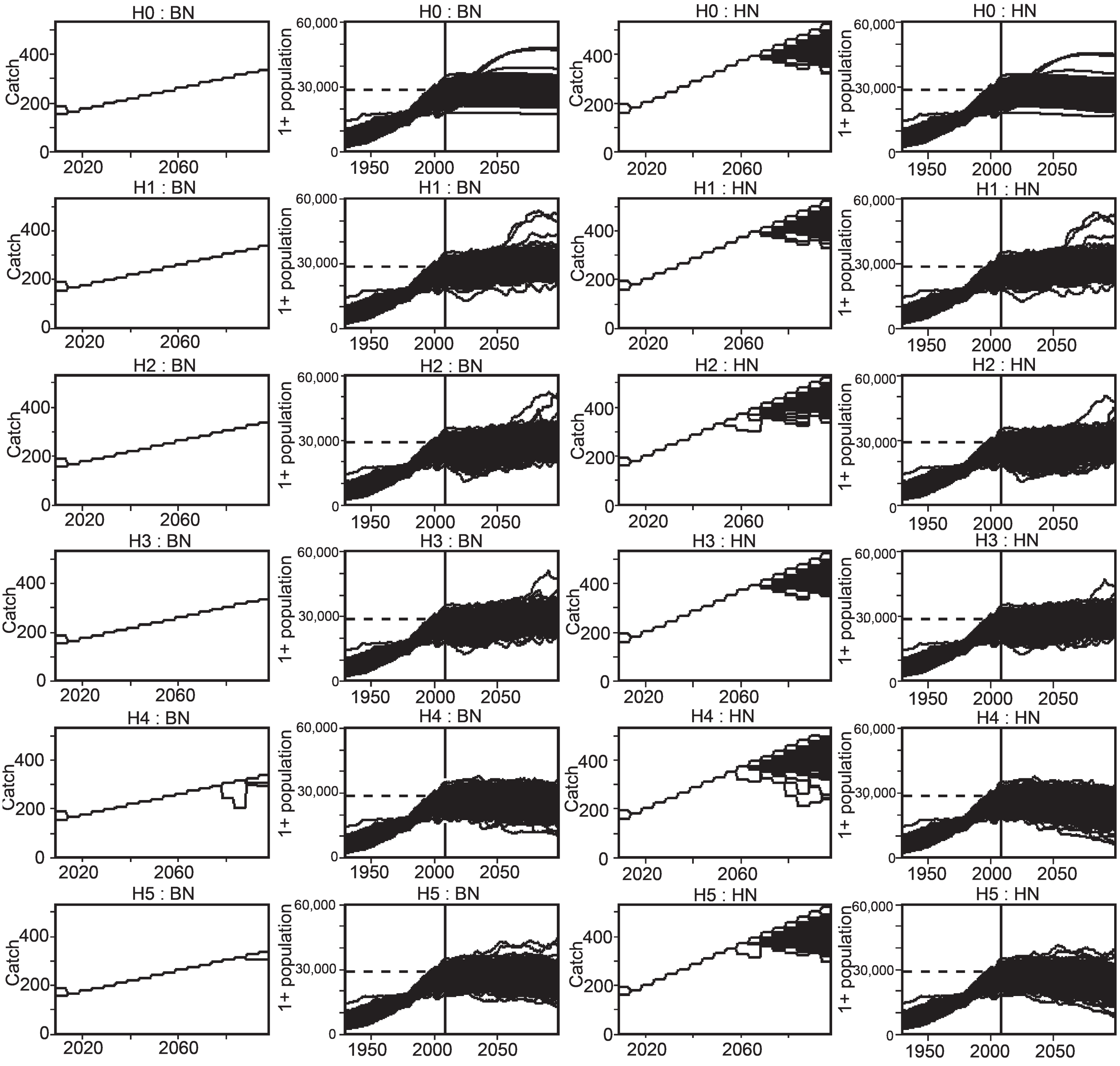

Fig. 3. Time-trajectories of future catches (first and third columns) and population trajectories from 1930–2098 (second and fourth columns) for the twelve scenarios (Table 1). The left and right pairs of columns are respectively for a final need levels of 340 and 530 whales per year. The results for each simulation are plotted as an individual line (thus a single visible line for catches represents a series of years where future catches were identical across scenarios).

process error as a function of future sea-ice resulted in an increasing trend in the size of process error deviations, while those scenarios which modelled environmental stochasticity as an independent process led to no such trend (Fig. 4). However, in terms of the median average need satisfaction, there was essentially no difference amongst all the scenarios; the *SLA* was able to achieve high need satisfaction for all of those examined here (Table 2).

The results of the 'deterministic' trials (H0) were more optimistic than those of the corresponding trials on which the *Gray Whale SLA* was based (GE01 and GE14) (compare table 2 of Breiwick *et al.* (2009) with the results for the two H0 trials in Table 2 of this paper). However, the differences in the values for the performance statistics are slight, and qualitatively the results of trial H0 and GE01 are identical. The differences in results are attributable to a variety of causes, including differences in the population dynamics models, in the data used to condition the operating model, and in the priors for the parameters of that model.

DISCUSSION

The approach taken here allows a forecast for an index of environmental variability to be incorporated into an operating model, which can be used to test management approaches given hypothesized interactions between the environment and population dynamics. These trials differ slightly from the standard set designed by the Standing Working Group of the AWMP during the original *Implementation* of the *Gray Whale SLA* (IWC, 2005a) in that they are conditioned on updated and newly available data, as well as a hypothesis regarding the effect of sea-ice on deviations in demographic rates. Hence, these analyses serve

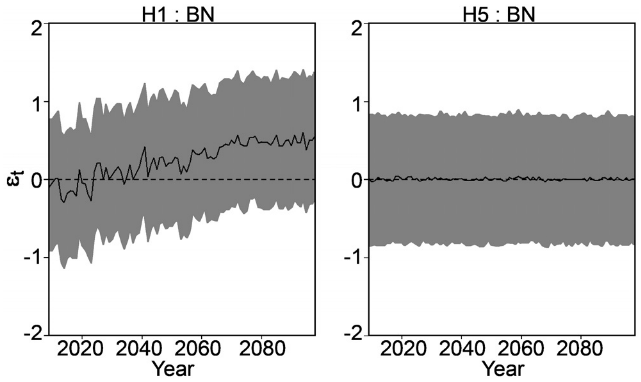

Fig. 4. The time-trajectories of future process error deviations for a case where these deviations are a function of future sea-ice (H1:BN; left panel) and where they are independent of the sea-ice index (H5: BN; right panel). The annual median is plotted as the solid line, the 90% probability interval envelope is shaded in gray, and the horizontal dashed line at zero is shown for reference.

to take account of new information that has become available since the original *Implementation*. The results provide evidence that the current state of nature is not outside the realm of plausibility envisioned during the simulation testing of the original *SLA*.

The magnitude of future additional mortality events was assigned in an *ad hoc* manner during the original *Implementation* of the *Gray Whale SLA*, i.e. future events were assumed to result in 20% declines in abundance (a likely large value, chosen to test the robustness of the *SLA*). In these analyses however, the operating model is conditioned in part on the strandings data, which allows the deviations in survival rates during the 1999/2000 mortality event and the resulting population size at the start of the future trajectories to be estimated directly. Likewise, the observed frequency and magnitude of those mortality events determined when conditioning are used to model the potential impact of future events. A set of several alternative trials was also preformed, to compare the results of the environmental forcing scenario to those for which future population dynamics were assumed to be deterministic, or to be subject to random environmental stochasticity (i.e. ignoring possible sea-ice impacts). For all of the scenarios considered here, the *Gray Whale SLA* was able to maintain stock size and satisfy need at higher levels. Therefore, there is no indication from these analyses that any revisions to the *SLA* are necessary.

While the *SLA* performed well under the scenarios considered in these analyses, there is still considerable uncertainty about how changes in sea-ice (or other environmental conditions) will affect future population dynamics. At present, the available information about the affects of environmental variability on cetacean population dynamics is largely correlative in nature, with the underlying mechanisms responsible for fluctuations in birth and survival rates not well understood. Although a plausible explanation has been hypothesised for ENP gray whales (i.e. that sea-ice may act as a physical barrier to prime feeding habitat), it is not straightforward to predict how other changes resulting from reductions in sea-ice will interact with the mechanisms that are currently influencing the dynamics of this population. Therefore, the conclusion that the *Gray Whale SLA* is robust to predicted changes in sea-ice should be tempered by uncertainty regarding the underlying assumption that current ecological processes will remain unchanged in the future, especially when so many other fundamental changes in ecosystems are expected as a result of climate change. Indeed, this one is one of the reasons *Implementation Reviews* are mandatory.

The assumption that the population dynamics were related to sea-ice led to more optimistic results. This was essentially the result of extrapolating (based on those years for which calf production and strandings data exist) a recent relationship between the environment and population dynamics into the future, under the assumption that such an effect (if it exists) would be invariant over time and independent of population density, among other factors. While more optimistic results would have been expected given the nature of the relationship between calf production and sea-ice cover, the magnitude of the effect could not be determined *a priori*. In addition, it was possible that the impact of trends in birth rate and survival could have 'confused' the *SLA* and led to poorer performance (e.g. the models underlying the *SLA*s could have concluded that the stock was depleted rather than close to carrying capacity) and reduced the strike limit.

The operating model used here could be modified to take into account alternative hypotheses with respect to predicted changes in the relationship between future environmental variability and population dynamics. For example, it would be relatively straightforward to model a change-point in the relationship between deviations in demographic rates and sea-ice, such that a loss of sea-ice might be beneficial up to some future time, after which the continued loss of sea-ice results in negative effects on population dynamics (e.g. by changing the sign of β after some future year). The operating model could then be used to test the performance of the *SLA* under such scenarios. A disadvantage of this approach would be that there are no data to determine the magnitude of negative effects, so any results would be speculative.

One of the appealing attributes of the framework for incorporating environmental data is its flexibility. As continuing research provides more insight into the mechanisms underlying the impacts of environmental variability on the population dynamics of ENP gray whales, the basic operating model used here can provide a basis for integrating this new information into assessments and evaluating alternative management approaches. For example, alternative environmental data (e.g. an index of El Niño/Southern Oscillation, a sea-ice index on the Chukchi Seas feeding grounds, or some weighted combination of different indices) could be substituted during the model fitting process to take alternative hypothesised relationships between environmental variability and population dynamics into account. Likewise, the framework could, with some modification, be applied to other populations of cetaceans for which environmental fluctuations are hypothesised to be an important determinant of population dynamics. Therefore, this framework should help to ensure that management strategies are robust to hypothesised impacts of future environmental variability on cetacean population dynamics.

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REFERENCES

A'mar, Z., Punt, A.E. and Dorn, M.W. 2009. The evaluation of two management strategies for the Gulf of Alaska walleye pollock under climate change. ICES *J. Mar. Sci.* 66: 1,614–32.

Brandon, J.R. and Punt, A.E. 2009. Assessment of the eastern stock of North Pacific gray whales: incorporating calf production, sea-ice and strandings data. Paper SC/61/AWMP2 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 29pp. [Paper available from the Office of this Journal].

Breiwick, J.M., Punt, A.E., Rugh, D.J., Laake, J.L. and Hobbs, R.C. 2009. Revised methods for estimating abundance of the eastern North Pacific stock of gray whales. Paper SC/61/AWMP1 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 10pp. [Paper available from the Office of this Journal].

Brownell, R.L., Makeyev, C.A.F. and Rowles, T.K. 2007. Stranding trends for eastern gray whales, *Eschrichtius robustus*: 1975–2006. Paper SC/59/BRG40 presented to the IWC Scientific Committee, May 2007, Anchorage, Alaska (unpublished). 11pp. [Paper available from the Office of this Journal].

Gulland, F.M.D., Pérez-Cortés, H., Urbán, J.R., Rojas-Bracho, L., Ylitalo, G., Weir, J., Norman, S.A., Muto, M.M., Rugh, D.J., Kreuder, C. and Rowles, T. 2005. Eastern North Pacific gray whale (*Eschrichtius robustus*) unusual mortality event, 1999–2000. *NOAA Tech. Mem. NMFS-AFSC-. 150.* 34pp. [Available at: *www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-150.pdf*].

Ianelli, J.N., Hollowed, A.B., Haynie, A.C., Mueter, F.J. and Bond, N.A. 2011. Evaluating management strategies for eastern Bering Sea walleye pollock (*Theragra chalcogramma*) in a changing environment. *ICES. J. Mar. Sci.* 68: 1,297–304.

International Whaling Commission. 2003. Report of the Scientific Committee. Annex E. Report of the Standing Working Group on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP). *J. Cetacean Res. Manage. (Suppl.)* 5:154–255.

International Whaling Commission. 2004. Report of the Scientific Committee. Annex E. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP). Appendix 3. Fishery Type 2: Implementation for Eastern North Pacific gray whales. *J. Cetacean Res. Manage. (Suppl.)* 6: 195–206.

International Whaling Commission. 2005a. Report of the Scientific Committee. Annex E. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP). Appendix 3. Fishery Type 2: *Implementation* for Eastern North Pacific gray whales. *J. Cetacean Res. Manage. (Suppl.)* 7: 127–38.

International Whaling Commission. 2005b. Report of the Scientific Committee. Annex E. Report of the Standing Working Group (SWG) on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP). Appendix 4. Specification of the component *SLA*s for the recommended gray whales SLA. *J. Cetacean Res. Manage. (Suppl.)* 7: 141–43.

International Whaling Commission. 2012. Requirements and Guidelines for *Implementations* under the Revised Management Procedure. *J. Cetacean Res. Manage.* 13: 495–506.

Overland, J. and Wang, M. 2007. Future regional Arctic sea ice declines. *Geophys. Res. Lett.* 34: L17705.

Perryman, W.L., Donahue, M.A., Perkins, P.C. and Reilly, S.B. 2002. Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Mar. Mammal Sci.* 18(1): 121–44.

Poole, M.M. 1984. Preliminary assessment of annual calf production in the gray whale, *Eschrichtius robustus*, from Pt Piedras Blancas, California. *Rep. int. Whal. Commn (special issue)* 6: 223–31.

Punt, A.E. and Breiwick, J.M. 2008. On standalone versions of the *Bowhead* and *Gray Whale SLAs*. Paper SC/M08/AWMP1 presented to the Workshop on Developing Assessment Methods and a Management Procedure for Greenlandic Fisheries, 26–29 March 2008, Copenhagen (unpublished). 11pp. [Paper available from the Office of this Journal].

Rayner, N.A., Parker, D., Horton, E., Folland, L., Alexander, L., Rowell, D., Kent, E. and Kaplan, A. 2003. Global analyses of sea surface temperature, sea ice and night marine air temperature since the late nineteenth century. *J. Geophys. Res.* 108: 4407 No. D14.

Rugh, D., Breiwick, J., Hobbs, R., Shelden, K. and Muto, M. 2008. Eastern North Pacific gray whale abundance in the winter of 2006–2007. Paper SC/60/BRG6 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 12pp. [Paper available from the Office of this Journal].

Rugh, D.J., Hobbs, R.C., Lerczak, J.A. and Breiwick, J.M. 2005. Estimates of abundance of the Eastern North Pacific stock of gray whales 1997 to 2002. *J. Cetacean Res. Manage.* 7(1): 1–12.