The forgotten whale: a bibliometric analysis and literature review of the North Atlantic sei whale *Balaenoptera borealis*

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ABSTRACT
1. A bibliometric analysis of the literature on the sei whale *Balaenoptera borealis* is presented. Research output on the species is quantified and compared with research on four other whale species. The results show a significant increase in research for all species except the sei whale. Research output is characterized chronologically and by oceanic basin.
2. The species' distribution, movements, stock structure, feeding, reproduction, abundance, acoustics, mortality and threats are reviewed for the North Atlantic, and the review is complemented with previously unpublished data.
3. Knowledge on the distribution and movements of the sei whale in the North Atlantic is still mainly derived from whaling records. Movement patterns and winter distribution are not clear. Surveys in some known summering areas show that the species has changed its distribution in parts of its previously known range.
4. With the present information, it is impossible to determine whether or not the North Atlantic sei whale population is subdivided into biological units. Abundance estimates are fragmentary and cover a restricted part of the summering habitat.
5. In the North Atlantic, sei whales seem to be stenophagous, feeding almost exclusively on calanoid copepods and euphausiids. On feeding grounds, they are associated with oceanic frontal systems, but how they find and explore these structures has not been fully investigated.

6. The available data on vital rates are based on whaling-derived studies and are 25 years old or older. Despite increasing human and environmentally induced pressures, there are no current estimates for mortality and population trends.
7. Current research needs include the clear definition of stock units, reliable abundance estimates, studies of distribution and migration that incorporate the identification of wintering areas, acquisition of up-to-date data on reproduction and mortality, and investigations into the consequences of environmental changes for the species.

INTRODUCTION

The sei whale *Balaenoptera borealis* is the third largest member of the Balaenopteridae family, after the blue whale *B. musculus* and the fin whale *B. physalus*, and is one of the least known mysticete whales. The species is cosmopolitan, inhabiting the world's temperate to subpolar oceans, with generally antitropical distribution centred in temperate zones. The populations in the North Atlantic, North Pacific and Southern Ocean are almost certainly separated, and may be further subdivided into geographical stocks (Horwood 1987). Sei whales are thought to undertake seasonal migrations from low-latitude wintering areas to high-latitude summer feeding grounds. The locations of winter calving grounds are unknown (Perry et al. 1999), and summer distribution on the feeding grounds exhibits great year-to-year variability (Jonsgård & Darling 1977). Throughout their range, sei whales occur predominately in deep waters. In feeding areas, they are most common over the continental slope or in basins situated between banks (Perry et al. 1999). Sei whales feed primarily on calanoid copepods and euphausiids, although small schooling fishes and squid form an important part of their diet in some areas (Horwood 1987).

Due to its smaller size, interest in this species by the whaling industry was low until the 1950s. After the decline of more valuable species such as blue, fin and humpback whales *Megaptera novaeangliae*, the whaling industry started targeting smaller species, particularly sei whales. Subsequently, sei whales were heavily exploited throughout their range and populations decreased drastically (Horwood 1987). Despite a period of intense commercial hunting, and a subsequent declaration by the International Whaling Commission (IWC) that the management of all whale populations was dependent on comprehensive knowledge of their ecology (Donovan 1989), little information existed on essential aspects of sei whales' life history and ecology.

By the end of the 1970s, it was recognized that the information available on population dynamics of sei whales and Bryde's whales *B. edeni* was insufficient for their proper management, leading to a special meeting on these species in 1977 (Anonymous 1977). Knowledge on the two species increased following that meeting but, subsequently, research interest diminished. With the onset of a moratorium on whaling during the 1985–86 pelagic and 1986 coastal seasons, most of the research effort shifted to other species such as right *Eubalaena glacialis, E. australis*, humpback, blue and fin whales. In

addition, more research effort was put into studying minke whales *B. acutorostrata*, the only species still killed in significant numbers for scientific and commercial reasons. In addition to the low level of scientific and commercial whaling interest in sei whales, the costs of studying cetaceans associated with pelagic habitats hindered research on the sei whale. Sei whales are also difficult to distinguish from Bryde's whales where the two species' ranges overlap, and are often mistaken for fin whales, impacting our understanding of the species' distribution and population size.

Joseph Horwood wrote an influential monograph on the species in 1987, summarizing all the knowledge accumulated on the sei whale to that date, which became the foremost reference on the population biology of the species. Despite the depth of that work, the author stated in the concluding remarks that '[it is] . . . obvious that many aspects [of the population dynamics] can profit by more research . . .' (Horwood 1987), after which he indicated directions for future research. Despite Horwood's advice, and possibly due to the persistence of the reasons mentioned above, sei whale research has advanced little since then. As in other regions, research on North Atlantic sei whales has been closely linked to whaling. Although commercial whaling ceased in the North Atlantic in 1988, most of the literature available still relies on whaling data, and scant new information has been published since whaling ceased.

In this review, we have three main objectives: (i) to undertake a bibliometric analysis in order to quantify the evolution of research on the sei whale, with emphasis on the North Atlantic; (ii) to summarize the state of knowledge about the species in the North Atlantic, by reviewing historical data, correcting some previous reports based on more recent knowledge and reporting the research produced in the last 20 years, including new unpublished data; and (iii) to identify knowledge gaps and further research needed for the proper management of this species.

METHODS
Bibliometric analysis
We used the Marine Mammal Database and Digital Library of the Natural History Museum of Los Angeles County (hereafter designated as MMD). This database was chosen because it is one of the most comprehensive literature databases specialized in marine mammals, with 52039 entries at the time of accession (28 July 2010). Records in this database date back to 1665, but there are great temporal gaps between entries until the mid-19th century. To avoid bias due to a poor representation of older references, we restricted our search to records published after 1860.

To enable comparison of the results with those from similar species, we searched for publications on blue, fin and humpback whales as well as on the two forms of minke whales *B. acutorostrata* and *B. bonaerensis*. We decided to combine the results for the two species of minke whales due to the difficulty of separating them in works published prior to the late 1990s. The database was filtered by the known vernacular English names as well as the current scientific denominations and synonymia for each species in the Title, Keywords and Abstract fields. We acknowledge that the method we used may miss some entries, but we consider that these false negatives are negligible in the scope of the total number of references detected. Moreover, concerning the comparison among species, there is no reason to think that the method favours the detection of any specific species in the literature over the others.

The database includes several types of contributions, but we used only peer-reviewed publications and scientific books or monographs. Conference proceedings, book reviews, non-peer reviewed technical reports, unpublished documents, unpublished theses, popular articles and similar were rejected. Duplicates and false positives (e.g. under 'sei' results such as 'seismic', 'seining', '*hosei*', etc.) were eliminated from the resulting bibliographic listings. Known mistaken species attributions (e.g. the Bonin Islands Bryde's whales that were wrongly reported as sei whales for a long time) were also eliminated from the listings.

Each publication on sei whales was then assigned to a unique oceanic basin, whenever that information was available (North Atlantic, South Atlantic, North Pacific, South Pacific, Mediterranean, Indian Ocean and Southern Ocean). Publications dealing with more than one of the above ocean basins or with global significance (e.g. some physiological studies) were assigned to a 'world' category, and those with no information on oceanic basin were classified as 'unknown'. Subsequently, descriptors were assigned to each publication according to the main focus of the publication. The descriptors used were as follows: phylogeny, anatomy, physiology, feeding ecology, reproduction/social ecology, distribution/movements, stock structure, acoustics, population assessment/management, pathology/natural mortality/threats, molecular biology/genetics, age determination/growth. As a result of the overlapping nature of some of the descriptors and depending on the focus of the publication, more than one descriptor could be assigned to the same publication.

We considered all publications as having equal weight since we were quantifying research activity, not the influence of individual publications over the subjects investigated (Price 1951).

The main bibliometric indicator of production used was Price's Law on scientific literature growth. This law is the most widely used indicator for the analysis of productivity of a specific scientific field, and states that scientific production follows an exponential growth (Price 1951). Failure in the fulfilment of this postulate indicates either that (i) a field has reached a saturation point in which the growth changes from exponential to linear and can ultimately decrease steadily towards zero or that (ii) artificial boundaries preclude the assignment of adequate resources to the progress of the subject under investigation.

A second indicator used in the present analysis is the national participation index (PI) for overall scientific production. The PI was calculated as the ratio of the number of publications per million people generated by country and the total number of publications on the subject for the period. Only the lead author was considered for country assignment of each publication since in many publications the affiliations of the co-authors were not mentioned. To calculate the number of publications per million people, we estimated the mid-decadal country populations using the average of the fifth and sixth year of each decade. All demographics were obtained from the U. S. Census Bureau except for the years 1880–89 that were derived from Anonymous (1891).

Literature review
We compiled data from published material and 'grey literature' from the MMD and from other sources, including other scientific libraries and the authors' personal libraries. We also contacted specialists that we knew had relevant unpublished information on North

Atlantic sei whales. Whenever possible, we tried to confirm species identification between sei and Bryde's whales. Problematic identifications are discussed in the text, especially with regard to whaling statistics.

RESULTS
Bibliometric analysis
At a global level, a total of 261 publications were detected on sei whales, 332 on blue whales, 515 on fin whales, 867 on minke whales and 954 on humpback whales. Research output was negligible prior to the 1940s and has increased more for the other species than for the sei whale in the last 20 years (Fig. 1). In order to assess whether the scientific output for each of the species follows Price's Law of exponential literature growth, we fitted linear and exponential models to the data. We used only data from 1940 onwards to coincide with the initial growth of scientific literature on these species. Except for the sei whale, there was a significant growth in research output for all species, and the exponential model best explained that growth (blue r^2: 0.52; fin r^2: 0.63; humpback r^2: 0.75; minke r^2: 0.75; $P < 0.05$ for all species). In some cases, the exponential and linear models both had a close fit towards the last 20 years, indicating a change from exponential to linear growth as predicted by Price's Law.
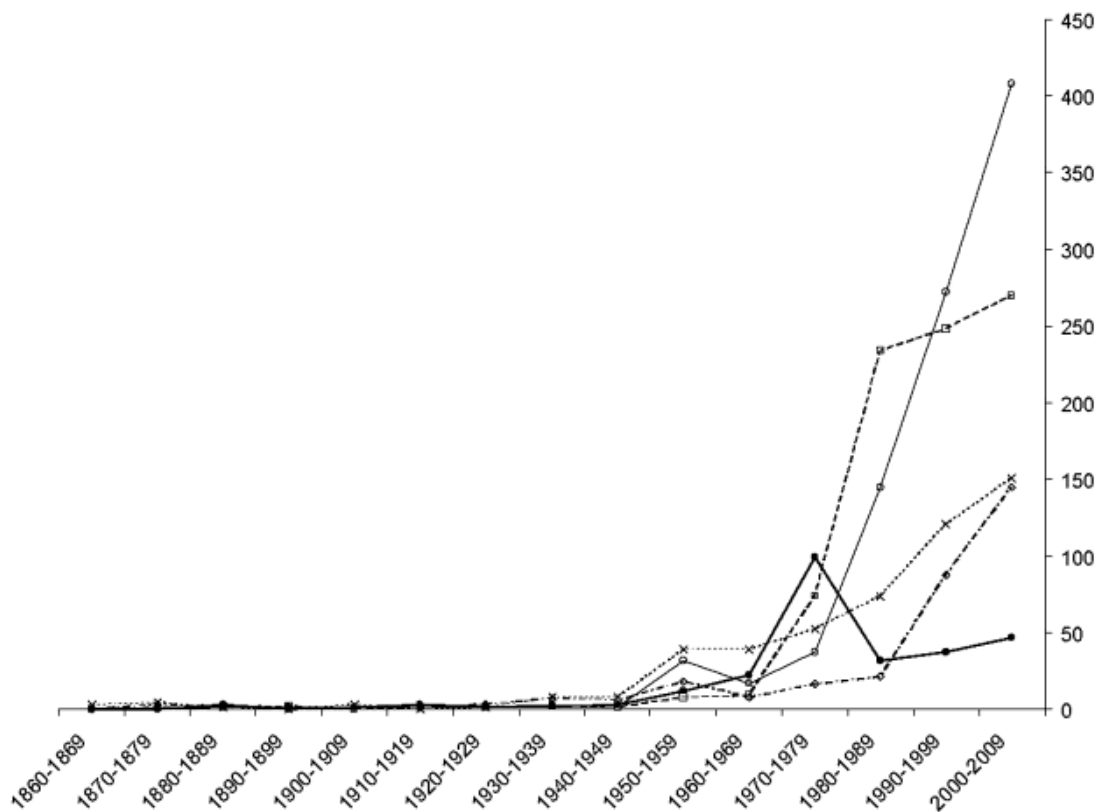

Fig. 1. Numbers of peer-reviewed publications on sei, blue, fin, humpback and minke whales in the Marine Mammal Database and Digital Library of the Natural History Museum of Los Angeles County, by decade, between 1860 and 2009. Closed circles: sei whale; open diamonds: blue whale; crosses: fin whale; open squares: Minke whale; open circles: humpback whale.
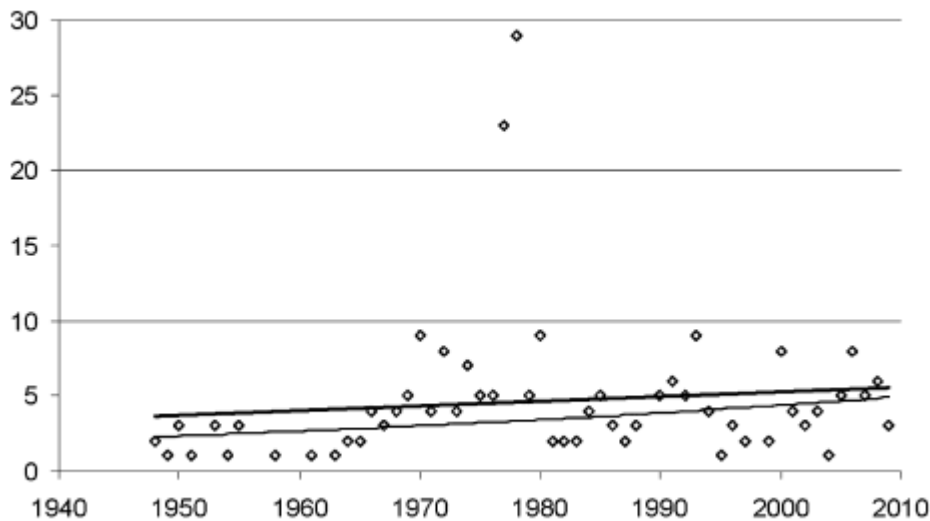
Fig. 2. Numbers of peer-reviewed papers on sei whales published per year. Linear and exponential models were fitted to the data to check for compliance with Price's Law on scientific literature growth. Linear model (thick line): $y = 0.0318x-58.298$ ($r^2 = 0.014$; $P > 0.1$). Exponential model (narrow line): $y = 1-11e0.0125x$ ($r^2 = 0.08$; $P < 0.01$).

For the sei whale, research output is almost stagnant, and the Price's Law postulate is not fulfilled (Linear model: $r^2 = 0.014$; $P > 0.1$. Exponential model: $r2 = 0.08$; $P < 0.01$; Fig. 2). The data points from 1977 to 1978 (corresponding to the outputs of the IWC special meeting on sei and Bryde's whales) were identified as highly influential on the fitting of the models by an analysis of residuals, and new models were fitted without those data. In the new models, the values for $r2$ were still low, indicating that most of the variance remained unexplained (Linear model $r2 = 0.09$; $P < 0.01$. Exponential model $r^2 = 0.13$; $P < 0.01$).

The distribution of publications by ocean basin is presented in Figure 3. Nearly one-third of the literature refers to the Southern Ocean, which can be explained by the importance of the modern whaling activity which developed there (Tønnessen & Johnsen 1982). Research concerning the North Atlantic sei whale is documented in 56 publications (21% of the total number). Half of those publications (28) were published after 1986 (when the whaling moratorium established by the IWC came into effect), but 50% (14) of those either used whaling data or were focused on management for whaling, showing that only half of the recent research on the North Atlantic sei whale is independent of whaling. The research output in subject categories by ocean basin, and for North Atlantic sei whales by decade, are presented in Tables 1 and 2, respectively. The subjects that have received the most attention are related to whaling (distribution and population assessment/management). Almost one-third of the publications on anatomy (30%, 13 publications) and almost half of the publications on distribution and movements (45%, 31) relate to the North Atlantic but, in contrast, relatively few publications exist on vital parameters such as age determination and growth, reproduction and natural mortality of the North Atlantic population.

Distribution/movements is the only subject for which there has been a clear increase over the years, in investigations on the North Atlantic sei whale (Table 2). In fact, it is the only subject that appears to have grown exponentially in accordance with Price's Law since the 1940s, although the sample size is small (exponential curve equation $y = 0.5771e^{0.4055x}$, $r^2 = 0.77$, $P < 0.01$, $n = 31$).
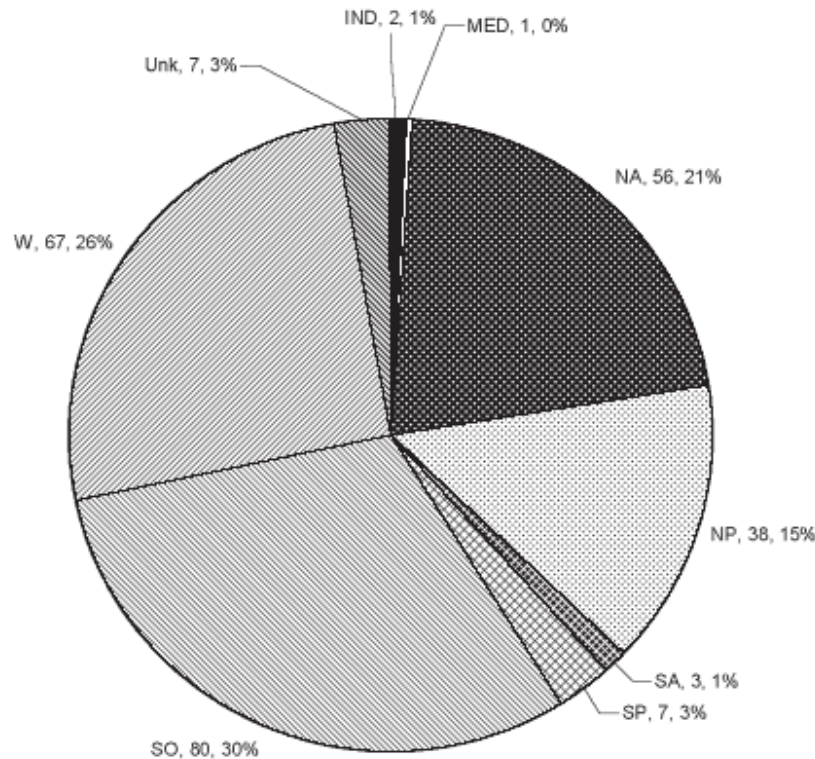

Fig. 3. Peer-reviewed publications on sei whales in the Marine Mammal Database and Digital Library of the Natural History Museum of Los Angeles County, USA, by ocean basin (Ocean, *n*, % of total). Ocean basins: IND, Indian Ocean; MED, Mediterranean; NA, North Atlantic; NP, North Pacific; SA, South Atlantic; SP, South Pacific; SO, Southern Ocean; W, World; Unk, unknown.

In the North Atlantic, although researchers from the United Kingdom and the United States produced most of the publications on the sei whale during the period 1880–2009 (17 and 13, respectively), Iceland and Norway have higher PI values (1.97 and 0.07, respectively; Table 3).
In the last 20 years, the distribution of publications has tended to be more balanced between nations, although the PI values vary widely due to different population sizes. It is not surprising that the nations listed in Table 3 were all involved in commercial sei whaling in the North Atlantic at some point in time, with the exception of the Netherlands (represented by a single publication on a stranding). Conversely, all the nations involved in commercial sei whaling in the North Atlantic are represented in that table, except for

Ireland, since whaling was conducted under the British flag before the Anglo–Irish treaty and ceased after that treaty.

Literature review
Taxonomy
In the last three decades, our understanding of cetacean origins has rapidly advanced with data from diverse fields such as palaeontology, anatomy, stratigraphy and, more recently, molecular biology (Uhen 2010). Immunological and amino acid comparisons made between the 1950s and the 1990s suggested a close relationship between the clades Cetacea and the Artiodactila (Gatesy 1998), supporting the association between these two groups postulated by Flower (1883a, b) based on morphological data. Traditionally, the Cetacea clade has been grouped as the Order Cetacea, but most of the post-1994 molecular studies have placed the cetaceans nested within the artiodactyls, leading to the fusion of these two clades into the Order Cetartiodactyla (Price et al. 2005, Uhen 2010). Despite the molecular evidence, reference to the Order Cetacea is still widespread among marine mammalogists both for convenience and in the interest of taxonomic stability. Classification within the Cetartiodactyla is still not fully resolved (Geisler & Uhen 2005, Price et al. 2005, Spaulding et al. 2009) and the clades Mysticeti (baleen whales) and Odontoceti (toothed whales), usually referred to as suborders by marine mammalogists, have not yet been ranked (Uhen 2010).
Despite the intense recent activity in cetacean phylogeny research, few researchers have dealt specifically with the sei whale. Two subspecies were proposed by Flower, the northern *B. borealis borealis* and the southern *B. borealis schlegelli* forms, but both morphological and genetic support for a Southern Hemisphere subspecies are weak (Perrin et al. 2010). In contrast, a maximum parsimony phylogeny of baleen whales revealed a strongly supported (bootstrap support > 95%) clade for North Atlantic sei whales (Baker et al. 2004).
A prioritized list of species in need of further taxonomic research was produced at a cetacean taxonomy workshop held in April 2004 (Taylor 2005). The list was based on both taxonomic uncertainty and conservation status, and taxa were ranked in three categories: high, medium and low priority (for taxonomic research). The two forms of sei whale are listed under medium priority, both due to taxonomic uncertainty and conservation status, indicating that the taxonomic status of the species is still not completely resolved and that taxonomic research is needed.

Distribution and movements
In most contemporary references, the main source of information on the distribution and movements of the sei whale are records from the whaling industry (e.g. Horwood 1987, Perry et al. 1999, Horwood 2009). These records, in the majority, reflect the preferred whaling areas, which were chosen based on several factors including a preference for known grounds, the presence of other favoured species, proximity to land stations and prevailing weather conditions. As such, these data do not reflect the entire distribution of the species and, in some cases, may no longer be accurate.

Table 1. Scientific literature production (numbers of published papers) on sei whales, by subject and by ocean basin, for the period 1860–2009

	Phylogeny	Anatomy	Physiology	Feeding ecology	Reproduction/ social ecology	Distribution/ movements	Stock structure	Acoustics	Population assessment/ management	Pathology/ natural mortality/ threats	Molecular biology/ genetics	Age determination/ growth
Indian Ocean						2				2		
Mediterranean						1				1		
North Atlantic	3	13	3	11	6	31	8	2	11	3	3	2
North Pacific	2	6	4	10	4	8	6	3	6	3	1	
South Atlantic				1		1				1		
South Pacific				1	1	5				1		
Southern Ocean		6	5	10	17	17	7	2	35	5		7
World	5	18	30	6	6	5	4		7	5	7	
Unknown				2	1	2	2		4	1		
Total	10	43	42	41	35	69	27	7	63	19	11	9

Table 2. Scientific literature production (numbers of published papers) on North Atlantic sei whales, by subject and by decade

	Phylogeny	Anatomy	Physiology	Feeding ecology	Reproduction/ social ecology	Distribution/ movements	Stock Structure	Acoustics	Population assessment/ management	Pathology/ natural mortality/ threats	Molecular biology/ genetics	Age determination/ growth
1880–89		3				2						
1890–99												
1900–09						1						
1910–19												
1920–29		1				2						
1930–39												
1940–49												
1950–59						1						
1960–69		1		1								
1970–79		2	1	2	2	6	4		4			1
1980–89		5		1	2	3	1		2			1
1990–99	2	1	2	2		6	2		4	1	2	
2000–09	1			5	2	10	1	2	1	2	1	
Total	3	13	3	11	6	31	8	2	11	3	3	2

Table 3. Distribution of publications on the North Atlantic sei whale among countries, by decade

	Canada	Denmark and Greenland	Iceland	Netherlands	Norway	Portugal	Spain	United Kingdom	United States
1880–89								3 (0.028)	
1890–99									
1900–09									1 (0.012)
1910–19									
1920–29									2 (0.009)
1930–39									
1940–49									
1950–59									1 (0.006)
1960–69									1 (0.005)
1970–79	3 (0.012)	1 (0.018)			1 (0.023)		1 (0.003)	2 (0.003)	3 (0.001)
1980–89	2 (0.007)	1 (0.018)	1 (0.379)				1 (0.002)	6 (0.010)	
1990–99	1 (0.003)		4 (1.362)		1 (0.021)		2 (0.005)	2 (0.003)	1 (0.0003)
2000–09		2 (0.024)	1 (0.226)	1 (0.004)	2 (0.029)	1 (0.006)		4 (0.004)	4 (0.001)
Total	6 (0.022)	4 (0.060)	6 (1.966)	1 (0.004)	4 (0.073)	1 (0.006)	4 (0.010)	17 (0.048)	13 (0.035)

Values in parentheses correspond to the national participation index, calculated as the ratio of the number of publications per million people generated by country and the total number of publications on the subject for the period.

The whaling records, however, document the oceanwide distribution of the species. Sei whales seem to prefer offshore, temperate waters and seldom venture into the colder waters of the polar seas (Horwood 1987, Perry et al. 1999), although larger individuals enter colder waters (Horwood 1986). Influxes into inshore waters may occur apparently in response to prey distribution (Jonsgård & Darling 1977, Payne et al. 1990, Schilling et al. 1992).

Sei whales undertake seasonal migrations from low-latitude breeding grounds to high-latitude feeding areas in both hemispheres (Horwood 1987). While feeding areas are fairly well defined in all oceans, the locations of breeding areas remain unknown. Catch data from the Southern Hemisphere and North Pacific suggest that migration is structured by sex and age class, and that pregnant females lead the migration both to and from the feeding grounds (Matthews 1938, Gambell 1968, Masaki 1976, Lockyer 1977a, Gregr et al. 2000, Best & Lockyer 2002).

Historical distribution. **Eastern North Atlantic.** In the northeastern North Atlantic, sei whales were first captured with the onset of modern whaling in Finmark (northern Norway; Cocks 1885, Collet 1886). Thereafter, modern whaling spread to other areas, and land stations were created in northern and western Norway, the Scottish islands (Orkney, Shetland and the Hebrides), the Faroe Islands, Ireland, Iceland, East Greenland, the Iberian Peninsula and northern Morocco (Haldane 1904, Southwell 1904, Thompson 1919, Jonsgård & Darling 1977, Sanpera & Aguilar 1992). Descriptions of sei whale distribution and movements were largely based on the records from these stations. Ingebrigtsen (1929) is still widely cited to describe the apparent spring–summer migratory sequence of sei whales in the northeastern North Atlantic (e.g. by Horwood 1987, Cattanach et al. 1993, Perry et al. 1999, Gregr et al. 2000) despite the fact that his assumptions remain unverified. According to Ingebrigtsen (1929), sei whales wintered in the southern part of the North Atlantic, possibly off southern Spain and Portugal and northwest Africa. They then migrated north up the mid-Atlantic and off the western continental slope of Europe to the areas around Iceland, Scotland, western Norway, and Finmark, and as far north as Bear Island and Spitsbergen.

The timing and extent of sei whale movements through western European waters has always displayed great seasonal and interannual fluctuation. Reports of years in which unusually large numbers of sei whales occur in an area, often followed by their disappearance from that area for several years, have been termed 'invasion years' (Jonsgård & Darling 1977).

Sei whales were captured along the shelf edges around the Scottish islands, from April to October with a peak in June (Haldane 1904, Thompson 1919, Horwood 1987). In Norway, sei whales first arrived at the waters off Møre, in the west coast, as soon as late April or early May (but more commonly in mid-May). Sei whales were captured closer to shore in the beginning of the season, between May and June, apparently moving offshore towards the end of the season (Jonsgård & Darling 1977). In Finmark, they were captured mostly from the western coasts (although they were also captured to the east in smaller numbers) from mid-May to August, with the largest catches in June (Cocks 1885, Collet 1886, Cocks 1887, 1888, 1889, Andrews 1916). In 1885, sei whales seem to have made an incursion in great numbers east of the North Cape – over 700 were captured by Norwegian and Russian whalers (Cocks 1886). In Iceland, sei whales first appeared in

late May or early June; the peak catches occurred in August or September (Jonsgård & Darling 1977, Horwood 1987, Sigurjónsson & Víkingsson 1997).

Off the Iberian Peninsula, sightings of sei and Bryde's whales are reported from logbooks of sperm whaling expeditions in the North Atlantic in the 19th century, in the Atlantic side of the Straits of Gibraltar but, at the time, they were not taken (Aguilar & Borrel 2007). Sanpera and Aguilar (1992) reviewed whaling off the Iberian Peninsula during the 20th century and described three major whaling grounds: off northwest Spain, off central Portugal, and in the Atlantic side of the Straits of Gibraltar. Sei whales were reported from the northwestern Spain and Straits of Gibraltar grounds, although some confusion over the species identification still persists. In the 1920s, sei whales were declared in the catch from the Straits of Gibraltar in small numbers, but the distinction between sei and Bryde's whales may be unreliable. In northeastern Spain, sei whales may have been confused with fin whales in the same way. (Sanpera & Aguilar 1992).

Horwood (1987 after Tønnessen & Johnsen 1982) reported that 66 sei whales were caught off the west coast of Portugal in 1925–27, but we believe that Tønnessen and Johnsen (1982) were referring to Spanish catches. Otherwise, the figures do not add up for Portugal, and catches are above 100% (749 sei whales are reported, and catches were 93% fin + 68/749 = 9% sei and blue + an undetermined number of sperm whales). Nevertheless, those figures do not agree with more recent reviews of Iberian whaling, which report no sei whales (Sanpera & Aguilar 1992) or just one sei whale (Brito 2008) captured off central Portugal, indicating that sei whales were never common in the grounds off central Portugal, at least during the whaling season.

From 1930 to 1945, whaling off the Iberian Peninsula was drastically reduced, resuming only in the late 1940s. After that period, there are no reported catches of sei whales from the central Portugal grounds, but relatively high catches of sei whales were declared in the Straits of Gibraltar grounds from 1950 to 1953. This contrasts with the figures for the 1920s catches, suggesting that there could be confusion in the identification of sei and Bryde's whales (Aguilar 1985, Sanpera & Aguilar 1992). Off northwest Spain, catches were resumed only after the 1950s, and no subsequent catches of sei whales were declared (Sanpera & Aguilar 1992).

Sei whales were reported, sometimes in large numbers in the beginning of the 20th century, from the area from Madeira Islands, past the Canary Islands towards the Cape Verde Islands (Jonsgård & Darling 1977). In the light of present knowledge, it is possible that those sightings were primarily of Bryde's whales (see discussion on current distribution).

From 1976 to 1979, the unregulated catcher boat *Sierra* and associated vessels operated in the eastern North Atlantic, spending the summer off the Iberian Peninsula and the winter off northwestern Africa (Best 1992). These vessels used to stay in the region 18–22°N, 20–25°W from November to May, reportedly in search of sei whales. The catch statistics for this operation are fragmented. Regarding sei whales, the only figures available are the catch of one whale in 1976 and 110 whales for the year 1978 (Best 1992). Although some confusion with Bryde's whales cannot be ruled out, the fact that a distinction is made between Bryde's and sei whales in the catch for the year 1976 indicates that some care was taken in differentiating the two species. Up to the present, this is the best indication of a well-defined sei whale wintering area in the Northeast Atlantic.

Western North Atlantic. Sei whales were seldom taken in the Davis Strait and western Greenland. Only eight whales were reported from whaling boats based in western Greenland in the periods between 1924–39 and 1946–50. Sei whales were considered rare, occurring only in years with warm water intrusions (Kapel 1979). Around the southeastern Labrador Sea, sei whales were uncommon in inshore waters; however, data from the Fisheries Research Board of Canada, collected between 1966 and 1973, indicated the occurrence of sei whales in parts of the offshore waters of the Labrador Sea (Mitchell 1975). Whaling off Newfoundland was episodic, with long periods of inactivity. Sei whales were taken in low numbers since the late 1890s (Mitchell & Chapman 1977). From 1966, an operation from Blandford, Nova Scotia, took a substantial catch of sei whales until 1972, when commercial whaling was terminated in Canada (Mitchell & Chapman 1977).

In the Labrador Sea, sei whales occurred from the first week of June (Mitchell & Chapman 1977). Off Nova Scotia, Mitchell (1975) described two 'runs' of sei whales taken by the Blandford station. One run began in early June, peaking in June–July, and another began in late August and early September, peaking in September–October. Mitchell (1975) hypothesized that the whales migrated from south of Cape Cod along the continental slope in June and July and then returned south in September–October. From stranding records along the western US coast, northern Gulf of Mexico and in the Greater Antilles, Mead (1977) hypothesized that sei whales from Nova Scotia migrate south along the Atlantic coast of the US, to winter in the waters of the Gulf of Mexico.

Current distribution. In recent years, most of the data on distribution come from sighting surveys, either dedicated or opportunistic, and there are a few accounts from strandings and incidental mortality. Much of the survey information has not been published in peer-reviewed journals and is available only through technical reports, sometimes making it difficult to assess and interpret.

Sei whales seem to be present at low densities over most of the areas covered by dedicated sighting surveys in the North Atlantic. However, that could be explained in part by the fact that most surveys cover areas over the continental shelves, and sei whales are known to prefer the deeper waters off the continental slope (Horwood 1987).

Mediterranean. In the Mediterranean, sei whales are thought to be occasional visitors – rare sightings and strandings are reported from Spain, Gibraltar, France and possibly Tunisia (Bompar 2000). Recent dedicated sighting surveys failed to detect sei whales (Notarbartolo-di-Sciara et al. 1993, Boisseau et al. 2010), supporting the idea that the species is an occasional visitor.

Eastern North Atlantic. Over the easternmost part of the North Atlantic, most sei whale sightings during the summer are concentrated in the deep waters of the Irminger Sea area between east Greenland and west Iceland and, in a lesser extent, in the Faroe–Shetland Channel (Sigurjónsson et al. 1989, Cattanach et al. 1993, Weir et al. 2001, Macleod et al. 2003, 2006, Anonymous 2009a).

Sighting rates in the Norwegian and adjacent waters are extremely low; just a few sightings are reported for the Norwegian Sea and near Jan Mayen (Øien 2009).

In the Bay of Biscay, sei whales are observed in late summer and early winter along the shelf edge, although with much lower sighting rates than those of most other species (Carlisle et al. 2001, Cresswell & Walker 2001).

A concentration of sei whales was reported in early summer near the frontal area just north and southwest of the Charlie Gibbs Fracture Zone (53°N) during the Census of Marine Life survey conducted over the Mid-Atlantic Ridge from 4 June 2004 to 2 July 2004 (Waring et al. 2008).

During a survey conducted in July 2007 along the continental shelves of Britain, Ireland, France and northern Spain, sei whales were only detected in small numbers off northwestern Spain in the areas of Castro Terrace and the Charcot Seamounts (Anonymous 2009b).

We are aware of only two records of sei whales along the Portuguese continental shore. In September 1978, a sei whale was stranded in Carrapateira, southwestern Portugal, in an advanced stage of decomposition (implying that it could have been drifting for several days; Sequeira et al. 1992). A single sei whale with an estimated length of 9m was sighted 8 nautical miles off Sagres (southwestern coast of Portugal) in October 2010 by a whale watching enterprise (Sara Magalhães pers. comm.). Pictures of the head and body were kindly provided to us, enabling confirmation of species identity. The estimated size of this individual is similar to the size estimated by Lockyer (1977b) for weaning in the Antarctic (8m long).

In the Azores Archipelago, the species was first recorded in 1989 (Gordon et al. 1990). Since then, it has been shown that the species is a regular visitor to these islands during the spring migration; sightings span from early spring to late summer, and relative abundance peaks in April and May (Silva et al. 2003, Santos 2008, Prieto & Silva 2010). The first confirmed record of sei whale presence in the Madeira Islands is from 2002 (Freitas et al. 2004). The fact that the species occurs simultaneously with the much more abundant Bryde's whale (that is present from late spring to early autumn) makes it difficult to characterize its seasonality in that archipelago (Luís Freitas pers. comm.).

In the Canary Islands, sei whales are seen only in low numbers in autumn and winter, apparently during migration to lower latitudes (López-Jurado et al. 1996, Carrillo et al. 2010).

The consistent presence of Bryde's whales during the summer months both in the Madeira and Canary archipelagos (López-Jurado et al. 1996, Luís Freitas pers. comm.) may have in the past created some confusion due to the difficulty in distinguishing both species. The discrepancy between the reports of large numbers of sei whales in that region in the beginning of the 20th century mentioned by Jonsgård and Darling (1977) and the more recent data mentioned above, indicating a less pronounced presence, may in part be because Bryde's whales in the region were misidentified as sei whales in the past.

Along the western coast of Africa, information on sei whales is very limited. During a dedicated sighting survey in April 2005, the Atlantic waters contiguous to the Mediterranean were surveyed between the latitudes of 20°N and 37°N (Boisseau et al. 2010). During this survey, only one sei whale was detected in off-shelf waters. Another dedicated sighting survey off southern Morocco between 24°N and 22°N in the Cintra Bay area, undertaken from January to February 1996, did not detect any sei whales (Notarbartolo-di-Sciara et al. 1998).

Off Mauritania, a sighting of a single sei whale was reported in March 2003, during a seabird and cetacean survey in offshore waters near the Chinguetti oilfield (Anonymous 2003a). However, the picture reproduced in the report shows a very falcate dorsal fin more characteristic of Bryde's whale. It is unclear whether this sighting was positively differentiated from Bryde's whale.

In mid April 2011, at least two sei whales were sighted in waters off Mauritania by naturalists on a touristic expedition vessel (Richard White pers. comm.). Pictures kindly provided to us enabled confirmation of species identity. These sightings occurred in the vicinity of the region where the unregulated whaling boat *Sierra* reportedly caught sei whales during winter (see discussion on historical distribution above).

Other records along the west coast of Africa come only from incomplete specimens and strandings, most of which have not been positively identified (Hazevoet & Wenzen 2000, Van Waerebeek et al. 2000, Weir 2010). Confirmed records include a stranding of an 11-m long individual in Mauritania in 1981, and a series of nine baleen plates recovered from the stomach of a tiger shark *Galeocerdo cuvier* captured off Senegal (Van Waerebeek et al. 2000). The Senegal specimen presents a problem in interpretation since it is impossible to know where the shark swallowed the baleen. Tiger sharks are known to move over great distances (e.g. Heithaus et al. 2007), and baleen probably has very low digestibility and, thus, has long permanency times in the stomach.

Hazevoet & Wenzel (2000) reviewed a stranding of a baleen whale calf in Cape Verde that occurred in November 1983 and concluded that it was probably a sei whale, although they could not rule out Bryde's whale that also occurs in the archipelago.

Western North Atlantic. In western Greenland, sei whale sighting rates are low and seem to be concentrated in two specific areas: the banks at 66°N at Lille Hellefiske and off the southern tip of Greenland (Compton et al. 2007, Anonymous 2009a, Laidre et al. 2010). Data from autonomous acoustic recording units deployed in the Davis Strait in 2007 showed that sei whales occurred in the area from late July to early October (when the equipment was collected) with two peaks: one in late August and a second, less pronounced, in late September (Kate Stafford pers. comm.).

During a July–August 2007 sighting survey in Canadian continental shelf waters along the Labrador and Newfoundland coasts, three sei whales were detected (Lawson & Gosselin 2009). One was off southern Newfoundland, and two isolated individuals were recorded over the Nova Scotia shelf.

Off the northeastern US coast, sei whales concentrate during spring in the deeper waters of the margins of eastern and southern Georges Bank, and make episodic incursions into shallower waters, including the Great South Channel, Stellwagen Bank and the southern Gulf of Maine (Payne et al. 1990, Schilling et al. 1992, Waring et al. 2009). Recently, sei whales have also been detected with an array of autonomous ocean gliders deployed in the southwestern Gulf of Maine during summer (Baumgartner & Fratantoni 2008, Baumgartner et al. 2008).

Over 20 cetacean species have been observed during aerial and shipboard surveys conducted during all seasons in the oceanic waters of the northern Gulf of Mexico, but the only baleen whale reported was Bryde's whale (Davis & Fargion 1996, Jefferson & Schiro 1997, Davis et al. 2000a, b, Baumgartner et al. 2001). Records of sei whales in the area are restricted to four strandings in eastern Louisiana (Jefferson & Schiro 1997).

Several sighting surveys undertaken in the Bahamas and Caribbean in late winter and spring did not detect sei whales either in coastal or offshore waters (Roden & Mullin 2000, Swartz et al. 2001, Yoshida et al. 2010). Mignucci-Giannoni (1998) reported two sightings of sei whales in waters off Puerto Rico and the Virgin Islands, but it is not clear in which circumstances these sightings were made and whether the whales were positively differentiated from Bryde's whale.

In the oceanic waters of the Central North Atlantic, the only information available comes from a pilot study using yachtsmen sailing from the Caribbean to the Azores in 1998 (Boisseau et al. 1999). No cetaceans were sighted to the west of a longitude of 43°W or south of a latitude of 32°N, but a possible sei whale was reported on June 16, northeast of the Azores at 43°50′N, 21°31′W. However, the sample was small (only two out of 50 boats reported their results), and the use of untrained observers might explain the low sighting rates and uncertainty in identification.

Recent surveys in the North Atlantic show that sei whales still use some of the areas identified from whaling data, and support the notion that after the 1960s sei whales may have drastically changed their distribution in some parts of their range (Cattanach et al. 1993), having apparently either abandoned or been extirpated from areas where they were previously recorded with some frequency, such as the Norwegian Sea.

Information from tropical waters on both sides of the North Atlantic is fragmented and imprecise, and the location of the breeding grounds is still unknown. In the offshore pelagic habitats of the Central North Atlantic, apart from localized surveys near the Atlantic islands, no survey has been conducted.

Distribution data are both scarce and sparse over temporal and spatial scales, and are clearly insufficient to understand the present distribution and movement patterns of the species over the North Atlantic, particularly with regards to winter distribution and the location of breeding grounds.

Stock identification
Although the term 'stock' represents the fundamental population unit for most management purposes, its formal definition varies broadly in scientific literature and management schemes. A typological definition may be unrealistic since it is dependent on management objectives (Dizon et al. 1992). The IWC, for some species and areas, does not clearly define 'stocks' or 'management units', leading to the designation of management areas that are not well founded as defining biologically isolated units (Donovan 1991).

Little attention was paid to the definition of stocks in the North Atlantic in the early years of the IWC. It was only after 1977 that the current stock boundaries for fin, sei and minke whales in the North Atlantic were established (Donovan 1991).

Eight concentrations of sei whales were identified for the North Atlantic by the IWC (southwest Norway, north Norway, Faeroe, Denmark Strait, Labrador Sea, Nova Scotia, Gulf of Mexico–Caribbean Sea and southeast North Atlantic). Although Horwood (1987) interpreted these as a first attempt at stock definition, in fact, the IWC did not suggest these areas as necessarily representing separate stocks (Donovan 1991). Mitchell and Chapman (1977) presented some evidence of distributional differentiation between the Labrador and Nova Scotia sei whales and proposed that these units constituted two

different stocks; both were considered separate from eastern Atlantic sei whales by the IWC (Donovan 1991).

The current IWC boundaries for the management areas of sei whales in the North Atlantic (Fig. 4) were adopted in 1977 based chiefly on statistical convenience and historic catch data rather than on scientific evidence of stock structure (Donovan 1991). Horwood (1987) suggested a separation of whales taken in Icelandic and Canadian operations based on reproductive data (see discussion on reproduction below). Daniélsdóttir et al. (1991) studied electrophoretic variation in sei whales from Icelandic catches from 1985 to 1988 and did not find significant differences in allele frequencies between samples from different years, indicating that those samples originated from a homogeneous population. No further information is available regarding genetic differentiation of sei whales in the North Atlantic.

Recently, movements of sei whales between the Azores and the Labrador Sea have been recorded with the aid of satellite telemetry (Olsen et al. 2009, Prieto et al. 2010). These movements show that the migration patterns of this species may be more complex than previously assumed, comprising not only the expected large latitudinal movements but also wide longitudinal displacements. These findings have clear implications for the interpretation of the current management areas for sei whales in the North Atlantic. Given the weak genotypic information on stock identity, the virtual lack of knowledge regarding the location of breeding grounds, and sparse evidence for stock separation on the feeding grounds, it is presently impossible to ascertain if the North Atlantic sei whale population is subdivided into biological units or if it represents a panmictic population.
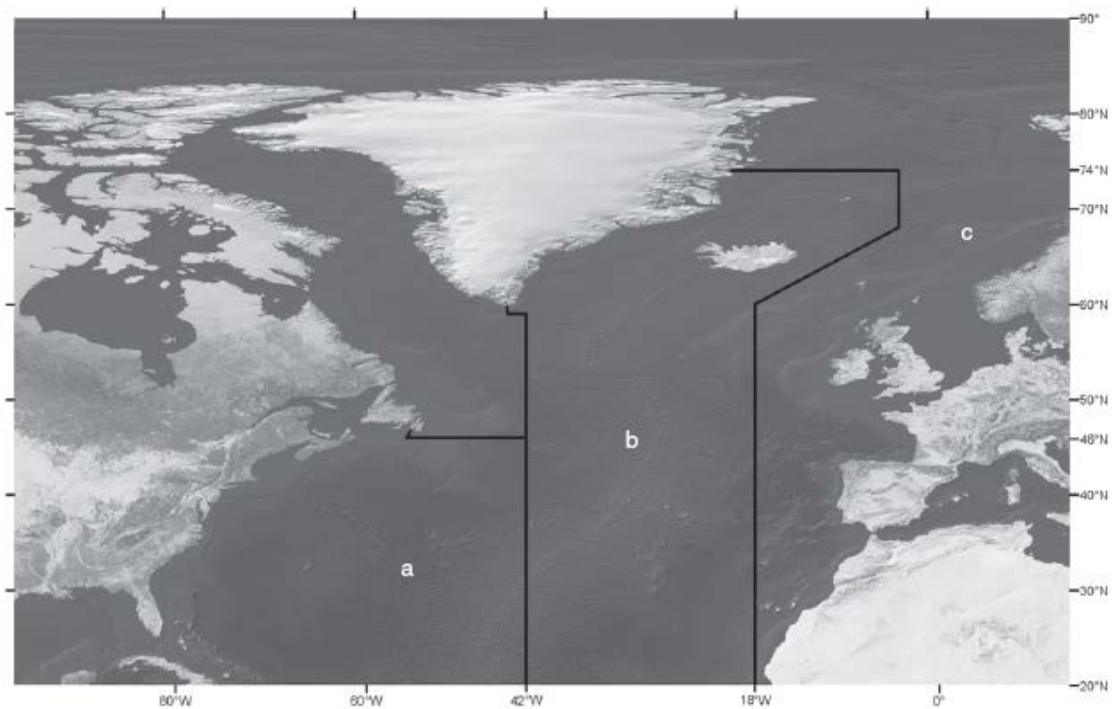

Fig. 4. International Whaling Commission stock boundaries for North Atlantic sei whales. (a) Nova Scotia, (b) Iceland–Denmark Strait, (c) Eastern.

Feeding ecology
The sei whale is the only rorqual species that seems to have evolved the ability to capture prey both by engulfment, as do the other rorquals, or by skimming on relatively low prey concentrations, as do the right and bowhead whales *Balaena mysticetus* (Gill & Hughes 1971, Watkins & Schevill 1979, Horwood 1987, Schilling et al. 1992). The ability to switch between feeding strategies results from anatomical adaptations of the internal baleen fringe, which is much finer than that of other rorquals (Collet 1886), and of the mouth cross section, which has some features reminiscent of right whales (Brodie & Víkingsson 2009).

This adaptation is reflected in the variety of prey recorded for the species. The sei whale has the most extensive list of prey of any baleen whale, including copepods, euphausiids, amphipods, decapods, cephalopods and fish, but the prey preferences are highly dependent on ocean basin and swarming characteristics of the prey, as shown in reviews by Budylenko (1978) and Horwood (1987).

Notwithstanding, in the North Atlantic, sei whales seem to be nearly stenophagous, feeding almost exclusively on the copepod *Calanus finmarchicus* and, to a lesser extent, on the euphausiids *Meganyctiphanes norvegica* and *Thysanoessa inermis* (Collet 1886, Andrews 1916, Horwood 1987, Sigurjónsson 1995). Off Iceland, this pattern seems to be inverted, and euphausiids are the main prey, followed by copepods (Sigurjónsson 1995, Sigurjónsson & Víkingsson 1997). In samples from whales taken in the Labrador Sea in 1971 and 1972, copepods were predominant in the stomach contents during the early whaling season (June–September); later in the season (October–November), they were replaced by euphausiids (Mitchell & Kozicki 1974). This pattern probably reflected seasonal changes in the zooplankton assemblage and abundance. Care should be taken in extrapolating that information to the present time, since copepods show substantial differences in abundance and distribution linked to the phase of the North Atlantic Oscillation, which has shifted from predominantly negative in the 1960s to predominantly positive since the mid-1980s (Fromentin & Planque 1996, Head et al. 2003).

In this ocean basin, even when apparently suitable schooling fish are available, sei whales demonstrate a preference for zooplankton (Watkins & Schevill 1979). Nevertheless, 2% of Icelandic whales examined consumed either sandeel *Ammodytes tobianus*, lumpfish *Cyclopterus lumpus* or capelin *Mallotus villosus* (Sigurjónsson & Víkingsson 1997).

Sei whales feeding on copepods seem to prefer the late copepodite stages (Schilling et al. 1992, Konishi et al. 2009). After the nauplius phase, copepods grow through five copepodite stages (CI-CV) and develop an oil sac filled with wax esters so that the latter stages have high caloric content (Miller et al. 2000). As proposed for right whales (Baumgartner et al. 2007), by preying on the late-stage copepodites, sei whales probably maximize their energy intake.

The stenophagy of sei whales found in the North Atlantic contrasts with the more euryphagic nature of the species found in other areas. In the North Pacific, for example, sei whales seem to switch between prey according to availability (Flinn et al. 2002, Konishi et al. 2009). In most cases, an individual focuses on one prey species during single feeding bouts, and only rarely do individuals have more than one prey species in their stomachs (Konishi et al. 2009).

Their ability to switch between feeding strategies theoretically allows sei whales to feed in the less productive wintering areas (perhaps with lower energetic gain) as has been reported for other areas (Kawamura 1973, Horwood 1987). Unfortunately, in part due to the scarcity of information about the winter distribution of sei whales in the North Atlantic, we could not find any information about their feeding ecology in lower latitudes.

After the last catches of sei whales in the North Atlantic by Iceland in 1988 under a special IWC permit for scientific research, very little research has been carried out on the feeding preferences of the species. We did not find any data on stomach contents from stranding records. This is not surprising since sei whale strandings are relatively rare due to the pelagic habits of the species.

Studies on the diet of North Atlantic sei whales using alternative methodologies, such as analysis of fatty acids, stable isotopes or faeces, are also scarce. The only information on sei whale feeding in the North Atlantic from non-lethal methods comes from an analysis of faeces collected during an episodic influx into the southern Gulf of Maine in 1986 that revealed only mandibles of *C. finmarchicus* (Schilling et al. 1992).

Some synoptic studies of the occurrence of potential prey and sei whales are available and support the diet preferences of the species in the North Atlantic. In western and southern Greenland, sightings of sei whales in September 2005 were in areas with the highest densities of krill *Meganyctiphanes norvegica* and *Thysanoessa* sp. (Laidre et al. 2010).

A concentration of sei whales reported in early summer 2004 near the frontal area of the Charlie Gibbs Fracture Zone, over the Mid-Atlantic Ridge, overlapped with the only area where concentrations of *C. finmarchicus* were found in the upper 100m of the water column (Skov et al. 2008). Similarly, off New England, the preference for *C. finmarchicus* is supported by the consistent synoptic occurrence of the whales with that copepod (Payne et al. 1990, Schilling et al. 1992, Baumgartner&Fratantoni 2008).

When preying on zooplanktonic organisms, sei whales show feeding periodicity, which seems to be associated with the diel vertical migration of the prey, and take advantage of prey concentrations near the water surface between dusk and dawn (Horwood 1987, Baumgartner & Fratantoni 2008). This may be a strategy to maximize foraging efficiency (Baumgartner & Fratantoni 2008).

On feeding grounds, baleen whales (and sei whales in particular) tend to associate with oceanic frontal systems such as fronts, eddies and upwelling systems (Nasu 1966, Moore et al. 2002, Tynan et al. 2005, Doniol-Valcroze et al. 2007, Bost et al. 2009). In the Pacific, sei whales tend to follow and be found in the warmer waters of the major mixing zones and tend to be associated with eddies broken from the fronts (Nasu 1966). Similarly, aggregations of sei whales have recently been found to be associated with fine scale frontal processes in the North Atlantic (Skov et al. 2008).

These associations with oceanic frontal systems probably enhance foraging efficiency by association with large concentrations of prey because of advection processes or due to increased prey biomass related to primary production (Skov et al. 2008, Bost et al. 2009). Nevertheless, the ways in which sei whales detect these systems and subsequently exploit them has not yet been investigated in detail. Since climactic changes may bring changes in the distribution and intensity of frontal systems, it is important to understand better the

role that these oceanographic features play in sei whale feeding behaviour and how predicted changes in climate may impact feeding ecology.

An affinity with submarine canyons is suggested by a sighting of more than 40 sei whales in a multispecies assemblage over and near Hydrographer Canyon in 1980 (Kenney & Winn 1987).

Reproduction

Horwood (1987) reviewed information on sei whale reproduction and, since then, no new information has become available for the North Atlantic. The most recent reproductive research in the North Atlantic was based on data collected in western Norway between 1951 and 1957 (Jonsgård & Darling 1977), from Iceland in 1967, 1969, 1972–75 and 1977–81 (Lockyer & Martin 1983), and from the northwestern Atlantic from 1966 to 1972 (Mitchell & Kozicki 1974). All reproduction studies on sei whales have been based on histological and morphological examination of material from catches.

Males. Male sexual maturity in cetaceans is normally assessed by examination of testes weight, spermatogenesis and histological examination of the testes tubules; animals are classified as immature, pubertal, active and resting (Perrin & Donovan 1984). The most commonly used techniques to calculate the body length and age at sexual maturity are not comparable for most purposes, and some care should be taken when comparing results from different studies (DeMaster 1984).

Horwood (1987) used the body length when 50% of males were sexually mature as to define the length at sexual maturity. He estimated lengths at 50% maturity of 12.0m from Canada, 12.7m from Iceland and 12.8m from Norway. The values from Canada are lower, but he noted that better agreement would be achieved if a different combined testes weight at maturity, comparable with that used in the other studies, was used in the Canadian study. The median age at sexual maturity was not calculated in the same manner since it was considered prone to being highly underestimated due to selection for large whales. Lockyer (1984) pooled all the available information to build a table of baleen whale reproductive parameters in which the mean length at sexual maturity estimated for North Atlantic male sei whales was 12.9m, and the mean age at sexual maturity, estimated by ear plug growth layer analysis was 8 years.

The evidence for seasonal cycles in spermatogenesis is equivocal for sei whales. Data from the northwest Atlantic suggest a seasonal cycle with increased activity towards the end of the summer (Mitchell & Kozicki 1974). The recent use of hormonal techniques in samples originating from Icelandic whaling showed a rise in hormonal activity during July–September, supporting a seasonal breeding cycle (Kjeld et al. 2003). Results for the Southern Hemisphere do not support that hypothesis since no seasonal cycles in spermatogenesis were found (Matthews 1938, Gambell 1968). That could be due to a low sensitivity of anatomical and histological methods to these cycles but could also reflect physiological differences between populations.

Females. Several methods and datasets have been used to estimate dates of conception of sei whales. Results indicate that conception occurs over a range of months, with a peak in June and July in the Southern Hemisphere, in November and December in the North Pacific and in December and January in the North Atlantic (Horwood 1987). Based on

the average length at birth (4.5m), the gestation period in the North Atlantic was calculated to be 10.7 months (Lockyer & Martin 1983).

Lockyer and Martin (1983) calculated a pregnancy rate of 0.40–0.44 and an ovulation rate of 0.59 for Icelandic sei whales, which is in disagreement with the ovulation rate of 0.26 calculated for the northwest Atlantic by Mitchell and Kozicki (1974). This discrepancy might be due to the method of calculation used by Mitchell and Kozicki (1974), in which the zero *corpora* classes are included in the regression of *corpus* number at age, thus rendering that estimate not directly comparable with others (Lockyer 1984). An ovulation rate of 0.26 and low pregnancy rate of 0.30 were interpreted by the authors as indications of a 3- to 4-year cycle, while all other studies from the North Atlantic and other oceans indicate a 2-year cycle (Lockyer 1984, Horwood 1987). However, it is noteworthy that after accounting for the bias against lactating females, Rice (1977) estimated a true pregnancy rate of 0.36 suggesting a 3-year pregnancy cycle for the great majority of female sei whales. Using hormonal methods, Kjeld et al. (2003) found an apparent pregnancy rate in mature females of between 0.37 and 0.38, but when indecisive results were accounted for, that value rose to 0.41, closely agreeing with the results from Lockyer and Martin (1983).

Two studies from the North Pacific indicated the existence of age-specific fecundity within the populations studied (Masaki 1976, Rice 1977). Lockyer and Martin (1983) did not detect evidence for age-specific ovulation in Icelandic females up to 45 years old. Using the same approach as described above for males, Horwood (1987) calculated the body length at 50% mature for females to be 13.1m for Iceland, 13.1–13.4m for Canada and 13.4m for Norway. As with males, he did not carry out the same analysis for age. Lockyer (1984) estimated the mean length at sexual maturity for North Atlantic female sei whales to be 13.3m and the mean age at sexual maturation (*tm*) to be 8 years.

Several studies on ear plug transition phase reported a decline in *tm* over time for sei, fin and minke whales. Although the calculations may be affected by several types of biases, at least for some cases, there is evidence for a real decline in the age at sexual maturation (Lockyer 1984).

For the Icelandic catches, Lockyer and Martin (1983) analysed the data for mean and confidence limits separately in groups of cohorts to avoid biases associated with using linear regression to describe the trends (see Lockyer 1984 for discussion). They detected a significant reduction in the *tm* between the periods pre-1940 and post-1940, in the order of 1.7 years.

It has been hypothesized that the decline in whale populations, due to intensive exploitation, may have led to a lower intra- and interspecific competition for prey that, in turn, may have led to faster growth rates inducing precocious puberty (e.g. Lockyer 1974, Laws 1977). Although the trends of decreasing age at sexual maturation seem, at least partially, to reflect the effect of intensive exploitation, the implications of that decline are still uncertain (Lockyer 1984).

After the cessation of sei whaling in the North Atlantic, few further studies on reproduction were undertaken, and those that were undertaken were based on whaling-derived samples (e.g. Kjeld et al. 2003). If, as it seems, there was an effect of exploitation on the reproductive parameters of the population, cessation of whaling may have reversed it, at least partially. However, other factors may have also influenced those parameters, such as a rearrangement of the North Atlantic ecosystem owing to changes in whaling,

fishing (including overfishing) and hydrometeorology (Merrick 1997, Beaugrand et al. 2002, Beaugrand 2004). Consequently, it is unlikely that published data on North Atlantic sei whale reproductive ecology remain unchanged. Since ecological and management models normally need reproductive components, it is important that new studies using recent samples are conducted to provide more up-to-date figures.

Recently, gonadal steroid hormones have been used to determine pregnancy in marine mammals (Baker et al. 2010). The dramatic differences in the concentration of these hormones in the blubber (Kellar et al. 2006) and hormonal metabolites in faecal samples (Rolland et al. 2005) of pregnant and non-pregnant cetaceans opened the possibility of assessing the pregnancy status of large numbers of free ranging cetaceans without the need for capture. There are some complications with the use of these techniques, since sometimes covariates are required to discriminate pregnancy fully (Gardiner et al. 1996), but in general results are reliable. The work by Kjeld et al. (2003) using blood samples from sei whales caught in Icelandic whaling operations was important in establishing ground values for steroid hormones of North Atlantic sei whales backed by anatomical and histological methods. That work proved that hormonal methods not only complement anatomical and histological methods but can in some instances actually be more sensitive. Nonetheless, the authors also pointed out disagreements between serum oestradiol values between sei and fin whales, advising further study.

To our knowledge, there have not been hormonal studies on the sei whale using tissues other than blood, but based on studies of other species there is no reason to think that data on reproduction could not be obtained from non-lethal techniques such as biopsy sampling or faecal collection. A hormonal study using blubber and skin from sei whales is necessary in order to test whether, and to what extent, the reproductive rate of the species can be assessed using these techniques. We acknowledge that recalculation of reproductive parameters using only hormonal techniques would be both technically and logistically challenging and may not be practical presently. Nevertheless, in the absence of other data sources, the feasibility of using hormonal methods should at least be investigated.

Abundance

There is no information on the pre-exploitation abundance of sei whales in the North Atlantic. The total catch of sei whales by modern whalers in the late 19th and 20th centuries has been estimated to be 16933 (Allison 2008). That figure is, however, probably affected by some confusion in the identification of sei and Bryde's whales and does not include any proportion of the 12322 unspecified species included in the catch (Allison 2008).

As discussed above, sei whales appear to occur at low densities over most of the areas covered by systematic sighting surveys in the North Atlantic either because the surveys encompassed areas not frequented by sei whales or were carried out during a season when they are scarce. Here, we only present the most recent estimates based on cetacean surveys specifically designed for abundance estimation. Previous estimates based on tagging from mark-recapture programmes (e.g. Mitchell & Chapman 1977) are considered inadequate given that, for such programmes to be effective, large numbers of animals have to be tagged and recaptured in each sampling period (Buckland et al. 1993). Similarly, estimates from early line transect surveys are likely to be negatively biased due

to poor sampling design and failure to correct for submerged animals and ship avoidance (Buckland et al. 1993).

No population estimate for the entire North Atlantic is available. Some estimates have been made for restricted areas of the eastern and western North Atlantic (Table 4). These abundance estimates cover only parts of the known summering habitat of North Atlantic sei whales, and where data are available, it is uncertain what fraction of the population was surveyed. If separate ecological units exist in the North Atlantic, it is possible that in some areas they overlap both spatially and temporally and have been treated as a single unit in abundance estimates.

Table 4. Recent abundance estimates and CVs for the North Atlantic sei whale

Area	Period	Abundance	CV	Reference
Southern Gulf of Maine to Maine (United States)	August 2002	71	1.01	Waring et al. 2009
Gulf of Maine to lower Bay of Fundy (United States)	June–July 2004	386	0.85	Waring et al. 2009
Southern Gulf of Maine to upper Bay of Fundy to Gulf of St. Lawrence (United States, Canada)	August 2006	207	0.62	Waring et al. 2009
Iceland–Denmark Strait (excluding southernmost blocks)	June–July 1987	1293	0.60	Cattanach et al. 1993
Iceland–Denmark Strait (including southernmost blocks)	July–August 1989	10300	0.27	Cattanach et al. 1993
CODA block 3 (northwestern Spain)	July 2007	366	0.33	Anonymous 2009a

CV, coefficient of variation; CODA, Cetacean Offshore Distribution and Abundance.

A series of synoptic multinational sighting surveys in the northeastern and central North Atlantic (NASS) were conducted in 1987, 1989, 1995 and 2001, from late June to early August, with some differences in area coverage between years (Sigurjónsson et al. 1989, Pike et al. 2009). Abundance estimates for sei whales were produced from the NASS surveys for the years 1987 and 1989, but the areas and survey periods differed between these 2 years. For the 1987 survey, a first estimate of 1243 sei whales was calculated by Gunnlaugsson and Sigurjónsson (1990) but, due to timing and coverage area, the estimate was considered to represent only part of the population previously targeted by Icelandic whalers. During 1989, the survey was undertaken later in the season (mid July to mid August) and extended to blocks farther south from the blocks surveyed in previous years. An abundance estimate of 10300 sei whales (coefficient of variation; CV = 0.268) was calculated for that survey; the data from 1987 were reanalysed using the same methodology yielding an estimate of 1293 sei whales (CV = 0.603). The difference between the two estimates was interpreted as being caused by the substantial survey effort made in 1989 in the area south of the area surveyed in 1987. The estimate for 1989 for a comparable area to the 1987 survey was 1590 whales (CV = 0.4) similar to the estimate for 1987 (Cattanach et al. 1993).

During the multinational Cetacean Offshore Distribution and Abundance in the European Atlantic survey (CODA), conducted in July 2007 along the British, Irish, French and

northern Spanish continental shelves, sei whales were only detected in one of the four survey blocks off northwestern Spain; the sei whale abundance estimate for that block was 366 whales (CV = 0.33; Anonymous 2009a).

Three recent abundance estimates are available for parts of the Canadian and US Atlantic Exclusive Economic Zone during the summers of 2002, 2004 and 2006. The 2004 estimate (386; CV = 0.85) is considered the best estimate for the Nova Scotia stock, although it is considered conservative because of uncertainties about population structure and whale movements between surveyed and unsurveyed areas (Waring et al. 2009).

Acoustics
Very few accounts of the acoustic characteristics and behaviour of the sei whale exist. Baumgartner et al. (2008) reviewed the scarce literature available and added some information from their own research, resulting in only five published reports describing sei whale calls. The current knowledge about sei whale call characteristics is summarized in Table 5. Recordings made in different areas and seasons present much dissimilarity that could be a result of geographic separation and population-specific acoustic characteristics, or because different types of calls have distinct ecological functions (Rankin & Barlow 2007, Baumgartner et al. 2008).

Mortality and threats
Natural mortality and threats. Killer whales *Orcinus orca* have been reported to prey on all great whales and are considered their only significant natural predator (Jefferson et al. 1991, Springer et al. 2006). The contribution of large cetaceans to the diet of mammal-eating killer whales is difficult to infer (Branch & Williams 2006).

Reciprocally, the scale and ecological significance that predation by killer whales have on large whale populations is still a matter of debate in the scientific literature (Reeves et al. 2006).

There are relatively fewer reports of killer whale predation on sei whales than on other species of large whales (Jefferson et al. 1991, Branch & Williams 2006), but that does not necessarily mean a lower incidence of predation since predation could be occurring farther offshore and be more difficult to detect.

Parasites have been known to cause major health problems in marine mammals (Dailey 2001) and are considered one of the most important sources of natural mortality for sei whales (Horwood 1987). Helminth parasites can cause severe complications, especially when infecting the liver, urinary and respiratory systems and brains (Lambertsen 1986, Lambertsen et al. 1986, Dailey 2001).

From a small sample from Iceland (*n* = 24) Lambertsen (1990) found a high incidence of the Acantocephalan *Bolbossoma* spp. in the colon. In the Antarctic, sei whales presented a high incidence of infection with several species of helminth parasites; most infections were restricted to the genitalia, stomach and intestine (Dailey & Vogelbein 1991). Nevertheless, the implications of these infections on sei whales' health and mortality are unknown.

Table 5. Summary of acoustic characteristics of known sei whale calls

Type of call	Minimum frequency (Hz)	Maximum frequency (Hz)	Average duration (s)	Phrase composition (parts)	Area	Reference
FM down-sweep	34.0	82.3	1.38	1–3	New England, United States	Baumgartner et al. 2008
FM up-sweep	–	3k	0.7	7–10	Nova Scotia-Newfoundland	Thompson et al. (1979) *in* Baumgartner et al. 2008
FM up-sweep	1.5k	3.5k	0.03–0.04	10–20	Nova Scotia	Knowlton et al. (1991)
FM down-sweep	44.6	100.3	1.2	–	Hawaii	Rankin and Barlow (2007)
FM down-sweep	21.0	39.4	1.2	–	Hawaii	Rankin and Barlow (2007)
FM down-, up-sweeps	200	600	1.1	–	Antarctic Peninsula	McDonald et al. (2005)
Tonal call	100	950	0.45	1–5	Antarctic Peninsula	McDonald et al. (2005)
Broadband signals	100	600	1.5	–	Antarctic Peninsula	McDonald et al. (2005)

FM, frequency modulated.

Marine mammal viral diseases have started to be investigated only recently but can induce high mortality rates and be persistent at a population level (Van Bressem et al. 1999, Dailey 2001). Very little information exists on the occurrence of viral diseases in sei and other baleen whales, and there are no records of epizootics in baleen whales (DeMaster et al. 2001). The only evidence for viral diseases in North Atlantic sei whales comes from Lambertsen (1990), who found inflammation consistent with a viral pathogen in the lungs of 14% of the sei whales examined in Iceland, but could not detect the causative agent.

An unknown disease with an incidence of 7% in sei whales off California caused the shedding of baleen plates, which impaired their ability to feed (Mizroch et al. 1984). There is no evidence for the same condition in North Atlantic sei whales.

Estimates of sei whale natural mortality rates have been impeded by several sources of bias. The estimates have been based on catch at age techniques that are likely to underestimate rates and may not be representative of the populations studied (Horwood 1987). A wide range of mortality rate estimates, between 0.05 and 0.1, have been presented with large confidence limits.

Lockyer (1977c) estimated mortality rates for Durban and South Georgia in the Southern ocean from age-frequency distributions and calculated that natural mortality in Durban was in the range of 0.047–0.066. For South Georgia, she argued that, though the amount of pelagic whaling for the area was difficult to assess, the natural mortality rate varied between 0.054 and 0.068.

For the eastern North Pacific, Rice (1977) used a similar approach to calculate mortality rates for animals with at least eleven earplug layers (the mean number at sexual maturity estimated for that population) and estimated a total (natural plus human-induced) mortality rate of 0.088 for females and 0.103 for males, but did not try to calculate the natural mortality rate.

Based on age-frequency distributions, Lockyer and Martin (1983) calculated instantaneous total mortality rates from 0.092 to 0.096 (males) and from 0.103 to 0.104 (females) for sei whales from Iceland but cautioned that these rates suffered from some sources of bias, including the irregular catching history of the species and a preference for larger (and hence older) animals in the catch. Natural mortality was not calculated in this study, and the authors only allude to an estimate of 0.06 from the Southern Hemisphere. The same authors also suggested that the age distributions within the catch might not be representative of the whole population due to geographic segregation of feeding grounds (Lockyer & Martin 1983).

Human-induced mortality and threats. In addition to direct exploitation, expanding anthropogenic activities in the marine environment, such as fisheries, shipping, pollution, military activities, and deep-water hydrocarbon extraction, probably impact sei whales.

Fisheries. Entanglement in fishing gear is a major source of mortality for many species of small and large cetaceans, particularly great whales occupying coastal habitats in heavily fished regions (Clapham et al. 1999). Sei whales primarily occupy pelagic habitats and are, therefore, less likely to encounter static fishing gear than coastal species such as humpback and minke whales. Serious injury and mortality of sei whales due to entanglement in fishing gear off the northeast United States and New Brunswick, Canada,

have been reported though at a much lower rate than for right, humpback, fin and minke whales (Glass et al. 2010).

Fisheries may also have ecological impacts on marine mammals through the large-scale removal of animal biomass from marine ecosystems, which can induce direct and indirect competition for resources between fisheries and marine mammals (Northridge 2009). The ways in which fishery-induced changes to the marine ecosystem may affect marine mammals are complex and have proved to be difficult to test (Northridge 2009). Nevertheless, in theory, the rapid removal of biomass from marine ecosystems could eventually lead to a collapse or change in the community structure that can reflect at several ecological levels with unpredictable consequences including to the great whales (DeMaster et al. 2001). The feeding strategy of sei whales should provide them with flexibility to switch between planktonic and fish prey. However, in the North Atlantic, the sei whale seems to be stenophagous, so the species' adaptability to rapid changes in prey assemblages in this ocean is questionable.

Ship collisions. Enhanced monitoring in recent years has resulted in an increasing number of ship collisions with great whales being documented, which have been attributed to increases in shipping traffic as well as to the increasing size and speed of ships (Laist et al. 2001, Hazel et al. 2007, Van Waerebeek et al. 2007). Between 1970 and 1990, it is estimated that between 13% and 20% of the strandings of great whales in the United States, Italy, France and South America were caused by collisions with ships (Laist et al. 2001). Sei whales are also affected by this increasing phenomenon (e.g. Laist et al. 2001, Van Waerebeek et al. 2007, Glass et al. 2010). Although reports of collisions with sei whales are comparatively less common than reports of collisions with other, more coastal, species (Laist et al. 2001), that could be due to the low probability of detecting an event when it occurs offshore. The oceanwide impact of ship strike rates on sei whale mortality is poorly understood but may be significant due to increases in merchant shipping traffic.

Noise. Human-generated noise in the oceans has been recognized as a potential threat to large whales since the early 1970s, but it was not until recently that the problem started receiving more attention (Clark et al. 2009).

Ocean noise levels have shown a continued increase in association with increasing human activities such as commercial shipping, seismic surveys, military activities, scientific research, etc. It has been estimated that in many parts of the world, between 1950 and 2000, there was an overall increase in low-frequency noise from shipping of in the order of 16dB (Anonymous 2003b).

Direct mortality caused by anthropogenic noise is a controversial issue, but the potential risk seems to be higher in deep diving cetaceans and less pronounced for baleen whales (e.g. Frantzis 1998, Jepson et al. 2003, Fernandez et al. 2005, Cox et al. 2006). Acoustic interference, or masking, can have detrimental effects on cetaceans by interfering with conspecific communication as well as by reducing their ability to detect other biologically important sounds and abiotic sound cues (Clark et al. 2009). Effects may be short- or long-term and may contribute to reduced survivorship and reproductive success as a result of persistent degradation of acoustic habitat over an animal's lifetime (Clark et al. 2009).

The acoustic repertoire of sei whales is poorly described (Baumgartner et al. 2008, this review), and the way they use their acoustic environment is virtually unknown. These parameters require further research to evaluate the impact of human-induced noise on sei whale ecology.

Contaminants. Currently, there is no evidence that organochlorine and heavy metal contaminants pose a major threat to baleen whales. Existing data on mysticetes support the view that feeding at lower trophic levels results in smaller contamination burdens than found in most odontocetes that feed at higher trophic levels (O'Shea & Brownell Jr 1994). Studies comparing contamination by organochlorine compounds in odontocetes and mysticetes from the same areas show levels of contamination at least one order of magnitude higher in the odontocetes (e.g. Focardi et al. 1992, Borrell 1993, Marsili & Focardi 1996, Haraguchi et al. 2000). That holds true for the North Atlantic sei whale, as has been shown by a study of Polychlorinated biphenyls (PCB) and Dichlorodiphenyltrichloroethane family compounds (DDTs) using samples from sei, fin, sperm *Physeter macrocephalus* and pilot *Globicephala melas* whales, white-sided dolphins *Lagenorhynchus acutus* and harbour porpoises *Phocoena phocoena* from the Northeastern North Atlantic, where sei whale total DDTs and PCB concentrations (mg kg-1) were from 14 to 136 times and from 23 to 146 times, respectively, lower than those of the odontocete species (Borrell 1993). Heavy metal contamination also tends to be lower in mysticetes and in the sei whale in particular; differences from odontocetes vary from non-existant to two orders of magnitude (e.g. Focardi et al. 1992, Haraguchi et al. 2000).

Climate change. Global warming is unequivocal (Anonymous 2007) and is likely to have detrimental impacts on marine mammal populations (Simmonds & Eliott 2009). Climate change is predicted to affect cetacean distribution, timing and range of migrations, abundance, mortality, reproductive success and prey resources (Learmonth et al. 2006, Simmonds & Isaac 2007).
Rates of temperature change in marine ecosystems have not been evenly distributed globally. Some of the more drastic increases in sea surface temperature have been reported for regions of the North Atlantic, including the Newfoundland–Labrador, west Greenland, Scottish and Icelandic shelves as well as the Faroe Plateau (Belkin 2009). These regions include much of the known sei whale summer habitat.
Marine ecosystems have a critical thermal boundary, where a small increase in temperature triggers abrupt ecosystem shifts at multiple trophic levels (Beaugrand et al. 2008); that process may already be causing ecosystem reorganization in marine copepod biodiversity in the North Atlantic (Beaugrand et al. 2002, 2008). In the northeastern North Atlantic and adjacent seas, there has been a shift in the copepod assemblage – warmer water species are moving poleward more than 10° in latitude, and there is an associated decrease in the number of subarctic and arctic species. West of the Mid-Atlantic Ridge, especially in the Labrador Sea, the trend is opposite – an increase and expansion to the south of the cold water species is taking place (Beaugrand et al. 2002). Those changes may have special implications for sei whales given that copepods seem to constitute their main prey in this ocean basin. Nevertheless, it is difficult to predict if sei whales will suffer or profit from these changes due to uncertainties about the ecosystem

reorganization and about sei whales' ability to cope with prey assemblage changes in the North Atlantic.

Resumption of whaling. Commercial sei whaling in the North Atlantic ceased in 1986 after the moratorium in commercial whaling implemented by the IWC. Under special scientific permits, however, Icelandic whalers captured 70 sei whales between 1986 and 1988. Aboriginal subsistence hunters in Greenland were allowed to take two whales in 1989 and one in 2006 (Allison 2008).
The resumption of commercial whaling in the North Atlantic is still a contentious issue within the IWC, and the possibility of operations targeting sei whales cannot be ruled out in the near future.

CONCLUSIONS AND RECOMMENDATIONS
In his seminal publication on the sei whale, Horwood (1987) identified research projects required to fill critical knowledge gaps, which in his opinion could be conducted using non-lethal techniques and existing data. Topics were as follows: (i) stock identity and genetics; (ii) distribution and migration; (iii) reproduction and mortality; and (iv) abundance estimation. To date, little progress has been made on these recommendations. Our bibliometric analysis shows that research on the sei whale has been almost stagnant for the last 20 years. There was a clear departure from the growth expected from Price's Law on scientific output. According to Price's Law, if scientific output on a subject does not follow exponential growth, either the field has reached saturation, which is clearly not the case, or not enough resources are being assigned to research.
The literature on virtually every aspect of the population biology of the North Atlantic sei whale is meagre and in most cases outdated. Furthermore, much of the research carried out over the last two decades relies on old whaling data, and little effort has been directed to applying current methodologies to understanding sei whale population biology. Meanwhile, some paradigms on population management and conservation have changed. The impacts of human activities are no longer restricted to single species and locations but have become global and transverse entire ecological communities. For example, as fishing pressure on several marine species increases, the lack of sustainable fishery management is a threat not only to the species being harvested but also to the equilibrium of the communities. Detrimental effects occur at all trophic levels (Sherman et al. 2009). As a result of these changes, it has been argued that marine research has shown a major shift in orientation to face an ever increasing environmental deterioration, and is now driven by the urgency to understand and ameliorate disturbed marine ecosystems, with implications for research priorities and the allocation of funds (Stachowitsch 2003). An example of that shift is a change in the focus of cetacean research from basic biological and ecological issues to conservation-related topics (Rose et al. 2011). One problem with this new paradigm is that it works against species or ecosystems for which there is little or no ongoing research. Since it is not possible to detect if they are facing conservation problems, investment is channeled away to other pressing issues, even if in reality they are in trouble. These species or ecosystems may end up being 'forgotten' by science, the general public and decision makers. That can create a paradox in which our ignorance about a resource puts it at risk by diverting investment to conserve other resources.

To avoid that paradox, it is important to focus efforts on gaining more information on those species and ecosystems for which our understanding is severely limited as is the case with cryptic species such as the sei whale.

The current research needs for the North Atlantic sei whale still include those identified by Horwood more than 20 years ago. To them are added the need to understand (i) the role of this species in the ecosystems it integrates into, and (ii) how changes in this ocean's marine environment will affect the species. The existing scientific knowledge on sei whales, largely derived from historical whaling data, is insufficient for making sound scientific and management decisions. This information is critically important given current human impacts on the marine environment and the likelihood of large-scale ecosystem changes due to climate change.

Research on the sei whale has been hindered in the past in part by its pelagic nature, which makes the study of the species both logistically difficult and expensive, compared with other more coastal species. With the aid of the most recent techniques to derive and analyse data, such as satellite telemetry and passive acoustic monitoring, it is now possible to conduct cetacean research efficiently even in pelagic habitats, and some of the research goals mentioned above can be achieved with fairly low human and financial investment. Other goals demand more investment but are essential to fill the data gaps. Among the most important are population assessments using synoptic multinational surveys that cover a wide latitudinal and longitudinal range and the clear definition of stock identity within the North Atlantic.

Overall, it is essential to bring research on North Atlantic sei whales out of its stagnancy and into the 21st century to ensure proper management of the species and the ecosystems it integrates with in the North Atlantic Ocean.

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