Population genetics and behavioural ecology of North Atlantic minke whales (Balaenoptera acutorostrata)

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Population Genetics and Behavioural Ecology of North Atlantic Minke Whales (*Balaenoptera acutorostrata*)

PhD Thesis of

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To my Parents

DECLARATION

The material contained in this thesis has not previously been submitted for a degree at the University of Durham or any other university. The research reported within this thesis has been conducted by the author unless otherwise indicated.

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ABSTRACT

Regional habitat use by a species, dictated by the spatial and temporal availability of resources, influences its distribution patterns and ultimately population genetic structure. Seasonal migrations between geographically separated breeding and feeding areas, as occur in many baleen whales, can complicate these relationships. Here I try to integrate the population structure of minke whales over the whole North Atlantic with regional habitat use and behavioural adaptations to a particular summer feeding ground, the Hebrides off West Scotland.

Whereas no genetic differentiation could be found between separate feeding areas as far apart as Canada, the UK and Svalbard, using microsatellites and mtDNA, the presence of two cryptic breeding populations was detected, which form mixed assemblages on feeding grounds across the North Atlantic. This implies fidelity to at least two breeding grounds irrespective of proximity to feeding areas, i.e. extensive seasonal migrations (over half the North Atlantic or more), which may require a re-assessment of current management stocks. These findings were consistent with the mobility and flexibility in habitat use and behaviour observed within the Hebrides. Results from Generalized Additive Models indicated that minke whale distribution was dependent largely on temporally variable parameters (temperature in spring, chlorophyll concentration in autumn), besides depth and, to a lesser extent, topography. However, fine-scale foraging behaviour was dictated primarily by the strength and direction of tidal currents. Distribution patterns according to environmental parameters changed through the season, but were largely consistent between the entire Hebrides (cell resolution of 4min) and a smaller core study area (2min), and over a time period of 15 years. Significantly higher sighting rates in areas of likely sandeel presence in spring, but not during the rest of the season, combined with prey samples from the core study area consisting almost entirely of sprat in August/September, indicate a switch in diet between early and late season and are consistent with the changes in habitat use. Site fidelity within the core study area was high only during periods of high feeding activity, but low at other times and between years, so that individual specializations to fine-scale feeding areas, as observed off Washington State, seem unlikely. Significant interannual changes in minke sighting rates between 2003-07, both within the core study area and over the entire Hebrides, were paralleled by changes in phytoplankton concentration, local sprat landings by the fishing fleet, and seabird breeding success and numbers counted at sea, particularly common guillemots. Auks were also the seabird guild that minke whales were most likely to associate with during foraging, taking advantage of tight bait-balls concentrated by them. The significant relationships with primary productivity make bottom-up control the most likely scenario for dictating concentrations of whale and seabird prey species in West Scotland. The ability to switch between different prey according to their availability through the season, and a distribution influenced by temporally variable parameters (temperature and chlorophyll concentration), combined with adjustments in foraging activity dependent on variable conditions at fine spatial scales (tides), enable minke whales to optimise exploitation of patchy prey concentrations.

GENERAL INTRODUCTION

Patterns of habitat use in a species relative to its size and mobility are ultimately influenced by the availability of resources. For organisms in the marine environment, such as whales, resource distributions are often patchy, and suitable habitat for mating and feeding may differ. This leads to a high level of mobility, which can influence population genetic structure.

Local food abundance in turn has implications for the degree to which an organism can afford to specialize. If prey is scarce, a generalist diet results in higher energy gain per unit time, whereas specialization on fewer prey types would be expected when food is abundant (MacArthur & Pianka, 1966). Generalists, probably in part as a result of evolutionary adaptation to low overall prey densities or an unreliable temporal and spatial distribution of food, are expected to show higher degrees of flexibility in their habitat use. This contrasts with specialists, which are often more restricted in their range due to lower tolerance of spatial changes in availability of their primary prey. It follows that spatial structuring of populations should be more pronounced in species with a specialist dietary niche than in generalists. However, individuals of a species can still show specializations with respect to both diet and / or feeding strategies between (ecotypes) or within areas, even if the species as a whole occupies a relatively generalist niche. By definition, ecotypes show differentiation between populations occurring in different environments (Turesson, 1922). The best known examples include sessile or sedentary organisms such as plants (e.g. yarrow; Clausen *et al.*, 1948) and some invertebrates (e.g. barnacles, Carballo *et al.*, 2005; or limpets, Conde-Padín *et al.*, 2009), but even extremely mobile mammals can show differentiation between ecotypes (e.g. inshore vs. offshore forms of the bottlenose dolphin, Hoelzel *et al.*, 1998). By contrast, individual specialization to diet or feeding strategies can occur within a given area and prey patch as a mechanism of reducing intraspecific competition for the same prey, but without leading to population differentiation. Examples include a wide range of wading birds, where individual feeding and foraging specializations can often be related to differences in morphology (e.g. between sexes or age groups), individual skills or social status (see review in Durell, 2000).

The relationship between habitat use and population structuring can be further complicated by seasonal migration between geographically separated breeding and feeding areas. In a number of bird species, e.g. the blackcap (Helbig, 1991; Berthold *et al.*, 1992), migratory routes are genetically determined. This suggests that seasonal site fidelity (at least in a stable environment) is adaptive, most likely because local environmental conditions require learning for efficient exploitation of resources. This may include knowledge of locations for suitable feeding and breeding sites or ontogenetic development of particular feeding strategies most suitable to the local environmental conditions and behaviour of prey. The importance of individual experience for foraging efficiency has been demonstrated in great tits, for example: individual captive birds preferred different feeding sites, reflecting the learned skills they had acquired during training (Partridge, 1976).

Most baleen whale species undergo seasonal migrations between low latitude breeding areas in winter (where they typically fast) and higher latitude feeding grounds in summer. The best-studied examples are the gray and humpback whales, whose breeding grounds are located within discrete areas, often close to land (Rice & Wolman, 1971; Clapham, 2009). However, where feeding conditions are favourable year-round (e.g. in the Arabian Sea for humpback whales, Mikhalev, 1997; or off Vancouver Island, Canada, for gray whales, Darling *et al.*, 1998), individuals may remain in their feeding areas for the entire year, resulting in partially migratory populations. This is also typical for various songbird species (e.g. blackcaps, robins or blue tits - Lack, 1943; Berthold, 1978; Biebach, 1983; Pulido *et al.*, 1996; Nilsson, 2006). By contrast to the well-studied humpback and gray whales, the breeding areas and migration routes of minke whales are poorly known. Population genetic studies are therefore restricted to samples taken on the summer feeding grounds. Some individual minke whales are known to show inter-annual site-fidelity to the same feeding areas both in the North Pacific (Dorsey, 1983; Dorsey *et al.*, 1990; Stern *et al.*, 1990) and North Atlantic (e.g. Gill *et al.*, 1995; Tscherter & Morris, 2007), and individual, habitat-specific, foraging strategies have been identified for the species in the eastern North Pacific (Hoelzel *et al.*, 1989).

Study species

The minke whale (*Balaenoptera acutorostrata*) is the most abundant of the balaenopterid or rorqual whales (also comprising blue, fin, sei, Bryde's and humpback) and has a worldwide distribution. Due to its smaller size (8m in males to 8.5m in females in the

northern hemisphere, with Antarctic animals being on average 0.5m longer; Horwood, 1990) by comparison to the other five species, the minke was generally not considered worth exploiting by the whaling industry before the second half of the 20th century, when the larger whales became depleted and internationally protected. Minke whaling continues today in the North Atlantic, North Pacific and Antarctic. Information on the population structure of the species therefore remains important for decisions on management stocks and has received increased attention over the last 20 years, particularly with the advances in molecular techniques.

Taxonomy

A high degree of allopatric differentiation between Antarctic, North Pacific and North Atlantic minke whales is now well established, not only on the basis of morphological (Horwood, 1990), but also genetic evidence using a wide range of markers (Amos & Dover, 1991; Hoelzel & Dover, 1991b; van Pijlen *et al.*, 1991, 1995; Wada *et al.*, 1991; Wada & Numachi, 1991; Hori *et al.*, 1994). Since the genetic distance between Northern and Southern Hemisphere minkes in some of the above studies (Wada *et al.*, 1991; Wada & Numachi, 1991; Hoelzel & Dover, 1991b) was comparable to or even exceeded that found between two other species in the genus, Bryde's and sei whales, the Antarctic form is now recognized as a separate species, *Balaenoptera bonaerensis*. A dwarf form, distributed off Australia, South Africa and South America, is more closely related to Northern hemisphere animals than to *B. bonaerensis* (Wada & Numachi, 1991; Hori *et al.*, 1994). The high genetic differentiation between North Atlantic and North Pacific minkes (Hoelzel and Dover, 1991; Amos and Dover, 1991; Hori *et al.*, 1994; van Pijlen et al., 1991, 1995; Martinez and Pastene, 1999), as well as morphological differences, have resulted in the recognition of two sub-species (*Balaenoptera acutorostrata acutorostrata* for the North Atlantic, and *B. a. scammoni* (previously *davidsoni*) for the North Pacific form; Perrin & Brownell, 2002).

Movements between breeding and feeding areas

Like other balaenopterids, North Atlantic minkes are thought to undertake seasonal migrations between high latitude feeding areas in summer and temperate breeding grounds in winter (Stewart & Leatherwood, 1985). Calves are born between November and March (mainly around December) after a gestation period of ca. 10 months (Jonsgård, 1951; Sergeant, 1963; Mitchell, 1975). Due to a relatively short lactation

period of ca. 4-5 months, calves are usually independent by the time they arrive on the summer feeding grounds, and mother-calf pairs are uncommonly seen.

Breeding populations of Antarctic minke whales, by contrast to humpback, gray or right whales, seem to be relatively dispersed in offshore waters (Kasamatsu *et al.*, 1995). In the western North Pacific, two breeding populations from either side of Japan form mixed assemblages on a common summer feeding ground in the Sea of Okhotsk (Wada & Numachi, 1991; Wada, 1991), and in the eastern North Pacific, some individuals appear to remain on their feeding grounds throughout the year (Everitt *et al.*, 1980; Dorsey, 1983; Dorsey *et al.*, 1990). Although southward migrations have been documented for North Atlantic minke whales at least in the northern parts of their range in the autumn (Skaug *et al.*, 2004), some individuals have been recorded as far north as west and southwest Greenland in winter (Kapel, 1980) and off Newfoundland in November and December (Sergeant, 1963). Sighting rates around the British Isles and Ireland are also highest during summer (with a peak in July and August), but occasional sightings also occur between November and March (Evans *et al.*, 2003; Anderwald & Evans, 2007), suggesting that small numbers of individuals may not migrate between feeding and breeding areas on a regular basis.

No discrete breeding grounds have so far been identified for minke whales in the North Atlantic. With very few strandings or sightings in inshore waters between November and April, they are thought to occur mainly offshore during winter (Jonsgård, 1951; Evans *et al.*, 2003). The extent of the seasonal migrations is also unknown, but minke whales are evidently capable of covering very large distances within short periods of time. Within three months (beginning of June to end of August), one subadult individual trapped in fishing gear off Skagen in Danish waters and subsequently satellite-tagged, travelled from Denmark to the north and west coasts of the UK, south past the Azores to NW of the Cape Verdes (ca. 18.5°N, 31°W), then turned north past Madeira and into the Mediterranean, where it was lost near the Balearic Islands (Teilmann *et al.*, 2005).

North Atlantic distribution

Balaenoptera acutorostrata acutorostrata is widely distributed over the entire North Atlantic from Baffin Bay to the West Indies in the west, and from Svalbard to the Azores in the east, although it is absent from the Baltic (Stewart & Leatherwood, 1985; Reid *et al.*, 2003). During summer, most sightings occur over the continental shelf of temperate

and subarctic regions, often close to the coast (e.g. in the St. Lawrence estuary, Iceland, Norway, around the British Isles and Ireland).

Both spatial and temporal segregation by age and sex have been reported for the species during migration and on the summer feeding grounds. Examples include:

By age:

- The Newfoundland minke whale fishery was dominated by mature animals, whereas juveniles were thought to remain further south during the summer (Sergeant, 1963).
- In both Greenland and eastern Canada, mature females dominated in catches during early summer, with increasing numbers of younger whales of both sexes later on (Mitchell & Kozicki, 1975; Solvik, 1976; Kapel, 1980).
- A high proportion of juveniles were observed off West Scotland in 2004 (Chapter 3), whereas mature animals usually dominate in the St. Lawrence (U. Tscherter, *personal communication*).

By sex:

- Off Norway, adult females tended to migrate closer to shore than males (Jonsgård, 1951, 1962).
- Minke whale catches in Newfoundland and Nova Scotia between 1966 and 1972 (Mitchell, 1974), as well as in the Barents Sea and in West Greenland in 1973 showed a strong bias towards females, whereas males predominated in East Greenland (Christensen, 1975).
- A bias towards females over years has been observed in the St. Lawrence estuary (D. Zbinden, U. Tscherter, *personal communication*).
- Christensen (1975) found a higher percentage of mature females in the 1973 catches from East and West Greenland (70%) than in the Barents Sea (40%).

Diet and feeding behaviour

Minke whales are the most catholic feeders among the mysticetes and take a wide range of fish species, as well as krill. However, in different parts of the North Atlantic, the relative importance of individual prey species varies: capelin (*Mallotus villosus*) dominates in the St. Lawrence (D. Zbinden, *pers. communication*), sandeels (*Ammodytes* spp.), capelin and krill in Greenland (Neve, 2000) and Iceland (Sigurjønsson *et al.*, 2000),

krill and capelin in the northern Barents Sea and around Svalbard, herring (*Clupea harengus*) in the southern Barents Sea (Lindstrøm *et al.*, 1997, 2002; Haug *et al.*, 1995, 2002) and Norwegian Sea (Vesterålen / Lofoten; Lydersen *et al.*, 1991; Lindstrøm *et al.*, 1997; Olsen & Holst, 2001), and sandeels in the North Sea (Olsen & Holst, 2001; Pierce *et al.*, 2004), although herring and sprat (*Sprattus sprattus*) are also taken around the British Isles (Pierce *et al.*, 2004). Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pollack (*Pollachius pollachius*), saithe (*Pollachius virens*), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*) and mackerel (*Scomber scombrus*) have also been recorded in stomach samples from some locations, but appear to be of less importance (Jonsgård, 1982; Lydersen *et al.*, 1991; Sigurjønsson *et al.*, 2000; Haug *et al.*, 1995; 2002; Olsen & Holst, 2001; Pierce *et al.*, 2004). These variations in diet may be predominantly a reflection of differences in prey availability between areas rather than true specializations.

Minke whales often feed near the surface (lunging sideways or vertically), enabling direct observations of feeding behaviour. Although a solitary species, groups of up to 15 individuals or more may occur in close proximity to each other in areas of high prey density. However, the animals normally behave independently of each other, and no evidence exists so far for cooperative feeding behaviour as has been observed, for example, in humpback whales (Sharpe, 2001).

Population size and causes of mortality

In the North Atlantic, the International Whaling Commission (IWC) currently recognizes four management stocks: East Canada, West Greenland, Central and Northeast (Rørvik & Jonsgård, 1981; Donovan, 1991). A population estimate of 174,000 (95%CI=125,000-245,000) was made for the Central and Northeast Atlantic combined, during 1996-2001, whereas the West Greenland stock size has been estimated at 10,800 (95%CI=3,600-32,400; http://www.iwcoffice.org). For the North Sea and adjacent waters (English Channel and Celtic Sea), an estimate derived from a line transect survey during July 1994 (SCANS) was 8,450 (95%CI=5,000-13,500; Hammond *et al.*, 2002). From SCANS II in July 2005, a point estimate for the equivalent area was slightly higher, at 10,500, out of a total of 16,395 over the NW European continental shelf (Hammond, 2008).

Besides humans, the only known predator of minke whales is the killer whale (*Orcinus orca*), at least in the Antarctic (Budylenko, 1981; Doroshenko, 1978) and eastern North

Pacific (Ford *et al.*, 2005). In the North Atlantic, the extent of killer whale predation on minke whales is unclear, but scars which were likely inflicted by killer whale teeth have been observed (Jonsgård, 1968). Due to the coastal distribution of minkes during summer, entanglement in fishing gear is an important source of mortality in most parts of their range (IWC, 1994). In east Scotland, one individual was struck by a ship (P.G.H. Evans, *personal communication*), and in the Bahamas, mid-frequency active sonar used by the military may have been responsible for the live-strandings of two minkes in 2000.

Minke whales are legally protected in most countries, with a moratorium on commercial whaling by the IWC since 1986. They are also listed on CITES Appendix I (except for the West Greenland stock, which is listed on Appendix II; http://www.cites.com; see also Evans, 2008: p. 657). Under objection to the IWC's moratorium, Norway has increased its annual quota in the Northeast Atlantic since 1993 to 1052 animals from 2006 onwards, although fewer animals have actually been taken (157 in 1993 to 597 in 2007, with a maximum of 647 in 2003; http://www.iwcoffice.org). Like Japan operating in the Antarctic (up to 856 whales killed in 2005) and North Pacific (ca. 200 per year), although on a much smaller scale, Iceland engaged in scientific whaling within Icelandic waters from 2003 to 2007 (with a maximum annual catch of 60 whales in 2006), and then resumed a limited commercial fishery in 2006 (with 6 individuals taken in 2007; http://www.iwcoffice.org). The fact that animals may form mixed assemblages of different breeding populations on summer feeding grounds (as in the western North Pacific) carries the danger that small breeding populations may be unknowingly depleted by whaling operations in feeding areas (Hoelzel, 1991).

Aims

The aim of this thesis is to shed light on how behavioural and ecological factors influence patterns of habitat use during the non-breeding season, and the extent to which these reflect population structure in a migratory species. The hypotheses are that a) habitat use within an area during the feeding season should be determined by biotic and abiotic factors associated with the optimisation of foraging efficiency; b) local environmental conditions in a feeding area require learning for efficient prey exploitation, and therefore fidelity to feeding sites should be adaptive; and c) if breeding populations show fidelity to the same feeding sites, this should be reflected by genetic differentiation between feeding grounds.

Moving to increasingly finer spatial scales in three chapters, I will try to answer the following main questions:

1) Does the summer distribution of minke whales on spatially separated summer feeding grounds reflect their population genetic structure over the entire North Atlantic, including data from previously unsampled areas?
2) Concentrating upon one particular feeding ground (the west coast of Scotland), what are the environmental parameters (fixed and temporally variable) that determine minke whale distribution, and does their relative importance differ between intermediate and fine spatial scales?
3) In the context of the biotic and abiotic conditions within a small core study area, what behavioural adaptations are shown by minke whales for efficient exploitation of local resources?

CHAPTER 1:

CRYPTIC MINKE WHALE POPULATION STRUCTURE IN THE NORTH ATLANTIC AS REVEALED BY MICROSATELLITE AND mtDNA MARKERS

INTRODUCTION

Cetaceans are highly mobile, and many species range over wide distances. Population structure within species can be influenced by geographic barriers (allopatry), colonisation of new habitats with associated bottlenecks and founder effects, adaptation to exploit local resources, as well as life history parameters such as social system, dispersal and migration. Bottlenose dolphins, for example, show strong population sub-structuring even within relatively localised areas, probably due to dependence on and adaptation to local habitat (Hoelzel *et al.*, 1998; Natoli *et al.*, 2004, 2005a), and killer whales due to different foraging specialisations (Hoelzel & Dover, 1991a; Hoelzel *et al.*, 2007). Other species, such as the gregarious short-beaked common dolphin (Natoli *et al.*, 2005b), or the migratory fin (Bérubé *et al.*, 1998) or sei whales (Wada & Numachi, 1991) show little differentiation over wide areas. In the small and thus potentially less mobile harbour porpoise, male-biased dispersal may link neighbouring populations through greater male-mediated gene flow, as inferred from lack of population sub-division found for microsatellites, while the maternally inherited mitochondrial DNA (mtDNA) shows stronger signs of sub-structuring between populations (Rosel *et al.*, 1999).

Migration and population structure

A detailed understanding of an exploited or endangered species' population structure over its entire geographic range is vital for its effective management and conservation. Despite the heavy exploitation of baleen whales in the 19th and 20th centuries, population identities for most species remain poorly understood. Mysticete population structure is particularly difficult to study due to their often long migrations between summer feeding grounds in high latitudes and winter breeding grounds in low latitudes. Mixing of different breeding stocks can occur in a single feeding area, as demonstrated e.g. for minke whales (Wada, 1991; Pastene *et al.*, 1992; Goto & Pastene, 1997), or conversely, individuals from different feeding grounds can congregate on a common wintering ground, as e.g. in humpback whales (Baker *et al.*, 1990). Both whaling and research efforts have focused mainly on the summer feeding grounds, whereas the winter distribution of most species, as well as their migration routes, are largely unknown (with the exception of North Pacific and Western North Atlantic humpback whales; Darling & McSweeney, 1985; Baker *et al.*, 1990; Baker *et al.*, 1993).

Minke whale population structure: Global

Allopatric differentiation between the two minke whale species of the Antarctic (*Balaenoptera bonaerensis*) and Northern hemisphere (*Balaenoptera acutorostrata*), respectively, as well as between the three subspecies from the North Pacific (*B. a. scammoni*), North Atlantic (*B. a. acutorostrata*) and the dwarf form in the Southern Hemisphere is now well established (Horwood, 1990; Amos & Dover, 1991; Hoelzel & Dover, 1991b; Wada *et al.*, 1991; Wada & Numachi, 1991; van Pijlen *et al.*, 1991, 1995; Hori *et al.*, 1994; Martinez and Pastene, 1999; see General Introduction). On a finer geographical scale, however, minke whale population structure remains less clear.

Within the Antarctic, the IWC set up six management areas for baleen whales (except Bryde's whale; Donovan, 1991), but most authors did not find any (van Pijlen *et al.*, 1991, 1995; Wada *et al.*, 1991; Wada & Numachi, 1991; Hoelzel & Dover, 1991b, Hori *et al.*, 1994) or only very little (Amos & Dover, 1991; Bakke et al., 1996) genetic differentiation between minke whales sampled in the adjacent management areas IV and V. However, Pastene *et al.* (1992) found differences in mtDNA haplotype frequencies between the eastern and western sectors, when the two areas were split into three adjacent regions, and also discovered spatial and temporal heterogeneity in haplotype distribution

when more individuals were examined subsequently (Pastene *et al.*, 1994, 1996), suggesting two populations.

Genetic differentiation has also been demonstrated in minke whales over a comparatively small area in the North Pacific: Wada & Numachi (1991) and Wada (1991) found significant differences in allozyme allele frequencies between animals caught off Korea and the Pacific coast of Japan. Wada (1991) compared these two populations with samples from the Sea of Okhotsk, where intermediate frequencies were found for the Adh-1 allele during April, suggesting that the two populations mix temporarily in the Sea of Okhotsk. Although Wada *et al.*'s (1991) mtDNA RFLP analysis did not reveal significant differences between minkes from Korea and the Pacific coast of Japan, a later study by Goto & Pastene (1997), using the same marker, confirmed the differentiation between these stocks.

Minke whale population structure: North Atlantic

For North Atlantic minke whales, most of the life history parameters influencing population structure, mentioned above, are not well known. They are usually solitary, but their mating system is unknown; regional and temporal segregation by both sex and age occurs in some areas, but it is not known whether sex-biased dispersal exists; animals which winter in the northern-most regions undergo latitudinal migrations, but it is not clear whether this also applies to minkes spending the summer in temperate seas such as around the British Isles. Finally, adaptation to local resources and site fidelity to summer feeding grounds seems to exist, which may influence population structure (see General Introduction).

Based on catch and sightings distribution, biological parameters such as sex and length distribution, marking data and the general desire to remain in accord with ICES boundaries, the IWC set up four management areas for minke whales in the North Atlantic in 1977 (Donovan, 1991; Rørvik & Jonsgård, 1981): East Canada, West Greenland, Central (East Greenland, Iceland and Jan Mayen) and Northeast (North Sea, Vesterålen / Lofoten, Barents Sea and Svalbard). These were further subdivided into the "IWC Small Areas" (Anon., 1992; Figure 1.1). Since these boundaries are based on feeding rather than breeding grounds, there is a danger of possible age and sex biases from individuals of the same breeding populations having influenced the decisions. Larsen & Øien (1988), for example, found that the apparent difference in sex ratio between West and East Greenland was caused mainly by sampling bias: in both areas,

females arrived earlier in the season and migrated further north, but since whaling effort in East Greenland was concentrated further south than on the west coast, more males were caught on the east coast.

Since the setup of the North Atlantic management units by the IWC, numerous studies have been carried out to compare the management stocks with the identities of actual populations. Although management stocks do not necessarily need to correspond to natural populations, biological information on population identity obviously needs to be taken into consideration in setting up management units for a species. Studies of (biological) stock structure in North Atlantic minke whales have included morphological, biochemical and genetic comparisons: Morphological studies by Christensen *et al.* (1990) found that minke whales caught in West Greenland tended to be bigger than animals from East Greenland and the Northeast Atlantic (including the North Sea), and that whales from both West and East Greenland had larger dorsal fins than those caught in the Northeast. However, the large overlap between groups did not allow the authors any conclusions about stock structure. The findings from genetic studies of stock structure within the North Atlantic so far have been very heterogeneous, depending on the markers used: allozyme analysis (Daníelsdóttir *et al.*, 1992; Daníelsdóttir *et al.*, 1995) and DNA-fingerprinting (Árnason & Spilliaert, 1991) indicated genetic differentiation between minke whales from West Greenland, Iceland and the Northeast Atlantic (Barents Sea for Daníelsdóttir *et al.*, 1992, and Árnason & Spilliaert, 1991; Svalbard, Barents Sea, Vesterålen / Lofoten and Norwegian North Sea for Daníelsdóttir *et al.*, 1995) and thus seemed to have been in general agreement with the morphological differences found by Christensen *et al.* (1990). However, mitochondrial DNA (mtDNA) analysis did not yield any significant differences between minke whales from West Greenland, Iceland and the Northeast Atlantic (Palsbøll, 1990: RFLP analysis, Bakke *et al.*, 1996: D-loop & NADH locus), although both studies detected two mtDNA lineages. RAPD-typing by Martinez & Pastene (1999) also identified two very closely related stocks within the Central / Northeast Atlantic: one cluster was formed by individuals from Jan Mayen (IWC Central stock) and Svalbard (Northeast), and the other by animals from the Norwegian North Sea, Vesterålen / Lofoten and the Barents Sea (all belonging to Northeastern stock). The highest level of genetic population sub-structure for North Atlantic minke whales so far has been detected by a combined microsatellite / mtDNA study by Andersen *et al.* (2003): whereas significant differences at the mtDNA level were found only between West Greenland and Central (East Greenland and Jan Mayen) females, the microsatellite

analysis revealed four sub-populations: West Greenland, Central (East Greenland and Jan Mayen), Northeast (Svalbard, Barents Sea and Vesterålen / Lofoten) and Norwegian North Sea. However, F_{st} values in their study were very low, which implies that most variance was explained by differences within regional populations.

A general consensus between studies so far has been the lack of sub-division between the IWC Small Areas within the Northeast Atlantic – Svalbard, Barents Sea and Vesterålen / Lofoten (see also Martinez *et al.*, 1997). These areas are therefore not re-examined in the present study, and only samples from Svalbard are used to represent this stock for comparison with other regions. The status of animals in the North Sea is less clear, however, with microsatellites being the only genetic marker so far to distinguish animals from the Norwegian North Sea as a separate population. The genetic relationship of Norwegian North Sea minkes with other populations, in particular with animals around the adjacent British Isles, is clearly in need of further investigation and is addressed in the present study. More importantly, however, previous studies on the population structure of North Atlantic minke whales appear to have placed their main emphasis on finding regional differences between summer feeding grounds. The possibility of seasonal mixing of populations on feeding grounds, as demonstrated around Japan (Wada, 1991), has so far not been examined in detail for the North Atlantic, and is therefore also addressed here.

Aims

Most minke whale population studies so far have relied on tissue samples of animals taken during commercial whaling operations, thus the main emphasis has been on finding regional differences between the traditional whaling grounds. The population structure and identity in regions where there has been no whaling for decades, such as British and Canadian waters, has not been investigated in any larger context yet, mainly because samples from these areas were scarce. However, in order to make informed management and conservation decisions on the species in the North Atlantic, it is essential to know the population structure over its entire range to account for the possibility of smaller, possibly isolated sub-populations, bearing in mind that population structure on the summer feeding grounds may not necessarily be spatially correlated since breeding takes place in lower latitudes. The two main questions asked in the present study are therefore:

1) Using neutral, high resolution genetic markers, how are minke whales from around the UK, Canada and Iceland related to animals from other regions in the North Atlantic, and do they represent separate populations?
2) Do minke whales from different breeding populations mix on summer feeding grounds, and if so, can they be identified from the mixed assemblages?

METHODS

Genetic markers

Amongst all the genetic methods applied in studies of North Atlantic minke whale population structure so far, VNTR markers (microsatellites and minisatellites) most likely provide the finest resolution. Microsatellites consist of short (1-6 bp) tandem repeat units normally between 50 and 200 bp in length, and are widely distributed throughout the nuclear genome (e.g. Tautz, 1993). Length polymorphisms are mainly caused by polymerase slippage during replication, usually resulting in changes of a single repeat unit, but also by unequal crossing-over during meiosis, resulting in differences of several repeat units (Weber & Wong, 1993; Di Rienzo *et al.*, 1994). The rapid evolutionary rates at microsatellite loci (ca. 10^{-4} to 10^{-3} per locus in mammals; Levinson & Gutman, 1987; Frankham *et al.*, 2002, p. 157; Jeffreys *et al.*, 1988) and the resulting high degree of polymorphism within species make them a valuable tool for examining population structure. In recent years, an increasing number of cetacean microsatellite primers have become available and thus facilitated fine-scale genetic analysis of populations.

Sex-biased dispersal is not uncommon in cetaceans (e.g. humpback whale, Palumbi & Baker, 1994; beluga, O'Corry-Crowe *et al.*, 1997; sperm whale, Lyrholm *et al.*, 1999; harbour porpoise, Rosel *et al.*, 1999; Dall's porpoise, Escorza-Treviño & Dizon, 2000; bottlenose dolphin, Möller & Beheregaray, 2004). Since both spatial and temporal heterogeneity in sex distribution in North Atlantic minke whales is well documented (Jonsgård, 1951, 1962; Mitchell, 1974; Christensen, 1975; Larsen & Oien, 1988; D. Zbinden, U. Tscherter, *personal communication*) and their mating system remains unclear, it is wise to include within a population genetic study of the species a marker which is inherited only maternally. Due to its lower effective population size (1/4) compared to nuclear DNA, the mitochondrial genome is more sensitive to genetic drift and thus well suited to study populations which have diverged relatively recently. The lack of proof-reading activity of the mtDNA polymerase results in 5-10 times higher evolutionary rates of mitochondrial compared to single copy nuclear DNA (Brown *et al.*, 1979). Within the mitochondrial genome, the control region (D-loop) is the fastest evolving region with substitution rates in humans between 2.8 (Cann *et al.*, 1984) and 5 times (Aquadro & Greenburg, 1983) higher than in the remainder of the molecule. For the intended fine-scale genetic analysis of population sub-structure, the mtDNA control

region was therefore amplified as a second marker for the UK, Irish and Canadian samples, and haplotype frequencies compared with those for other regions within the North Atlantic found by Bakke *et al.* (1996) and Andersen *et al.* (2003).

Samples

The areas covered in this study are the east and west coasts of the UK, the Norwegian North Sea, Ireland, Spain, coastal Norway (Vesterålen / Lofoten), Svalbard, Jan Mayen, Iceland, West Greenland and the Gulf of St. Lawrence, Canada.

Tissue samples included skin and muscle samples stored in NaCl saturated 20% DMSO (Amos and Hoelzel, 1991) or 100% Ethanol (Table 1.1). Samples from the UK were either provided by the Scottish and English strandings co-ordinators from stranded animals (38 samples) or by biopsy-sampling live minke whales in the Western Isles, Scotland, under permit from Scottish Natural Heritage (5 samples). Irish, Spanish and Canadian samples were taken exclusively from stranded animals, and Norwegian, Icelandic and West Greenland samples from whaling operations (Figure 1.1). No whales were killed in order to provide material for the present study. Where tissue samples originated from whaling operations, the animals were taken for other purposes as part of the whaling programmes of the countries concerned, and sub-samples were kindly provided by the relevant national institutes administering the tissue samples and other biological material.

For most regions, several years of sampling had to be included in order to get a large enough sample size. A separate analysis based on year to year differences was therefore not possible. In addition to the North Atlantic samples, 30 individuals from the Sea of Japan (JP) were included in the analysis as an outgroup.

Table 1.1. Number (N), sex (f:m) and tissue origin of samples from the different regions.

Origin	N (f:m)	Tissue	Stored in:	Source	Years
UK (UK)	43 (29:14)	skin	salt / DMSO, 1 x gin	38 x strandings, 5 x biopsing	1993 – 2005
West Greenland (GR)	36 (28:8)	muscle	salt / EDTA / Tris	whaling	1980 & 1982
Iceland (IC)	60 (27:33)	skin	EtOH	whaling	2003 & 2004
Gulf of St. Lawrence (CN)	15 (13:2)	skin, 2 x muscle	salt / DMSO	strandings	1996, 2002 & 2003
Norwegian North Sea (NS)	36 (22:14)	muscle	salt / DMSO	whaling	2004
Svalbard (SV)	48 (47:1)	muscle	salt / DMSO	whaling	2004
Jan Mayen (JM)	17 (17:0)	muscle	salt / DMSO	whaling	2004
Ireland (IR)	4 (3:1)	skin	salt / DMSO	strandings	2001 – 2003
Spain (SP)	3 (1:1, 1 not sexed)	skin	salt / DMSO	strandings	2003 & 2004

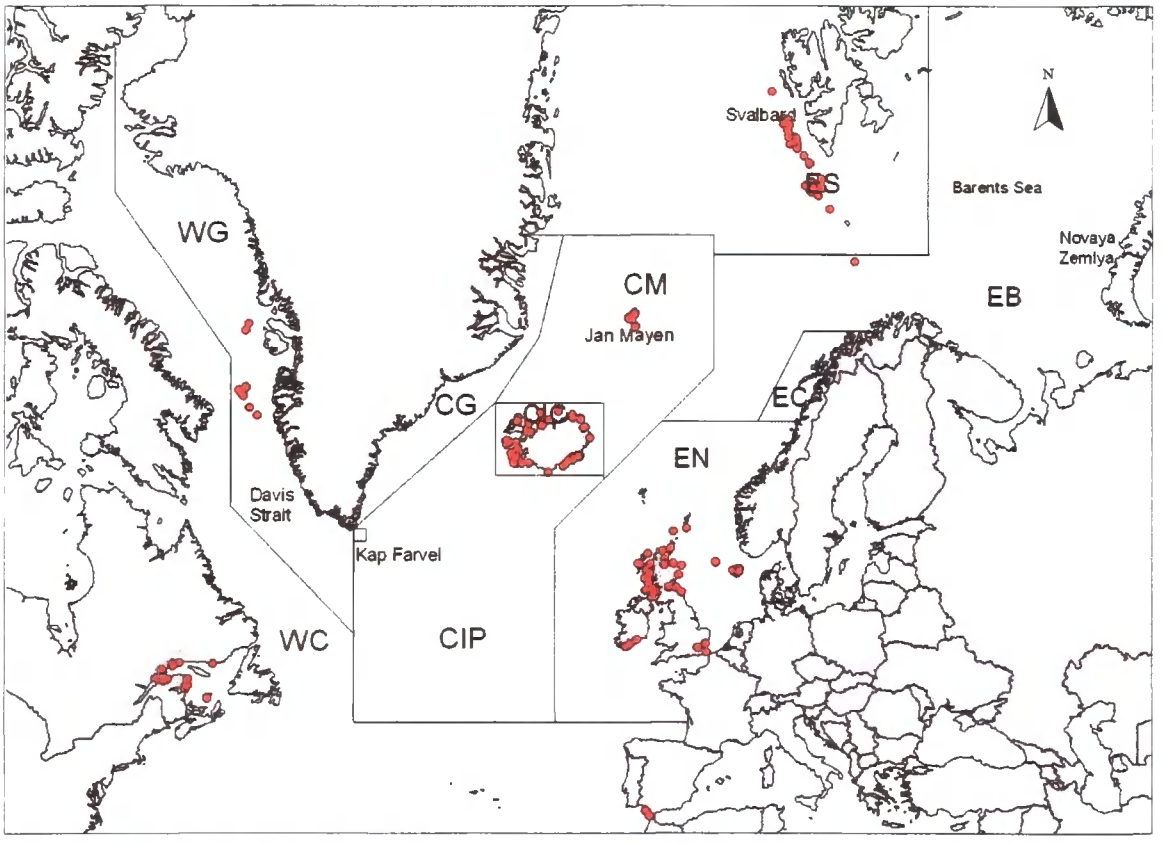


Figure 1.1. IWC Small Areas (Anon., 1992) and sampling locations of the 262 North Atlantic minke whale tissue samples. For West Greenland, only locations from the 1980 catches are plotted, but samples in 1982 were taken in the same area (F. Larsen, *personal communication*). IWC management units: Eastern Canada (WC), West Greenland (WG), Central (CG, CM, CIC and CIP) and Northeast (ES, EB, EC and EN).

Biopsy-sampling

In the Hebrides, biopsy-samples were taken from live animals under permit from Scottish Natural Heritage (SNH), using a 6mm in diameter by 12mm deep biopsy dart (provided by Dr. Finn Larsen) fired from a cross-bow. The dart was sharpened at the edge, and barbs inside the cylinder retained the sample (Palsbøll *et al.*, 1991). The depth of the dart allowed samples to be taken from skin and a small proportion of the blubber beneath the skin. The dart was fired from a distance of approximately 10m to the animal, taking a sample from the upper side, under the dorsal fin. Such samples have been collected from minke whales with no indication that the distribution or long-term behaviour of the subject whales has been disrupted. The dart was retrieved free-floating in the water, and all samples were stored at -20°C in a saturated NaCl salt / 20% dimethylsulphoxide (DMSO) solution (Amos & Hoelzel, 1991) until DNA-extraction in the laboratory.

Laboratory work

Nuclear DNA was extracted from the skin and muscle samples following a standard proteinase K, phenol / chloroform extraction protocol for whole cell DNA (Milligan, 1998: 46-47).

Microsatellites: Ten microsatellite loci were then amplified using specific primer sets (Valsecchi and Amos, 1996; Andersen *et al.*, 1997; Palsbøll *et al.*, 1997; Bérubé *et al.*, 2000; Table 1.2) in the polymerase chain reaction (PCR). Two thermal profiles were used: Protocol 1) 5min at 95°C, 35 cycles of [45s at 94°C, 1.5min at annealing temperature, 1.5min at 72°C], 1.5min at 50°C, 8min at 72°C; Protocol 2) 3min at 95°C, 35 cycles of [1min at 94°C, 30s at annealing temperature, 10s at 72°C], 15min at 72°C. Protocol 2 was used for Igf-1 only. Annealing temperatures were optimised for minke whales and ranged from 45°C to 62°C (Table 1.2). Amplifications were carried out in 20µl volumes with the following concentrations: 2mM of each dNTP, 500ng/µl primers, 50ng/µl fluorescent labelled primer (Hex, Fam or Ned), 0.4 units Biotaq DNA polymerase and 0.5-2.5mM $MgCl_2$. Amplified DNA was subsequently analysed for length variation on 6% polyacrylamide denaturing gels using fluorescent imaging on an automated ABI PRISM 377 DNA sequencer. An internal standard marker (Genescan-500 ROX, Applied Biosystems, Warrington, UK) was used to determine allele sizes.

The gender of individuals with unknown sex was determined using specific primers for the ZFY/ZFX gene (Bérubé and Palsbøll, 1996).

Table 1.2. PCR conditions used for the 10 microsatellite loci, repeat number and allele sizes.

Locus	Annealing temperature (°C)	$MgCl_2$-concentration (mM)	Repeat No.	Allele size	derived from:	Reference
EV1	61.0	1.5	2	122-174	*Physeter macrocephalus*	Valsecchi & Amos, 1996
EV37	53.0	1.0	2	175-213	*Megaptera novaeangliae*	Valsecchi & Amos, 1996
GATA028	45.0	2.0	4	155-225*	*Balaenoptera spp.*	Palsbøll *et al.*, 1997
GATA098	62.0	2.5	4	78-102	*Balaenoptera spp.*	Palsbøll *et al.*, 1997
GATA417	50.5	1.0	4	201-249	*Balaenoptera spp.*	Palsbøll *et al.*, 1997
ACCC392	49.0	0.5	4	192-266**	*Balaenoptera spp.*	Palsbøll *et al.*, 1997
GT509	55.5	1.0	2	191-217	*Megaptera novaeangliae*	Bérubé *et al.*, 2000
Kwm2a	47.0	0.9	2	144-162	*Orcinus orca*	Hoelzel *et al.*, 1998
Igf-1	53.5	1.0	2	141-153	Bovidae, *Phocoena phocoena*	Kirkpatrick, 1992; Andersen *et al.*, 1997
Texvet 7	52.6	1.5	2	162-180	*Tursiops truncatus*	Shinohara *et al.*, 1997; Rooney *et al.*, 1999

* A large allele gap of 22bp was detected between 163bp and 185bp.
** A large allele gap of 38bp was detected between 200 and 238bp.

Mitochondrial DNA: A 500bp fragment of the mitochondrial DNA (mtDNA) control region was amplified in the UK, Irish and Canadian samples using light-strand MT4 (5'-CCTCCCTAAGACTCAAGGAAG-3'; Árnason *et al.*, 1993) and modified heavy-strand Dlp5 primers (5'-GGATGTCTTATTTAAGRGGAA-3'; Baker *et al.*, 1996). The thermal profile for mtDNA amplification was the same as protocol No. 1) used for microsatellite amplification (see above). The annealing temperature was set to 55°C, and $MgCl_2$-concentration was 1.5mM. Buffer, dNTP, primer, polymerase and DNA concentrations were the same as used for the microsatellites, but reaction volumes were increased to 50µl. PCR products were purified with QIAgen PCR purification columns according to the protocol provided by the manufacturer (Qiagen GmbH, Germany) and sequenced using the ABI dye-terminator method.

Analysis

Microsatellites

A) REGIONAL COMPARISONS

The level of polymorphism was calculated as number of alleles per locus and population, effective number of alleles, allelic richness, and observed (H_o) and expected (H_e) heterozygosities. Effective number of alleles per locus is calculated as

$$n_e = 1 / \sum p_i^2$$

where p_i the frequency of the i^{th} allele (Frankham *et al.*, 2002: 81-82).

Allelic richness, which controls for variation in sample size by a rarefaction method (Hurlbert, 1971; El Mousadik & Petit, 1996; Petit *et al.*, 1998), is calculated as

$$r = \Sigma \left(1 - \left(\binom{2N-N_i}{2n} \Big/ \binom{2N}{2n}\right)\right)$$

where N the number of individuals in the population in question, n the number of individuals in the smallest population sampled, and N_i the number of alleles of type i. It is implemented in the program Fstat 2.9.3 (Goudet, 2001).

The advantage of both these measures is that they are less influenced by rare alleles and less sensitive to different sample sizes. Allelic richness permits direct comparison with the smallest sample and gives higher estimates than effective number of alleles. Since the same n is used for all populations, however, the presence of one or two populations with extremely low sample sizes will influence the estimates for all other populations, yielding less representative values. The effective number of alleles, on the other hand, only depends on the allele frequencies in the population that the measure is being calculated for, and was therefore used in addition to allelic richness to include the two smallest geographic populations.

Only geographic populations with ≥ 10 samples were included in the tests for Hardy-Weinberg and linkage disequilibrium, F- and R-statistics, Mantel test and test for sex-biased dispersal. Samples from Ireland (n=4) and Spain (n=3) were only included in estimates of the most probable number of putative populations in STRUCTURE 2.1.

Hardy-Weinberg equilibrium: All loci in each population were tested for possible deviations from Hardy-Weinberg equilibrium (heterozygote deficiency or excess) using the program MICROCHECKER 2.2.3 (van Oosterhout *et al.*, 2004), which is also capable of detecting possible null alleles, large allele drop-out or scoring errors due to stuttering. After randomising genotypes from the observed alleles for each locus and population, probabilities of observed homozygote frequencies were calculated using a cumulative binomial distribution. P-values were derived using a rank-based approach, and Fisher's combined probability test was then calculated (van Oosterhout *et al.*, 2004). Bootstrap values for Monte Carlo simulations were set at 1000, and confidence intervals were Bonferroni-corrected. The frequency of possible null alleles was estimated using the van Oosterhout *et al.* (2004) null allele estimator.

Linkage disequilibrium: Fisher's exact test (Rousset & Raymond, 1995) with Markov chain settings of 10,000 dememorisation steps, 100 batches and 5000 iterations per batch was performed for all combinations of loci using the program GENEPOP 3.4 (Raymond & Rousset, 1995) in order to test for linkage disequilibrium amongst loci.

Population differentiation: Genetic differentiation among geographic populations was investigated using both the infinite allele model (F_{st}; Weir & Cockerham, 1984) and stepwise mutation model (Rho_{st}; Goodman, 1997). The advantage of the stepwise mutation model is that it takes into account the inter-dependence of microsatellite allele sizes, as well as their high mutation rates (e.g. by comparison to isozyme loci; Slatkin, 1995). The infinite allele model on the other hand is based on random genetic drift as the primary cause for differentiation between populations and generally shows lower variance by comparison to the stepwise mutation model (Slatkin, 1995). Compared to the process of genetic drift, neutral mutations occur more slowly in the genome and become important only after relatively long periods of separation between populations. For recently diverged populations, the infinite allele model can therefore be more powerful than the stepwise mutation model. Thus, both models were included in the analysis. F_{st}

values were calculated using the program MICROSATELLITE ANALYSER (MSA; Dieringer & Schlötterer, 2002). Rho_{st} values were calculated in RST CALC (Goodman, 1997), based on a standardised dataset as implemented in the program. Slatkin's R_{st} (Slatkin, 1995) may be biased if the dataset includes populations with unequal sample sizes and widely differing variances between microsatellite loci, in that case underestimating differentiation of loci with low variances. In order to overcome the bias introduced by different variances among loci, RST CALC (Goodman, 1997) standardises the dataset before calculating Rho_{st} to express allele sizes as standard deviations from the global mean, and differences in sample sizes are addressed by calculating variance components (Goodman, 1997). The number of both permutations and bootstrap values for the test statistics was set at 1000. The population JM showed only one allele for the locus Igf-1, which would have resulted in a division by zero in the calculation of the test statistics and thus caused the program to crash (S. Goodman, *personal communication*). The locus IGF-1 therefore had to be excluded for the comparison of Rho_{st} values with the population JM.

In addition to F_{st} and Rho_{st}, the most probable number of putative populations (K) which best explained the pattern of genetic variability was estimated using a Bayesian approach implemented in the program STRUCTURE 2.1 (Pritchard *et al.*, 2000). The admixture model with correlated allele frequencies was chosen with a burn-in length of 50,000 and 500,000 Monte-Carlo Markov-Chain repeats, and the average admixture coefficient for individuals (α) was inferred with a uniform prior for α (initial value = 1, max = 10, SD = 0.025). For each putative K, four independent runs were performed in order to check whether the results remained constant, i.e. whether the chosen burn-in length and repeat number were appropriate. All populations were included in the first model ($1 \leq K \geq 14$), then the outgroup Japan was excluded in order to get a higher resolution for the North Atlantic samples (also $1 \leq K \geq 14$). Bayesian clustering methods as implemented in STRUCTURE rely on Hardy-Weinberg and linkage disequilibrium between populations. Thus, the performance of the program decreases with decreasing F_{st} values (particularly if $F_{st} \leq 0.02$; Latch *et al.*, 2006). In order to uncover cryptic population structure associated with individuals from different breeding populations mixing on the summer feeding grounds where the samples were taken, only the three largest populations (UK, IC and SV) were therefore included in a third model, ($1 \leq K \geq 8$), and last, the program was run for each of these three populations separately ($1 \leq K \geq 5$). Evanno *et al.* (2005) found that the log probability calculated by STRUCTURE could provide an incorrect estimate of the number of clusters especially in cases where population structure did not

follow a typical island model. A measure based on the second order rate of change of the likelihood function with respect to K (ΔK) yielded a more accurate estimate of the true number of populations in their simulations. For the first model including all putative populations, ΔK was therefore calculated in addition to the log probability as

$$\Delta K = m(|L(K+1)-2L(K)+L(K-1)|) / s[L(K)]$$

where m corresponds to the mean and s to the standard deviation of the four runs for equal K, and L is the log likelihood value Ln(P(X|K)) in the STRUCTURE output (Evanno *et al.*, 2005). This was compared with the highest number of putative populations suggested by STRUCTURE.

B) POPULATION COMPARISON BASED ON STRUCTURE RESULTS

Based on the highest likelihood run of the software STRUCTURE, all North Atlantic samples were re-assigned to one of two populations according to their highest coefficient of admixture (likelihood assignment). Polymorphism of these two new populations, Hardy-Weinberg and linkage equilibrium, as well as F_{st} and Rho_{st} were calculated using the same methods as described for the geographic comparisons. In addition, Fisher's exact test for population differentiation was applied, using the program GENEPOP 3.4 (Raymond & Rousset, 1995). Test parameters were set at 10,000 dememorisation steps, 1000 batches and 10,000 iterations per batch.

An individual-based assignment test, implemented in the program GeneClass2 (Piry *et al.*, 2004), was performed as a second method using a Bayesian approach (Rannala & Mountain, 1997), but with higher power than the method implemented in STRUCTURE 2.1 (Pritchard *et al.*, 2000). Individuals were assigned back to their source population using scores, which were calculated as:

$$Score_{i,l} = L_{i,l} / \sum^{k} L_{i,j}$$

where $L_{i,l}$ the likelihood value of the individual i in the population l, and k the number of populations (Piry *et al.*, 2004). The probability of each individual belonging to each reference population was calculated according to Paetkau *et al.* (2004), with a minimum

of 10,000 simulated individuals and a type 1 error probability of 0.01. Finally, the assignment results were verified independently in a factorial correspondence analysis (FCA) using the software GENETIX (Belkhir *et al.*, 2002).

The effective sizes of the two putative populations were estimated using the program *IMa* (Hey & Nielsen, 2007). The two loci containing a multi-step allele gap (GATA028 and ACCC392) were excluded from these calculations in order not to violate the assumptions of the stepwise mutation model. After several trial runs, parameters were adjusted to a burn-in length of 2,000,000 steps, metropolis coupling of 80 chains, geometric increments of 0.99 and 0.6, generation time of 22 years (Taylor *et al.*, 2007), and a mutation rate of an estimated 10^{-5} (per locus per year; Shug *et al.*, 1998; Yue *et al.*, 2002). A stepwise mutation model was assumed. Trend lines over the course of the run and update acceptance rates were used to check for sufficient mixing of the Markov chain. The final run included 6,380,375 steps after burn-in and saved 319,019 trees per locus.

Effective population size was calculated from IMa according to Hey (2007) as:

$N_e = q / (4UG)$,

where q = estimate of $4N_eu$ obtained by IMa,
U = mutation rate / locus / year (here 10^{-5})
G = number of years per generation (here 22 years).

Mitochondrial DNA

A) REGIONAL COMPARISONS

All sequences were cut to the same length as Bakke *et al.*'s (1996) published control region sequences and aligned using the program ClustalX1.81 (Thompson *et al.*, 1997).

Gene and nucleotide diversity (Nei, 1987), Tajima's D (Tajima, 1989), Fu's F_S (Fu, 1997), genetic differentiation (conventional F_{st} from haplotype frequencies (Weir & Cockerham, 1984) and Φ_{st} (Excoffier *et al.*, 1992)), and mismatch distribution were calculated in ARLEQUIN2.0 (Schneider *et al.*, 1999). For calculations involving mutation

rate, Ho *et al.*'s (2007) estimate of 5 x 10^{-7} (per site per year) was used, which had been derived for the HVR1 of the mtDNA control region for various mammals, incorporating ancient DNA data. Estimates of genetic distance for the calculation of nucleotide diversity and Φ_{st} used the Tamura-Nei model (Tamura & Nei, 1993) with a gamma correction of α=0.47 (as estimated for the human control region by Wakeley, 1993). The number of permutations for all test statistics was set to 10,000. Due to the small sample size for Ireland (n=4), Irish and British samples were pooled for the geographic comparison. This combined population and the Canadian samples were then compared with the haplotype distributions found by Bakke *et al.* (1996) and Andersen *et al.* (2003) for the remaining North Atlantic regions. The tests for genetic differentiation were performed both for the total sample and for females only (in the latter case excluding Bakke *et al.*'s (1996) data, since the individuals' sexes in his analysis were not published).

B) POPULATION COMPARISON BASED ON STRUCTURE RESULTS

Diversity indices, Fst and Φ_{st} were calculated for the populations inferred from STRUCTURE in the same way as for the geographic comparisons. Only the sequences amplified in the present study (i.e. UK, Ireland and Canada) were included in these analyses.

Phylogeny

Phylogenetic trees were constructed for the whole North Atlantic, using sequences found in the present study combined with haplotypes published by Bakke *et al.* (1996) and Andersen *et al.* (2003). A haplotype from the Antarctic (A1; Bakke *et al.*, 1996) and North Pacific (named here P1; GenBank Accession No. AY878077, Baker *et al.*, 2000) were used as outgroups. Both a neighbour-joining (Kimura 2-Parameter model with gamma correction of α=0.47 to correct for multiple hits at the same site, taking into account differences in substitution rates between transitions and transversions) and maximum parsimony tree (close-neighbour-interchange with search level 1 and 10 replications for random addition of trees) were constructed using the program MEGA version 3.1 (Kumar *et al.*, 2004). Phylogeny for both trees was inferred from 1000

bootstrap replications. In addition, a Bayesian approach for inference of phylogeny, as implemented in the program MRBAYES (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), was applied. The General Time Reversible method (GTR) was chosen as a standard nucleotide substitution model, with a gamma-shaped mutation rate variation including a proportion of invariable sites. The Monte-Carlo Markov-Chain length was set initially to 1,000,000, then increased to 10,000,000 repeats, and the sampling frequency was set to 100. Parameter values and trees were then summarised using 25% (i.e. 25,000) of the samples, and the consensus tree drawn in the program TREEVIEW (Page, 1996).

Finally, a median-joining network was constructed from all North Atlantic haplotypes (i.e. UK / Ireland and Canada, plus sequences published by Bakke *et al.*, 1996, and Andersen *et al.*, 2003, for all other regions) using the NETWORK software (www.fluxus-engineering.com; Bandelt *et al.*, 1999). The transversion to transition weight was set at 5:1, and deletions were weighted the same as transitions. In order to create higher resolution networks, epsilon was incrementally increased from 0 to 10 and 20, but no difference was observed between the settings for 10 and 20. Before drawing the network, the MP option (Polzin & Daneschmand, 2003) was enabled to delete redundant links and median vectors.

RESULTS

In all regions except Iceland, the sex distribution was biased towards females (Table 1.1).

Microsatellites

A) REGIONAL COMPARISONS

Polymorphism: The locus Igf-1 showed the lowest heterozygosity and number of alleles in all North Atlantic regions, but considerably more polymorphism for samples from the Sea of Japan (Table 1.3). Very few private alleles were observed between regions within the North Atlantic, but the Japanese population showed two or more private alleles for 8 out of 10 loci. Both heterozygosity and effective number of alleles were comparable between North Atlantic regions, though Ireland and Spain showed fewer alleles, as expected due to their very small sample sizes.

Hardy-Weinberg equilibrium: Deviations from expected Hardy-Weinberg allele frequencies were detected for two loci: Texvet 7 (for Greenland, Jan Mayen and Japan) and Kwm2a (for Jan Mayen and Japan), and were all due to homozygote excess (Table 1.3, Appendix 1.1). A shortage of heterozygous genotypes with alleles of one repeat unit difference indicated scoring errors due to stuttering for Texvet 7 for the Greenland ($p<0.025$), Jan Mayen (though not significant; $p>0.05$) and Japanese ($p<0.001$) samples, and a general excess of homozygous genotypes for most allele sizes suggested the presence of possible null alleles in all three regions for this locus. Texvet 7 was therefore excluded from any further analyses.

Although a possible presence of null alleles was suggested for Kwm2a in the Jan Mayen and Japanese populations, the excess of homozygotes for the Japanese samples was not significant ($p>0.05$), and a binomial analysis could not be performed for the Jan Mayen samples because >50% of alleles were the same size. Whereas inclusion of Texvet 7 changed the pattern of differentiation, exclusion of Kwm2a did not (F_{st} test, Appendix 1.2), and the locus was therefore retained in the analysis.

No evidence for large allele drop-out was detected in any locus - population combination.

Linkage disequilibrium: Chi-square values and significance levels from Fisher's exact test for each locus pair across all populations are listed in Appendix 1.3. After Bonferroni correction, only the locus pairs EV1–EV37 and GATA417-ACCC392 still showed significant linkage disequilibrium ($p<0.0014$). However, in comparisons for each region separately, no consistent pattern could be found, and in both cases this high significance was due to the Japanese population, which showed a p-value of <0.00001 for both locus combinations. Since the population from the Sea of Japan only served as an outgroup in this analysis, the loci were retained.

Table 1.3. Number of alleles (n, with number of private alleles in brackets), effective number of alleles (n_e), allelic richness (r; only for $N \geq 15$), observed (H_o) and expected (H_e) heterozygosities for each locus and region. For Texvet 7, a_0 indicates the estimated null allele frequencies for populations which showed a significant heterozygote deficiency. Abbreviations for populations are as in Table 1.1. JP=Japan.

	UK (N=43)	GR (N=36)	IC (N=60)	CN (N=15)	NS (N=36)	SV (N=48)	JM (N=17)	IR (N=4)	SP (N=3)	JP (N=30)
Texvet 7										
n	5	6	6	5	5	6	5	2	3	10 (4)
n_e	4.0	3.6	3.3	3.4	2.3	3.3	3.2	1.3	2.6	4.4
r	4.9	5.3	4.7	5.0	3.8	4.7	4.9	-	-	8.0
H_o	0.721	0.556*	0.683	0.867	0.500	0.646	0.471*	0.250	0.667	0.414*
H_e	0.761	0.734	0.704	0.726	0.580	0.708	0.711	0.250	0.733	0.786
a_0		0.118					0.163			0.233
EV1										
n	8	8	12 (1)	9 (1)	9	9 (1)	7	5	4	17 (8)
n_e	5.0	5.0	6.0	6.2	5.6	5.4	4.0	3.2	3.6	7.1
r	6.6	6.7	8.7	9.0	7.5	7.0	6.8	-	-	12.3
H_o	0.860	0.917	0.850	1	0.861	0.771	0.706	0.750	0.667	0.900
H_e	0.809	0.811	0.841	0.867	0.835	0.823	0.774	0.786	0.867	0.873
Kwm2a										
n	7	7	6	7	7	7	5	4	3	8 (2)
n_e	3.6	2.6	3.0	4.0	2.9	3.5	2.7	3.6	2.0	4.0
r	6.2	6.1	5.7	7.0	6.4	6.3	5.0	-	-	6.4
H_o	0.814	0.722	0.600	0.667	0.583	0.729	0.412*	1	0.333	0.600*
H_e	0.727	0.619	0.673	0.775	0.661	0.722	0.647	0.821	0.600	0.760
GATA028										
n	10	10	9	6	11 (1)	11 (1)	8	6	5	9 (2)
n_e	5.4	4.7	4.8	3.2	5.7	6.1	4.6	4.6	4.5	5.7
r	8.0	8.3	6.9	6.0	8.5	8.6	7.6	-	-	8.1
H_o	0.837	0.694	0.800	0.733	0.861	0.896	0.765	1	0.667	0.833
H_e	0.823	0.799	0.800	0.713	0.835	0.845	0.804	0.893	0.933	0.838

*Loci which showed heterozygote deficiency when tested for Hardy-Weinberg disequilibrium in MICROCHECKER 2.2.3. Populations IR and SP were not tested due to small sample sizes.

Table 1.3, continued. Number of alleles (n, with number of private alleles in brackets), effective number of alleles (n_e), allelic richness (r; only for N≥15), observed (H_o) and expected (H_e) heterozygosities for each locus and region. For Texvet 7, a_0 indicates the estimated null allele frequencies for populations which showed a significant heterozygote deficiency. Abbreviations for populations are as in Table 1.1. JP=Japan.

	UK (N=43)	GR (N=36)	IC (N=60)	CN (N=15)	NS (N=36)	SV (N=48)	JM (N=17)	IR (N=4)	SP (N=3)	JP (N=30)
GT509										
n	8	10	12 (1)	5	10	12 (1)	9	3	4	11
n_e	5.1	5.3	5.4	4.4	5.5	4.9	4.6	2.5	3.0	6.1
r	6.7	7.7	8.0	5.0	7.8	8.1	8.6	-	-	8.7
H_o	0.884	0.750	0.800	0.867	0.833	0.833	0.706	0.500	1	0.767
H_e	0.812	0.824	0.822	0.798	0.829	0.805	0.807	0.679	0.800	0.851
Igf-1										
n	2	2	3	2	3	3	1	1	1	5 (3)
n_e	1.1	1.1	1.1	1.5	1.1	1.2	1.0	1.0	1.0	2.8
r	1.9	1.9	2.1	2.0	1.8	2.2	1.0	-	-	4.3
H_o	0.116	0.139	0.133	0.400	0.056	0.167	0	0	0	0.567
H_e	0.111	0.131	0.126	0.331	0.055	0.156	0	0	0	0.658
GATA417										
n	10	9	10 (1)	8	9	10	9	4	4	5 (2)
n_e	6.6	6.1	7.1	5.1	6.4	6.8	6.4	2.9	3.0	3.0
r	8.5	7.5	8.3	8.0	8.3	8.4	8.7	-	-	4.7
H_o	0.930	0.943	0.900	0.867	0.833	0.938	0.882	0.750	0.667	0.500
H_e	0.858	0.848	0.867	0.832	0.856	0.863	0.868	0.750	0.800	0.682
EV37										
n	7	9 (2)	6	5	8	8 (1)	6	2	2	6 (3)
n_e	3.4	2.9	2.6	2.3	3.4	3.3	2.5	1.3	1.8	3.2
r	5.9	6.0	5.1	5.0	6.3	6.4	5.8	-	-	4.9
H_o	0.814	0.694	0.717	0.733	0.889	0.792	0.647	0.250	0.667	0.700
H_e	0.711	0.663	0.623	0.579	0.719	0.703	0.622	0.250	0.533	0.694
GATA098										
n	7	7	7	4	6	5	4	3	2	5
n_e	4.3	4.1	4.1	3.1	3.8	3.7	3.3	2.9	1.8	3.2
r	6.0	5.5	5.4	4.0	5.3	4.9	4.0	-	-	4.7
H_o	0.791	0.750	0.750	0.800	0.778	0.646	0.706	0.750	0.667	0.800
H_e	0.776	0.765	0.762	0.706	0.747	0.735	0.718	0.750	0.533	0.695
ACCC392										
n	6	5	7 (1)	6	7	6	4	3	4	7 (3)
n_e	2.7	2.3	3.3	2.1	2.9	2.5	2.5	1.7	3.6	4.0
r	5.6	4.6	5.7	6.0	5.8	5.1	4.0	-	-	6.5
H_o	0.628	0.556	0.683	0.600	0.667	0.604	0.529	0.250	1	0.900
H_e	0.639	0.576	0.705	0.543	0.660	0.605	0.619	0.464	0.867	0.765

*Loci which showed heterozygote deficiency when tested for Hardy-Weinberg disequilibrium in MICROCHECKER 2.2.3. Populations IR and SP were not tested due to small sample sizes.

Population differentiation: After Bonferroni correction, significant genetic differentiation could only be detected between the North Atlantic and Sea of Japan, but not amongst different regions within the North Atlantic. This result remained the same, no matter whether F_{st} or Rho_{st} was used (Tables 1.4 and 1.5). The exclusion of IGF-1 due to invariance for the comparison with the JM population resulted in higher Rho_{st} values for comparisons of all North Atlantic populations with Japan, but did not alter the results for populations within the North Atlantic (Appendix 1.4).

Table 1.4. F_{st} values for pairwise regional comparisons. Abbreviations for regions are the same as in Table 1.1. F_{st} values are listed above, significance values below the diagonal.

	UK	GR	IC	CN	NS	SV	JM	JP
UK	-	0.00074	-0.00241	0.00911	0.00087	-0.00287	0.00862	0.19172
GR	0.37	-	0.00017	0.01116	0.0063	0.00206	0.01387	0.21049
IC	0.86	0.43	-	0.00809	-0.00059	-0.00197	0.00498	0.19604
CN	0.06	0.04	0.07	-	0.01066	0.00266	0.01067	0.18945
NS	0.35	0.04	0.55	0.05	-	-0.00279	0.00108	0.19735
SV	0.87	0.21	0.81	0.28	0.84	-	0.00226	0.18681
JM	0.05	0.01	0.13	0.10	0.39	0.28	-	0.20565
JP	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	-

* p-values which were still significant after Bonferroni correction ($p<0.0028$).

Table 1.5. Rho_{st} values (averaging variance components over loci; Goodman, 1997) for pairwise regional comparisons. Abbreviations for regions are the same as in Table 1.1. Rho_{st} values are listed above, significance values below the diagonal. The JM population was monomorphic for the locus IGF-1, which therefore had to be omitted from the comparison of JM with the other regions in order to avoid a division by 0.

	UK	GR	IC	CN	NS	SV	JM	JP
UK	-	0.00269	0.00511	0.00538	0.00813	0.00335	*0.03511*	0.33694
GR	0.33	-	-0.00517	-0.00265	0.00531	-0.00453	*-0.00309*	0.35499
IC	0.17	0.84	-	-0.00357	0.00221	-0.00184	*0.01144*	0.35189
CN	0.25	0.55	0.57	-	0.01447	0.00201	*0.00813*	0.37588
NS	0.15	0.26	0.29	0.14	-	-0.00231	*0.01333*	0.35192
SV	0.23	0.78	0.63	0.36	0.61	-	*0.00408*	0.34604
JM	*0.02*	*0.61*	*0.17*	*0.35*	*0.19*	*0.38*	-	*0.4459*
JP	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	*<0.0001**	-

* p-values which were still significant after Bonferroni correction ($p<0.0028$).

Results on the most likely number of populations using the Bayesian approach in the program STRUCTURE 2.1 (Pritchard *et al.*, 2000) were not entirely clear-cut: when the outgroup Japan was included in the model, the highest likelihood was indicated for $K \approx 3$ populations, with Japan clearly separated from the North Atlantic, and two populations within the Atlantic Ocean (Table 1.6, Figure 1.2). These two latter populations were independent of their regional origin. However, for all models excluding the Sea of Japan samples, STRUCTURE indicated the presence of only one population. The simulation for the model including all North Atlantic populations without the outgroup Japan showed considerable variation between the four independent runs for the same K and was therefore repeated at a higher burn-in of 500,000 and run length of 1,000,000. However, the outcome remained the same as for the shorter run-lengths (Table 1.6).

Although K=3 showed a higher likelihood than K=2 for the model including the outgroup Japan, Ln(P(X|K)) reached a plateau after K=2, before decreasing again (Appendix 5a). Pritchard & Wen (2003) and Evanno *et al.* (2005) had pointed out such a plateau, or even slight increase in likelihood after the true K was reached in their simulations, and the plot of ΔK (calculated according to Evanno *et al.*, 2005) indeed showed a peak at K=2 (Appendix 5b). According to this result, the most likely number of populations within the North Atlantic was just one, despite the higher likelihood for the presence of two populations in this particular model. Nevertheless, the possibility of two populations within the North Atlantic required further investigation, since previous F_{st} values for regional comparisons had already been well below the threshold at which STRUCTURE could still detect population differentiation (Latch *et al.*, 2006). Based on the highest likelihood assignment for each individual in the model including the outgroup Japan (named STR1), all North Atlantic samples were thus re-assigned to one of the two populations suggested by STRUCTURE for this model, and the other tests of population differentiation repeated for these new groupings, named STR2 and STR3, respectively.

Table 1.6. Results from STRUCTURE 2.1. K = putative number of populations, Ln(P(X|K)) = estimated ln probability of K, Var (Ln(P(X|K))) = Variance of estimated ln probability of K, α = average admixture coefficient for individuals. The simulation for the model "without Japan" was repeated at a higher burnin and run length. Note that α>>1 for all models which do not include the outgroup Japan, indicating high admixture for North Atlantic individuals between regions.

Model	K	Ln(P(X|K))	Var (Ln(P(X|K)))	α
all populations	1	-9015.1 to -9014.9	51.3 - 51.5	-
	2	-8318.3 to -8317.5	116.8 – 118.0	0.0289 – 0.0290
	3	-8283.4 to -8279.8	300.3 – 306.0	0.0334 – 0.0337
	4	-8314.9 to -8310.5	523.3 – 530.1	0.0363 – 0.0365
without Japan	1	-7350.5 to -7350.1	39.9 – 40.6	-
	2	-7403.3 to -7378.8	134.8 – 189.4	5.4079 – 6.9910
	3	-7545.8 to -7463.7	320.4 – 489.1	5.1823 – 6.2015
burnin=500,000,	1	-7350.8 to -7350.0	39.9 – 42.2	-
run length=1,000,000	2	-7398.3 to -7364.9	99.6 – 177.8	6.3349 – 6.6248
	3	-7504.6 to -7447.4	288.6 – 405.7	5.7248 – 6.5004
UK, IC, SV	1	-4287.5 to -4282.3	32.1 – 41.3	-
	2	-4330.3 to -4267.9	13.2 – 151.3	5.8040 – 6.6388
UK	1	-1223.1 to -1215.8	21.5 – 31.6	-
	2	-1222.8 to -1212.2	17.4 – 33.0	3.7329 – 6.1312
IC	1	-1700.5 to -1695.1	24.8 – 33.6	-
	2	-1713.9 to -1700.7	34.5 – 70.3	4.0981 – 7.2609
SV	1	-1377.7 to -1369.5	22.7 – 35.2	-
	2	-1384.0 to -1371.5	28.8 – 48.9	4.3602 – 5.5829

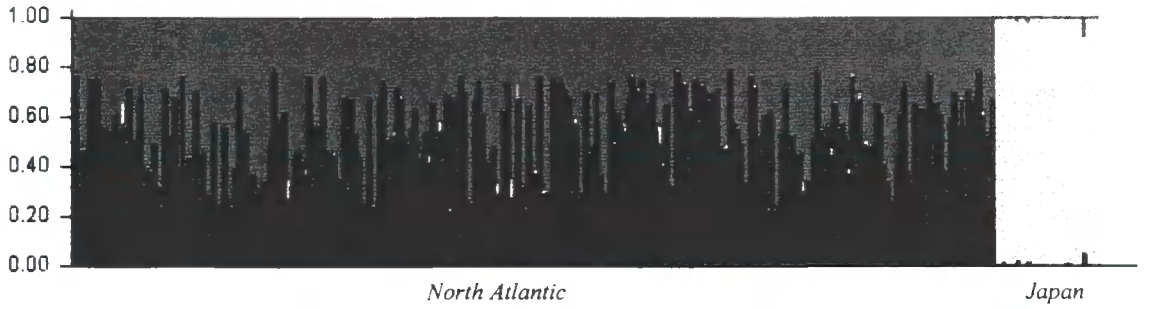


Figure 1.2. Estimated proportion of the coefficient of admixture (likelihood assignment) for each individual's genotype that originated from population k for k=3. Each individual is represented by a column.

B) POPULATION COMPARISON BASED ON STRUCTURE RESULTS

Polymorphism: Overall genetic diversity was similar between the two populations derived from STRUCTURE, although STR2 showed marginally lower average heterozygosities and allelic richness than STR3 (STR2: average H_o=0.675, H_e=0.668, r=8.4. STR3: average H_o=0.722, H_e=0.690, r=8.56). Private alleles were observed between the two populations in all loci except Kwm2a (Table 1.7).

Hardy-Weinberg equilibrium: As in the regional comparisons, Texvet 7 showed a deviance from expected Hardy-Weinberg allele frequencies for STR2 due to an excess of homozygote genotypes, possibly as a result of the presence of null alleles. Texvet 7 therefore remained excluded from the analysis. No homozygote excess could be detected for any of the other loci in either population.

Linkage disequilibrium: All pairs of loci were in linkage equilibrium. GATA028 – EV37 only showed a marginally significant linkage disequilibrium after Bonferroni correction (Chi^2=17.748, df=4, p=0.00138; $p_{corr.}$=0.001389; Appendix 1.6) and were retained in the analysis.

Table 1.7. Number of alleles (n, with number of private alleles in brackets), effective number of alleles (n_e), allelic richness (r), observed (H_o) and expected (H_e) heterozygosities per locus (excluding Texvet 7) for the two populations revealed by STRUCTURE.

	STR2 (N=133)	STR3 (N=129)
EV1		
n	13 (5)	10 (2)
n_e, r	5.4, 12.8	5.7, 10
H_o	0.842	0.845
H_e	0.819	0.828
Kwm2a		
n	7	7
n_e, r	3, 7	3.1, 7
H_o	0.632	0.705
H_e	0.673	0.683
GATA028		
n	12 (3)	9
n_e, r	5.9, 11.9	4.4, 9
H_o	0.820	0.806
H_e	0.833	0.777
GT509		
n	9	14 (5)
n_e, r	4.3, 8.9	5.9, 14
H_o	0.797	0.829
H_e	0.770	0.833
Igf-1		
n	2	3 (1)
n_e, r	1, 2	1.2, 3
H_o	0.045	0.217
H_e	0.044	0.197
GATA417		
n	11 (2)	9
n_e, r	6.9, 11	6.2, 9
H_o	0.887	0.914
H_e	0.857	0.842
EV37		
n	9 (2)	10 (3)
n_e, r	2.6, 9	3.3, 10
H_o	0.692	0.822
H_e	0.616	0.702
GATA098		
n	6	7 (1)
n_e, r	3.8, 6	3.8, 7
H_o	0.729	0.752
H_e	0.741	0.741
ACCC392		
n	7	8 (1)
n_e, r	2.9, 7	2.5, 8
H_o	0.632	0.612
H_e	0.663	0.605

Population differentiation: By contrast to the regional comparisons, both F_{st} and Rho_{st} showed a highly significant differentiation between STR2 and STR3 (F_{st}=0.020814, p=0.0001; Rho_{st}=0.0248, p<0.00001). Interestingly, the F_{st} value between the two populations was at the threshold for which the resolution power of STRUCTURE is known to decrease (Latch *et al.*, 2006). Fisher's exact test also showed a clear separation between STR2 and STR3 (Chi^2="infinity", df=18, p<0.00001).

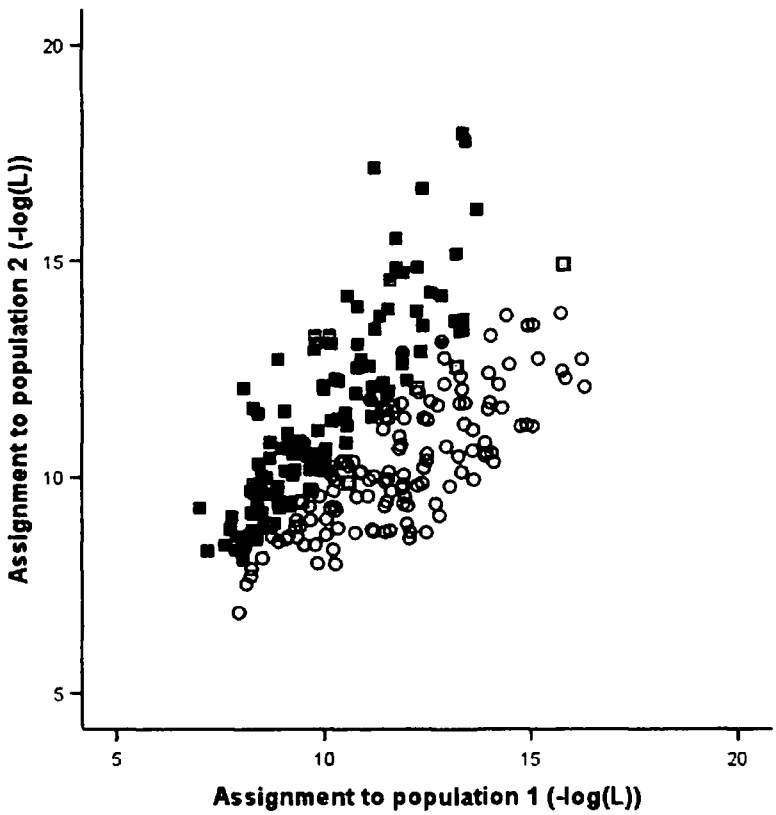


Figure 1.3. Log likelihood plot for Geneclass assignment results of STR2 and STR3. Correctly assigned individuals: filled squares = STR2, open circles = STR3. Incorrectly assigned individuals: light grey squares = STR2 assigned to STR3, dark grey circles = STR3 assigned to STR2.

Assignment of individual genotypes to their most likely source population using the program GeneClass2 (Piry *et al.*, 2004) corroborated these results: 94.7% of individuals were assigned correctly back to STR2 and STR3 respectively, based on ranks only (quality index = 85.33%), and 87.4% of individuals were assigned correctly based on probabilities (quality index = 70.15%). There was no difference in assignment success between the two populations: based on ranks, eight individuals from STR2 (6%) were assigned incorrectly to STR3, and six individuals (4.6%) from STR3 to STR2 (Appendix

1.7a). A log likelihood plot (Figure 1.3) illustrates the separation between the two populations despite the relatively close proximity of the clusters. Both populations were represented in all areas within the North Atlantic for which representative sample sizes were available (Figure 1.4; Appendix 1.7b). Amongst these areas, animals from both populations were present in approximately equal proportions around the UK, Iceland and Svalbard, whereas STR2 dominated in the Norwegian North Sea (69%), and STR3 in West Greenland (67%; comparing these two samples, $\chi^2 = 9.4$, p= 0.0022). Andersen *et al.* (2003) found their strongest F_{st} between West Greenland and the Norwegian North Sea. STR2 also dominated in Jan Mayen, Ireland and Spain, but due to low sample sizes, relative frequencies between the two populations in those areas are most likely not representative. Within the UK, STR2 and STR3 showed a proportion of 1:1 (13:13 individuals) on the west coast, whereas STR3 dominated on the east coast (70.5%, i.e. STR2:STR3 = 5:12 individuals), although this subdivision was also based on low sample sizes and is therefore not very meaningful.

The factorial correspondence analysis (Figure 1.5) confirmed the relatively close proximity between the two populations observed in the likelihood plot, and showed some degree of overlap. The first two dimensions explained 5.4% of the total variation.

Effective population size estimates based on microsatellite loci assessed using *IMa* (Hey & Nielsen, 2007) suggested a smaller size for STR2 (210; HPD90: 107-562) than for STR3 (5,437; HPD90: 2,039–9,380). These estimates were stable over multiple runs, and the posterior distributions reasonably tight and non-overlapping. The magnitude of these estimates depends on the estimated mutation rate, which varies over several orders of magnitude for microstatellite loci (see review in Brohede, 2003). The actual rates for these loci in the minke whale are not known, but the average rate assumed (10^{-5}) allows for easy calibration (e.g. if average $u=10^{-4}$, estimated N_e for STR2 would be 21). Estimates for migration rate and splitting time were not resolved.

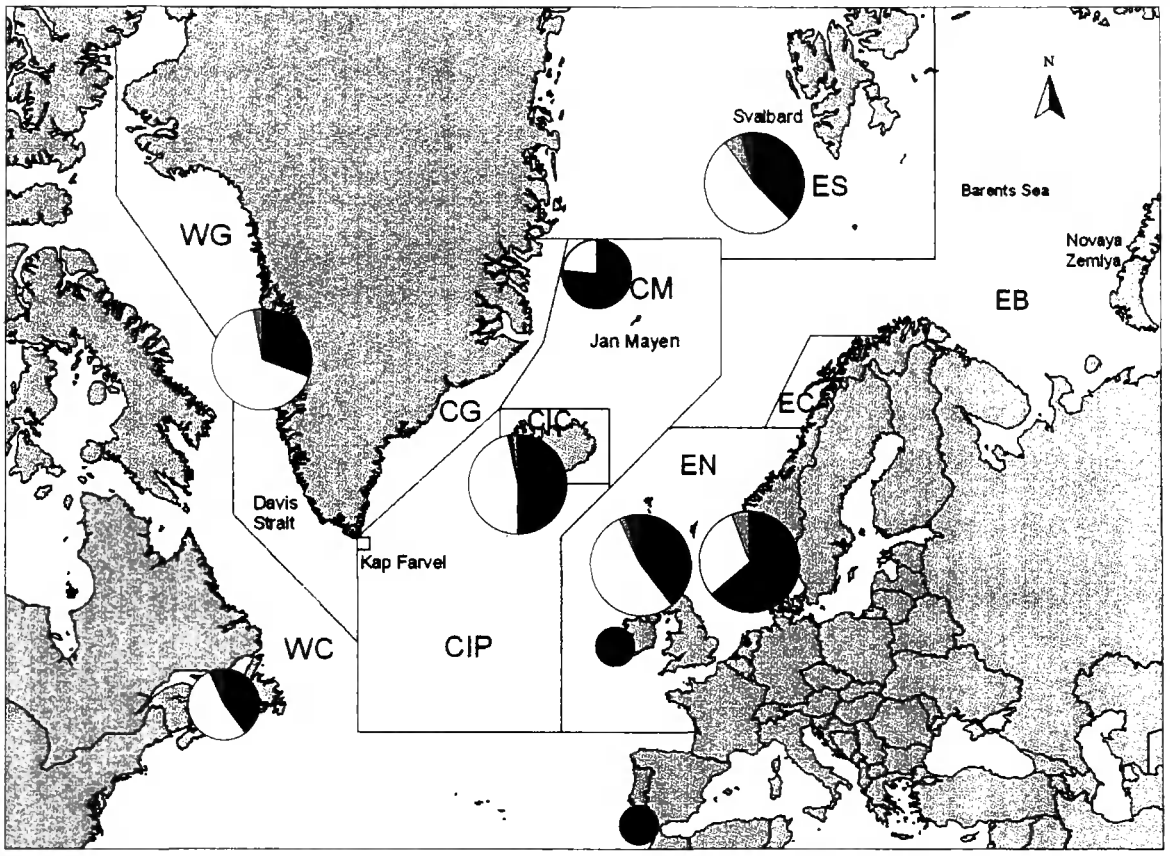


Figure 1.4. Geographic distribution of STR2 and STR3 in North Atlantic according to Geneclass assignments. Black = STR2, white = STR3, light grey = putative STR2 individuals assigned to STR3, dark grey = putative STR3 individuals assigned to STR2. Sizes of pie charts indicate sample sizes for different areas: largest charts represent areas with $n \geq 36$, medium-sized charts $10 < n < 20$ (Jan Mayen and Canada), and smallest charts areas with $n \leq 5$ (Ireland and Spain).

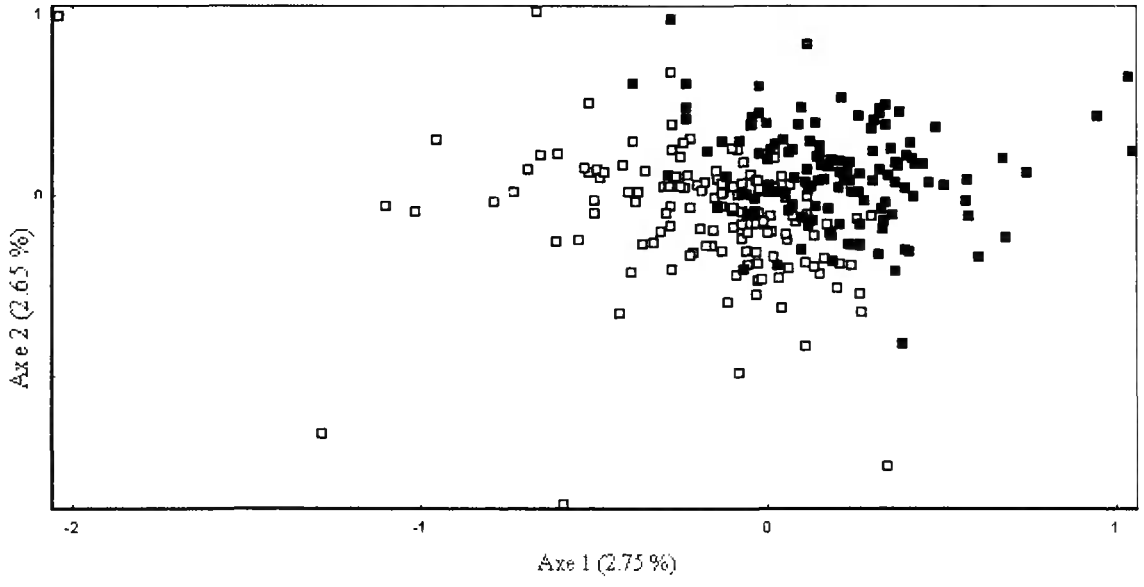


Figure 1.5. Two-dimensional representation of the factorial correspondence analysis. Individuals are projected on the factor space defined by the similarity of their allelic states.

Mitochondrial DNA

A) REGIONAL COMPARISONS

A total of 28 haplotypes were found amongst the 62 samples from the UK, Ireland and Canada (Table 1.8), of which 8 haplotypes had not been observed by Bakke *et al.* (1996) or Andersen *et al.* (2003). The 28 haplotypes were defined by 21 polymorphic sites: 3 inversions / deletions (TA, ATA and TATA), 2 transversions and 16 transitions. In agreement with Bakke *et al.* (1996) and Andersen *et al.* (2003), the most common haplotype was N1.

Gene and nucleotide diversities were very similar between the UK / Ireland and Canada (Table 1.9). Gene diversities for both locations were somewhat higher than the North Atlantic average (Table 1.9), but comparable with the values found by Andersen *et al.* (2003). Nucleotide diversities, on the other hand, were comparatively low, though at the higher end of values found by Bakke *et al.* (1996) and Andersen *et al.* (2003) for the other North Atlantic regions. Tajima's D values were not significant for either UK / Ireland or Canada, nor for the entire NA, confirming neutrality. Fu's F_S, however, was very large, negative and highly significant for the UK / Ireland and also the entire North Atlantic sample, which suggests a possible population expansion for North Atlantic minke whales (Table 1.9).

Table 1.8. Haplotype distribution for the pooled UK / Ireland (UK/IR) versus Canada (CN) samples. Haplotypes N1 – N48 are identical with Bakke *et al.*'s (1996) and Andersen *et al.*'s (2003) corresponding sequences obtained from GenBank.

Haplotype	UK/IR (n=47)	UK/IR females (n=32)	CN (n=15)	CN females (n=13)
N1	12	10	4	4
N2	0	0	1	1
N3	2	1	0	0
N4	3	2	1	0
N5	1	0	0	0
N6	1	0	0	0
N9	4	4	1	1
N10	2	0	1	1
N11	1	0	0	0
N18	0	0	1	1
N19	2	2	0	0
N20	2	1	0	0
N21	0	0	1	1
N22	1	1	0	0
N23	1	1	0	0
N24	1	1	0	0
N25	3	3	0	0
N26	0	0	1	0
N33	1	1	2	2
N48	2	2	1	1
N52	1	0	0	0
N53	1	0	0	0
N54	1	1	0	0
N55	1	1	0	0
N56	1	0	1	1
N57	1	0	0	0
N58	1	1	0	0
N59	1	0	0	0

Neither F_{st} nor Φ_{st} could detect any population differentiation between UK / Ireland and Canada or between these two samples and any of the other regions in the North Atlantic (Table 1.10). Although Φ_{st} values increased for the comparisons CN – EN, UK/IR – C, CN – WG and also UK/IR – CN when only females were considered in the analysis (Table 1.11), the results remained the same as when both sexes were included.

Table 1.9. Gene diversity, nucleotide diversity, Tajima's D and Fu's F_S for the combined UK / Ireland (UK/IR), Canadian (CN), and entire North Atlantic (Entire NA; including Bakke *et al.*'s (1996) and Andersen *et al.*'s (2003) published sequences).

	Gene diversity	Nucleotide diversity	Tajima's D	Fu's F_S
UK/IR	0.923 ± 0.029	0.0077 ± 0.0047	-0.94338	-15.94452***
CN	0.933 ± 0.054	0.0076 ± 0.0048	-0.74164	-3.56790**
Entire NA	0.886 ± 0.011	0.0077 ± 0.0046	-0.84002	-26.20247**

*p<0.05, **p<0.02 (as appropriate for Fu's F_S; Fu, 1997; Schneider *et al.*, 2000), ***p<<0.001

Table 1.10. F_{st} and Φ_{st} values for the total sample (males and females combined). UK/IR = UK & Ireland, CN = Canada. WG = pooled West Greenland sample for 1982, 1996, 1997 and 1998 from Andersen *et al.* (2003); C = Central North Atlantic, consisting of Bakke *et al.*'s (1996) samples from Iceland (n=41) and Andersen *et al.*'s (2003) samples from East Greenland (n=30) and Jan Mayen (n=24); NE = North East Atlantic, consisting of Bakke *et al.*'s samples from Svalbard (n=15), NW Norway (n=26), and the Barents Sea (n=5), and Andersen *et al.*'s (2003) samples from the same areas (Svalbard, n=16; NW Norway, n=14; Barents Sea, n=33). EN = Norwegian North Sea (Andersen *et al.*, 2003).

	CN (n=15)	WG (n=166)	C (n=95)	NE (n=109)	EN (n=23)
UK/IR (n=47):					
F_{st}	-0.01758	-0.00602	-0.00134	-0.00515	-0.00282
Φ_{st}	-0.00428	-0.00866	0.00222	-0.00758	-0.00539
CN:	-				
F_{st}		-0.01012	-0.00299	-0.00992	0.00370
Φ_{st}		0.00682	-0.00658	-0.01660	0.00029
all p-values >0.05					

Table 1.11. F_{st} and Φ_{st} values for females only. Population abbreviations are the same as in Table 1.10. Bakke et al.'s (1996) samples were excluded from the analysis because the individuals' sexes were not known.

	CN (n=13)	WG (n=128)	C (n=44)	NE (n=53)	EN (n=14)
UK/IR (n=32):					
F_{st}	-0.01417	-0.00743	-0.00037	-0.00994	-0.01950
Φ_{st}	0.00242	-0.00900	0.01472	-0.01121	-0.00121
CN:	-				
F_{st}		-0.00941	-0.00324	-0.01072	0.00714
Φ_{st}		0.01668	-0.00299	-0.02195	0.01852
all p-values >0.05					

B) POPULATION COMPARISON BASED ON STRUCTURE RESULTS

The haplotype distribution between STR2 and STR3, based on the samples from UK, Ireland and Canada, is listed in Table 1.12. In line with the results for the microsatellite loci, STR2 showed somewhat lower gene and nucleotide diversities than STR3 (Table 1.13), with the gene diversity of STR2 even slightly below the minimum found by Andersen *et al.* (2003). The F_{st} value between the two populations, both including all individuals (F_{st}=0.02892, p=0.039) and females only (F_{st}=0.04493, p=0.033), confirmed the differentiation between the two populations inferred already from the microsatellite results. However, Φ_{st} values were low and non-significant (all individuals: Φ_{st}=-0.00084, p=0.43; females only: Φ_{st}=-0.0121, p=0.6). As in the regional comparisons, Tajima's D remained non-significant, and Fu's F_S large, negative and highly significant, supporting the possibility of an expansion for both populations (Table 1.13).

Table 1.12. Haplotype distribution for the two populations STR2 and STR3, based on the samples from UK, Ireland and Canada. Haplotypes N1 – N48 are identical with Bakke *et al.*'s (1996) and Andersen *et al.*'s (2003) corresponding sequences obtained from GenBank.

Haplotype	STR2 (n=28)	STR2 females (n=21)	STR3 (n=34)	STR3 females (n=24)
N1	11	9	5	5
N2	0	0	1	1
N3	0	0	2	1
N4	1	0	3	2
N5	1	0	0	0
N6	1	0	0	0
N9	0	0	5	5
N10	0	0	3	1
N11	1	0	0	0
N18	1	1	0	0
N19	0	0	2	2
N20	1	1	1	0
N21	0	0	1	1
N22	1	1	0	0
N23	0	0	1	1
N24	0	0	1	1
N25	2	2	1	1
N26	1	0	0	0
N33	2	2	1	1
N48	1	1	2	2
N52	0	0	1	0
N53	0	0	1	0
N54	1	1	0	0
N55	1	1	0	0
N56	1	1	1	0
N57	0	0	1	0
N58	1	1	0	0
N59	0	0	1	0

Table 1.13. Gene diversity, nucleotide diversity, Tajima's D and Fu's F_S for STR2 and STR3, based on the samples from UK, Ireland and Canada (n=62).

	Gene diversity	Nucleotide diversity	Tajima's D	Fu's F_S
STR2	0.820 +/- 0.074	0.0056 +/- 0.0035	-1.01337	-10.04960*
STR3	0.939 +/- 0.022	0.0074 +/- 0.0044	-0.57577	-10.87144*

*$p<0.00001$

Phylogeny

The Neighbour-Joining, Maximum Parsimony and Bayesian phylogenetic trees, based on haplotypes from the whole North Atlantic (i.e. including sequences from Bakke *et al.*

(1996) and Andersen *et al.* (2003), in addition to those from UK, Ireland and Canada), supported only one matriline with respect to the mtDNA control region (Figures 1.7, 1.8 and 1.9). Only four and three branches within the North Atlantic were supported by bootstrap values of ≥50% in the neighbour-joining and maximum parsimony trees, respectively.

The results from Fu's F_S test (Tables 1.9 and 1.13), suggesting a population expansion for North Atlantic minke whales, were in agreement with the mismatch distribution (Figure 1.6): using the parametric bootstrap test implemented in ARLEQUIN2.0 (Schneider *et al.*, 1999), no significant deviation from the sudden expansion model was detected (SSD=0.0073; p=0.6), and the raggedness index of the curve was low (0.0136; p=0.81). Tau was estimated at 5.851 (95% CI = 2.158 - 10.265). Based on a mutation rate of 5 x 10^{-7} per site per year (Ho *et al.*, 2007), this would suggest an expansion time of 16,957 (6,260 - 29,768) years before present (Rogers & Harpending, 1992). The curve in Figure 1.6 is not strictly unimodal, however, making it difficult to pinpoint the time of expansion from tau. The two peaks may represent two periods of expansion. The low value of Φ_{st} between STR2 and STR3 and the largely star-shaped structure of the Bayesian tree (Figure 1.9) are further indications of a relatively recent population expansion in North Atlantic minke whales (Ingman *et al.*, 2000), as suggested by Fu's F_S test (Tables 1.9 and 1.13) and the mismatch distribution (Figure 1.6).

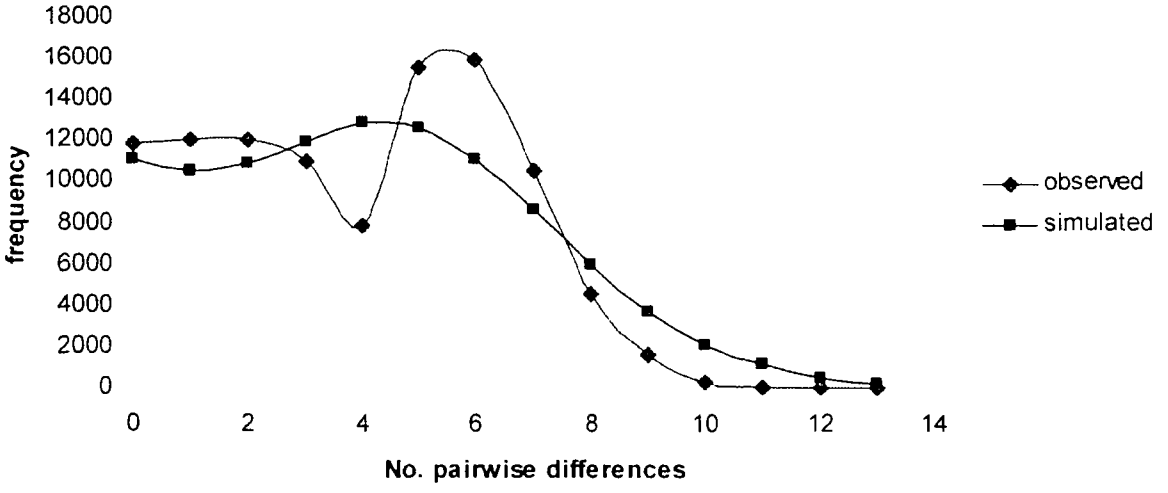


Figure 1.6. Mismatch distribution based on all North Atlantic haplotypes (i.e. including sequences from Bakke *et al.* (1996) and Andersen *et al.* (2003), in addition to those from UK, Ireland and Canada). Two periods of expansion may be represented here, with the earlier, lower peak suggesting an older expansion.

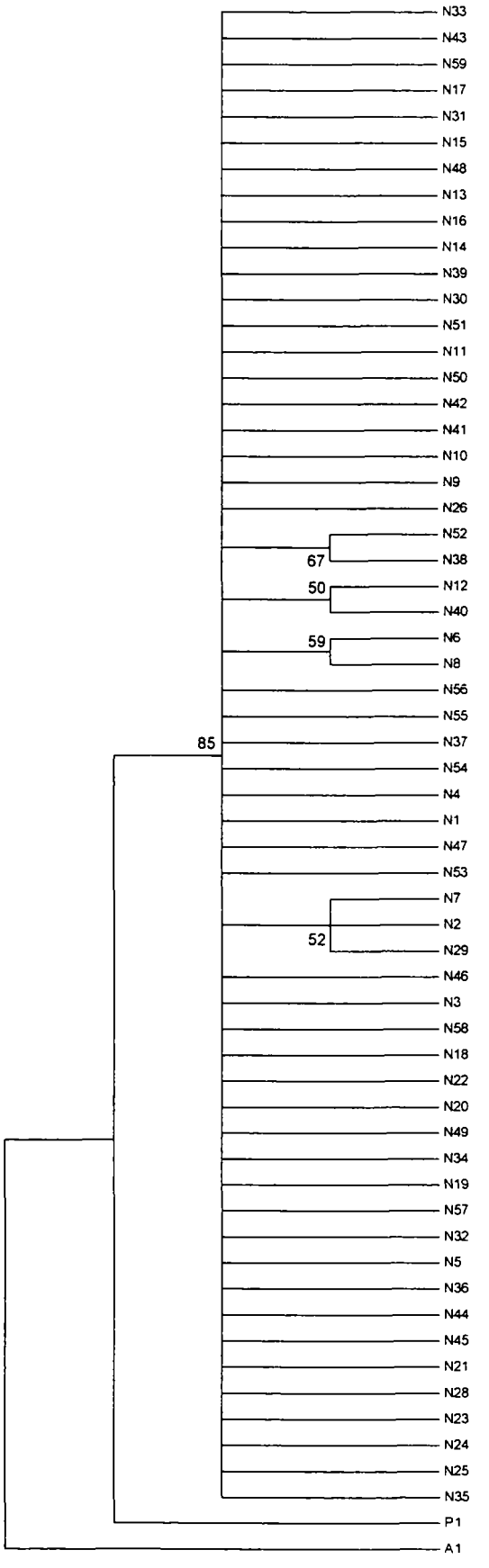


Figure 1.7. Neighbour-joining consensus tree for all North Atlantic haplotypes using Kimura 2-Parameter model (cut-off=50%). For haplotype names, see Table 1.8. A1 = Antarctic haplotype (Bakke *et al.*, 1996), P1 = North Pacific haplotype (Baker *et al.*, 2000). Bootstrap values are given as percentage over 1000 replications.

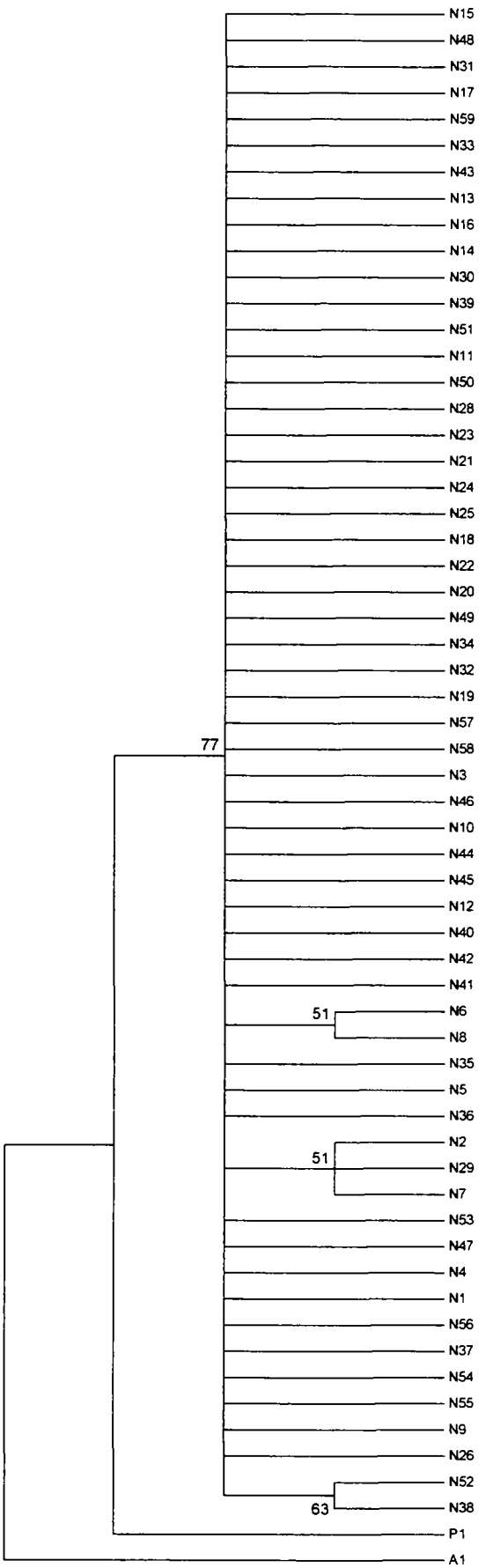


Figure 1.8. Maximum Parsimony consensus tree for all North Atlantic haplotypes (cut-off=50%). For haplotype names see Table 1.8. A1 = Antarctic haplotype (Bakke *et al.*, 1996), P1 = North Pacific haplotype (Baker *et al.*, 2000).

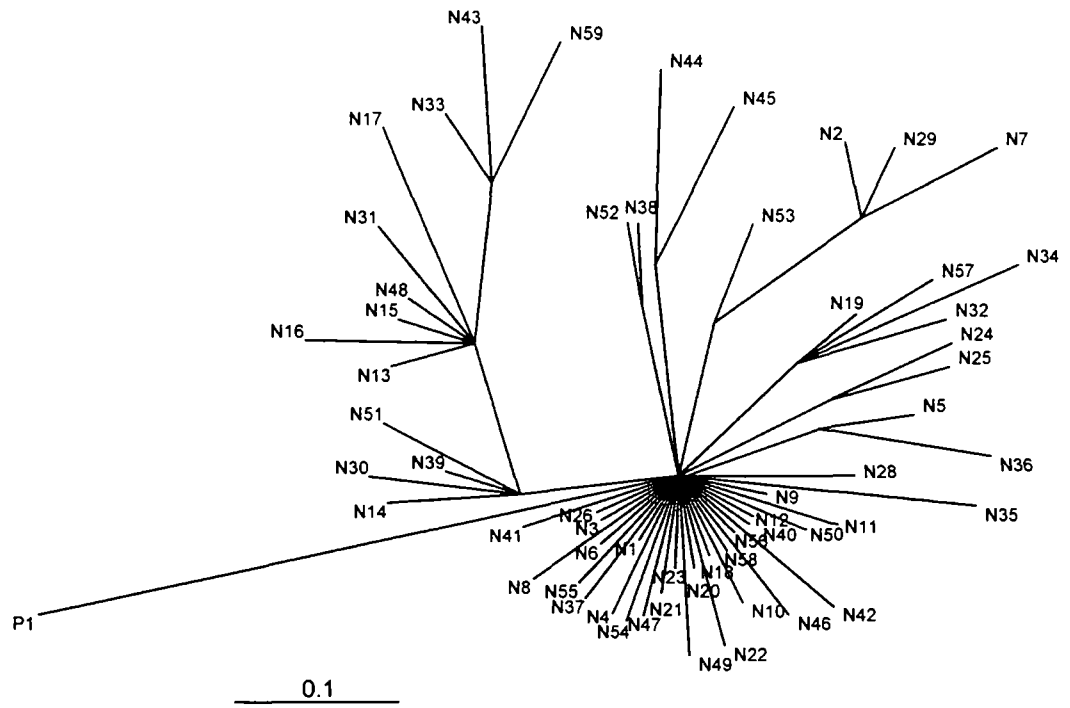


Figure 1.9. Bayesian consensus tree for all North Atlantic haplotypes inferred from MRBAYES (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) according to the General Time Reversible model. For haplotype names see Table 1.8. P1 = North Pacific haplotype (Baker *et al.*, 2000).

Relatively few median vectors were necessary to construct the phylogenetic network for all North Atlantic haplotypes using the program NETWORK (www.fluxus-engineering.com; Bandelt *et al.*, 1999). There were few cases of homoplasy, resulting in little reticulation and thus a reasonably simple network (Figure 1.10). Haplotype N1 appeared to be the centre and thus possible origin of the network, although it might have become the dominant haplotype within the North Atlantic by chance. When the two outgroups A1 (Bakke *et al.*, 1996) from the Antarctic and P1 (Baker *et al.*, 2000) from the North Pacific were included, A1 was connected to the North Atlantic phylogeny via N36 and then linked to N1 via N5. P1 was joined to the network by the simultaneous connection of its last median vector to N1, N26, N9 and N38 (data not shown). This direct connection between N1 and the more closely related outgroup P1 pointed further towards the possibility of N1 representing the ancestral node for the North Atlantic haplotypes. The high number of short branches originating from N1 made it the likely centre for at least a local expansion. On the other hand, there were some branches which

were longer and contained several extensions, suggesting a relatively old expansion for the North Atlantic minke whale population.

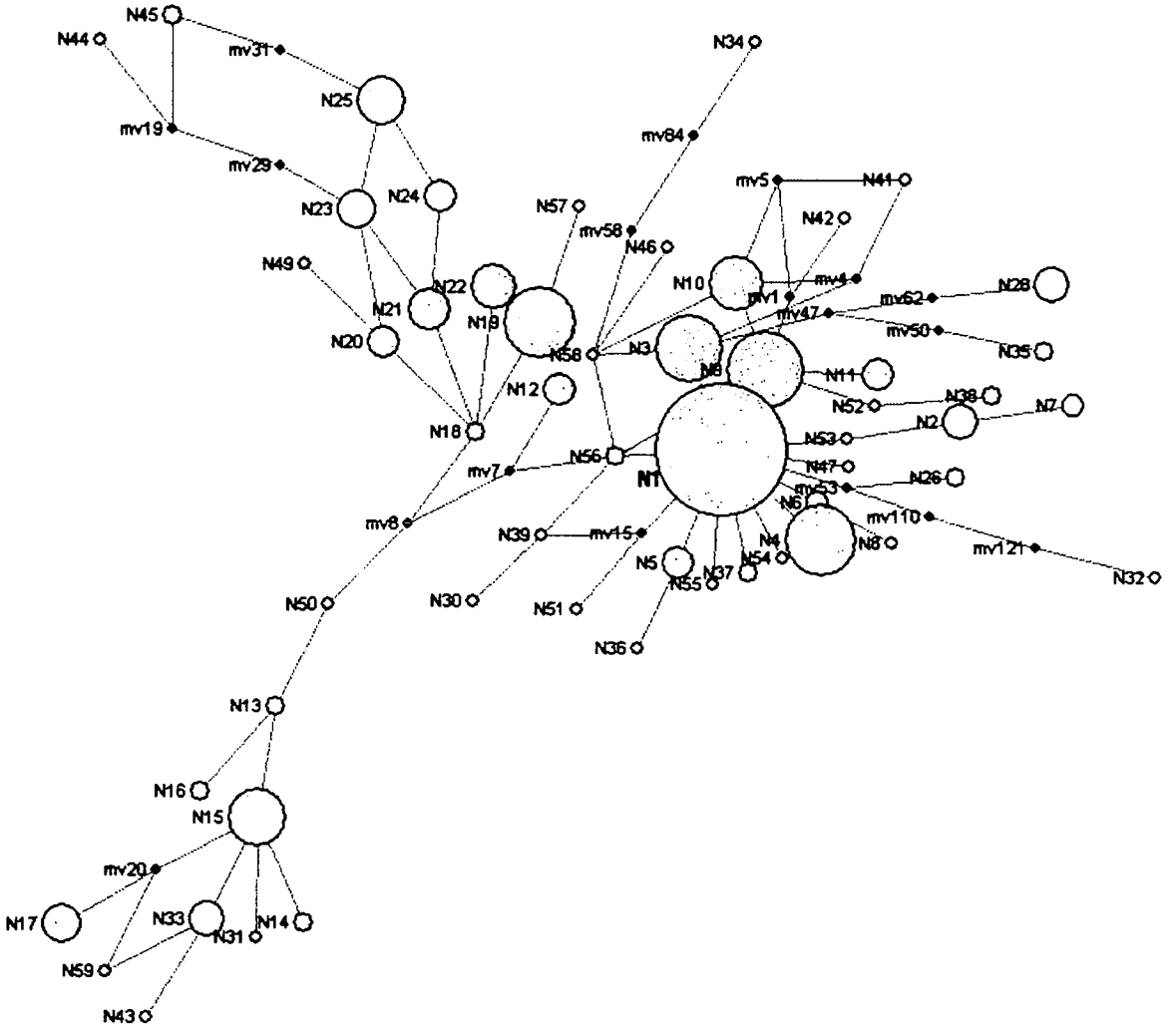


Figure 1.10. Median-joining network using all North Atlantic haplotypes (i.e. including sequences from Bakke *et al.* (1996) and Andersen *et al.* (2003)). Grey nodes represent the haplotypes, black nodes represent median vectors. Node sizes are proportional to haplotype frequencies, except for N1, which had to be reduced in size to make neighbouring nodes visible.

DISCUSSION

The aim of this study was to investigate the population structure of North Atlantic minke whales over as much of the sub-species' range as possible based on both microsatellites and the mtDNA control region in order to help towards appropriate management. For the first time, a relatively high number of samples from non-whaling regions, which had not been investigated before, were included in the analysis in order to give a fuller picture of possible sub-populations, as well as the species' history in the North Atlantic. In the light of seasonal migration, combined with the lack of knowledge about locations of winter breeding grounds, particular attention was paid towards the possibility of mixed assemblages of different populations on the summer feeding grounds, from where the samples originated.

Population structure and comparisons with previous studies

Neither the microsatellite nor mtDNA analysis could detect any clear differentiation between minke whales from the different regions within the North Atlantic examined in this study. However, the existence of two separate populations could be demonstrated, which were independent of their regional origin, and this result was consistent between microsatellites and F_{st} for mtDNA, as well as between different analyses based on the microsatellite loci. These two populations, named STR2 and STR3, were represented in approximately equal proportions in all areas with large enough sample sizes, except for the Norwegian North Sea, which showed a higher proportion of animals from STR2, and West Greenland, with a higher proportion of individuals from STR3. Even though the STRUCTURE analysis had indicated the presence of only one population when the outgroup Japan was excluded, and ΔK (Evanno *et al.*, 2005) suggested that the true number of populations including the outgroup was only two, F_{st}, Rho_{st}, Fisher's exact test and the Geneclass results on the microsatellites, as well as Fst with respect to the mtDNA control region (based on the sub-set of samples from UK, Ireland and Canada only), all confirmed the differentiation between STR2 and STR3. The calculated F_{st} value of 0.0208 between the two populations with respect to the nine microsatellite loci was comparatively low and fell almost exactly on the threshold for which the performance of STRUCTURE is known to decrease (Latch *et al.*, 2006). On the borderline, it therefore

seems worth investigating further apparently contradictory results from STRUCTURE in order to arrive at a reliable estimate for K. If the differentiation between STR2 and STR3 in the STRUCTURE runs with the outgroup Japan included had indeed been simply an artefact, the assignments would have been random, and the groups would not have assorted as two populations which could be separately defined by F_{st} and independent tests.

Previous studies, using a variety of markers, have reached different conclusions about the regional genetic structure of minke whales in the North Atlantic, and the mixing of two populations on the summer feeding grounds, as indicated here, could account for some of these discrepancies. Palsbøll (1990) and Bakke *et al.* (1996) suggested the presence of two closely related maternal lineages within the regions they examined using mtDNA loci (RFLP analysis, control region and NADH dehydrogenase locus). However, in the present study, the two populations were inferred from microsatellites and the F_{st} value for the mtDNA control region, whereas Φ_{st} was non-significant (probably due to low genetic distance between haplotypes), and all phylogenetic trees including all known North Atlantic haplotypes indicated only one matriline. The fact that F_{st} indicated differentiation between STR2 and STR3 with respect to the mitochondrial control region while only one matriline could be found for the whole North Atlantic could be explained by the time since separation of the two populations. If STR2 and STR3 have diverged relatively recently, there may not have been sufficient time available for two different matrilines to form. However, this does not exclude the possibility for differences in the relative haplotype frequencies between the two populations indicated by F_{st}. In Bakke *et al.*'s (1996) case, the two matrilines may have been an artefact caused by low sample size. With a greater number of haplotypes identified both in Andersen *et al.*'s (2003) paper and in the present study, the "gap" between Bakke *et al.*'s (1996) two groups of haplotypes was filled, and the grouping into the two lineages thus disappeared.

A detailed comparison with Andersen *et al.*'s (2003) paper is of particular interest, since the same class of markers was used:

1) *Statistical power*. Whereas Andersen *et al.* (2003) included 16 microsatellite loci, the present work used only 9 loci in the final analysis (of which 6 were identical between the two studies). This lower number of loci clearly resulted in lower statistical power

compared to Andersen *et al.*'s (2003) work. Indeed, in their study, even F_{st} values as low as 0.007 and therefore probably of little or no biological importance, became statistically significant and thus resulted in the inference of population differentiation between all four suggested regions, when it seems that some of these apparent regional differences might be explained simply by different relative frequencies of STR2 to STR3 between those regions (see below).

2) *Sampling effect.* To provide reasonably low errors associated with allele frequency estimation, and therefore accurate Fst estimates, sample sizes per population should be greater than 20, and much higher when F_{st} is small (A.R. Hoelzel, *personal communication*). It is notable that in the present study, with only one exception (GR – NS), all pairs of regions which showed significant differentiation with respect to F_{st}, Rho_{st} or Fisher's exact test prior to type 1 error correction, included the two regions with the smallest sample sizes, JM (n=17) and CN (n=15). The same applied to Andersen *et al.* (2003): with the exception of East vs. West Greenland, the only significant F_{st} values detected between IWC Small Areas in their work were between the Norwegian North Sea (n=23) and Svalbard (n=16), the Norwegian North Sea and Jan Mayen (n=24), and Jan Mayen and Svalbard. In both studies, the relatively low sample sizes for the respective regions may have resulted in unrepresentative sampling of genotypes, leading to a potential bias in the results. In the case of the Norwegian North Sea and Svalbard, more representative sampling should have been achieved in the present study by comparison with Andersen *et al.* (2003) due to the higher numbers of samples for these areas, but for Jan Mayen, both studies only had low numbers of samples available. If sampling bias is indeed an issue, this might partly explain the high F_{st} values that Andersen *et al.* (2003) found in comparisons with the Norwegian North Sea. It would also mean that the only trustworthy significant regional differentiation according to F_{st} prior to type 1 error correction in the regional comparisons of the present study was between West Greenland and the Norwegian North Sea (GR – NS), two of the regions farthest apart from each other, and, not surprisingly, those with the highest difference in proportions of STR2 to STR3 amongst the regions with sufficiently large sample sizes (STR2 dominated in the Norwegian North Sea, STR3 in West Greenland). These were also the two regions between which Andersen *et al.* (2003) found the highest F_{st} value with respect to their 16 microsatellites. Irrespective of sample size, the high F_{st} values in Andersen *et al.*'s (2003) study involving the Norwegian North Sea could thus also be explained by its higher

proportion of individuals from STR2, but since the relative frequencies of STR2 and STR3 are unknown for East Greenland, coastal Norway and the Barents Sea, this cannot be verified.

3) *Hardy-Weinberg equilibrium.* One of the originally ten loci in the present work had to be excluded due to Hardy-Weinberg disequilibrium in two North Atlantic regions and the outgroup. Inclusion of this locus (Texvet7) in the analysis would have changed the results, increasing F_{st} values for some pairs of regions and decreasing them in others. Andersen *et al.* (2003) retained several locus – population combinations for which a significant Hardy-Weinberg disequilibrium was detected in the analysis. The significant heterozygote deficiencies in some regions might have been an indication of a Wahlund effect, supporting the presence of the two populations found in this study within those areas.

4) *Interannual variation.* Andersen *et al.* (2003) used samples which were taken during whaling operations within the same year (except for West Greenland). This was not possible for all regions in the present study since a lot of samples were taken from strandings. If minke whales visit different feeding grounds between years, the combination of samples from different years would result in mixing of different breeding stocks for the same region, and it might be argued that the presence of two populations in almost all regions in the present study could have resulted from the combination of samples from different years. However, the sample set from the UK, with the widest temporal coverage (1993-2005), showed the same degree of mixing between STR2 and STR3 as Svalbard, where all samples originated from the same year (2004). Moreover, Andersen *et al.* (2003) did not find any consistent differences between individuals sampled from West Greenland in different years, and results from all photo-ID studies carried out on minke whales in different regions of the world so far (Dorsey, 1983; Dorsey *et al.*, 1990; Gill & Fairbairns, 1995; U. Tscherter, *personal communication*) have indicated that the animals are relatively faithful to their summer feeding grounds. It is therefore unlikely that large interannual variation exists within regions, and the relative frequencies of STR2 and STR3 within and between regions with sufficiently large sample sizes should be relatively stable over the time period the samples in the present study originated from.

Using allozyme markers, Daníelsdóttir *et al.* (1992, 1995) found significant regional differentiation between minke whales from West Greenland, Iceland and Norway. As with the comparison between the Norwegian North Sea and West Greenland in Andersen *et al.*'s (2003) study, this may be explained by the different relative frequencies of STR2 and STR3 between these regions: West Greenland has a higher proportion of animals from STR3, Iceland a ratio of ca. 1:1, and at least the Norwegian North Sea a higher proportion of individuals from STR2. Unfortunately, neither the Barents Sea nor coastal Norway were included in the present analysis, so the relative frequencies of the two populations in those areas are as yet unknown.

Species biology and population structure

Considering the high mobility of minke and other baleen whales, combined with the apparent lack of physical barriers within ocean basins, little or no population structure within the North Atlantic would intuitively be expected. By contrast to highly specialised species such as the northern bottlenose whale, which depends on deep submarine canyons and shows low levels of genetic diversity combined with regional differentiation (Dalebout *et al.*, 2001), the North Atlantic minke whale is a generalist, occurring over a wide range of habitats and feeding on a broad selection of prey species. This generalist niche would be expected to result in higher dispersal ability and thus higher levels of admixture between populations. Nevertheless, two distinct populations can be recognised which form mixed assemblages on their summer feeding grounds. Thus, there appears to be a similar situation in the North Atlantic as in the western North Pacific, where individuals from two different breeding populations temporarily meet on a common summer feeding ground (Wada, 1991). The movement between breeding and feeding areas seems to occur at a larger scale in the North Atlantic, however, with individuals from both populations present on every feeding ground covered by the present study. In contrast to the western North Pacific, the approximate locations of the breeding grounds of the two populations are entirely unknown, and it is also uncertain if localised breeding areas exist at all. There does not seem to be much differentiation between western and eastern North Atlantic, since animals from one population would be expected to dominate on feeding grounds either in the east or west under this scenario, with increased mixing around Iceland. The absence of such a pattern suggests that the breeding grounds of both populations are either located somewhere in the Central North Atlantic (or from where

distances to all feeding grounds are similar), that there are no localised breeding areas, or that distances between breeding and feeding grounds are of little importance to minke whales.

Phylogeny

Whereas the lower levels of genetic diversity in North Atlantic minke whales compared to North Pacific and Antarctic (with respect to nucleotide diversity of the mtDNA control region (Bakke *et al.*, 1996); at enzyme loci (Wada & Numachi, 1991); and microsatellites (this study)) point towards a population bottleneck, the strongest evidence for recent expansion comes from the mtDNA analysis: Fu's F_S test and the largely star-shaped structure of the Bayesian consensus tree, as well as the phylogenetic network for all known North Atlantic haplotypes, strongly support the hypothesis of a relatively recent rapid population expansion within the North Atlantic. A recent expansion of both populations may explain the presence of only one matriline, as well as the low Φ_{st} value between STR2 and STR3, as the time since divergence may have been too short for the evolution of differences at the sequence level. Bérubé *et al.* (1998) suggested that extant North Atlantic fin whale populations might have been founded after the last glaciation, i.e. as recently as ca. 18,000 years ago. For the North Atlantic minke whale population, the calculated tau value places the main period of expansion at ca. 17,000 years before present, which would be consistent with a post-glacial expansion as detected for fin whales. However, the shape of the mismatch distribution (Figure 1.6) suggests the possibility of two separate events of expansion. Pastene *et al.* (2007) suggested earlier population expansions for both North Atlantic and North Pacific minke whales associated with increasing carrying capacities through the re-establishment of upwelling systems following the Pliocene global warming period ca. 1.5 million years ago. Although the precise timing of expansion events depends on an accurate estimate of mutation rate, which remains controversial, an older expansion might explain the well-developed branches with numerous extensions in the phylogenetic network (Figure 1.10), whereas the newer event (after the last glaciation) might be responsible for the partly star-shaped structure around haplotype N1.

Management units

The IWC set up four management units for minke whales in the North Atlantic: East Canada, West Greenland, Central and NE Atlantic. Most genetic studies on North Atlantic minkes to date have focused on finding population differentiation between these management stocks, concentrating particularly on the whaling areas. Results from the present work do not support the division into the four separate stocks. However, genetic population structure should only be one criterion for defining management units. Distribution, life history parameters, local conservation threats such as bycatch, pollution, direct human exploitation or competition with fisheries, as well as different national legislation, also need to be taken into account (e.g. Donovan, 1991; Lockyer, 2003). The effective population size of STR2 was estimated to be more than an order of magnitude lower than that of STR3, which was also consistent with its lower genetic diversity. Unfortunately, only the relative population sizes between STR2 and STR3 are of practical use for management considerations here due to the uncertainties in substitution rates for the absolute estimates. Based on data from 1996-2001, the minke whale population in the NE and Central stocks combined was estimated at ca. 174,000 animals, with a 95% CI of 125,000–245,000 (www.iwcoffice.org). Besides a management plan that takes into account the presence of mixed assemblages of two breeding populations, precautionary measures might involve considering the Norwegian North Sea as a separate stock due to its higher relative frequency of the smaller and less diverse population STR2. The same may apply to Jan Mayen with just over 75% of individuals from STR2, although this is as yet based on a low sample size.

CHAPTER 2:

MINKE WHALE HABITAT PREFERENCES AND DIET ON THE WEST COAST OF SCOTLAND:

POSSIBLE IMPLICATIONS FOR CHANGES IN RELATIVE ABUNDANCE

INTRODUCTION

The spatial and temporal distribution of animals is dictated by their physiological tolerance to different environmental conditions, accessibility to optimal habitat, the availability of food and suitable breeding sites, and the avoidance of predators (Begon *et al.*, 1986). Marine mammals can tolerate a wide range of environmental conditions, and obvious physical boundaries to limit their distributional ranges seem largely absent from the marine environment. Baleen whales can range over vast distances, and in most species, breeding and feeding are both spatially and temporally segregated, with breeding often occurring in lower latitudes during the winter months and feeding in higher latitudes during summer. Since they have few natural predators (notably killer whales) due to their large size, it is therefore reasonable to assume that their distribution and abundance in an area during summer is a reflection of the availability, density and quality of their prey. However, in those instances where a species feeds on a variety of prey or can switch between different prey types seasonally or regionally according to their relative abundance, this relationship can become less obvious. In the absence of detailed

information on the spatial and temporal distribution and abundance of its prey (and prey choice), as well as for conservation purposes, it is often more straightforward to examine the distribution of a species with respect to the characteristics of its habitat in order to understand what makes particular areas important as feeding grounds. The distribution of resources is almost always patchy (relative to the mobility of an animal), and an investigation into habitat use at different spatial scales may also provide insights into how a species finds its prey.

Although the winter breeding grounds of North Atlantic minke whales are unknown, the implication from their population genetic structure is that they can range over wide distances seasonally between breeding and feeding areas (see Chapter 1). A common feature of most known minke whale summer feeding grounds in the North Atlantic is that they are located in the seasonally productive waters of the continental shelf, often very close to land, such as around Iceland, the British Isles and Ireland, in the St. Lawrence Estuary, and off Svalbard, Novaya Zemlya and northern Norway in the Barents Sea. The species is known as a catholic feeder, taking a wide range of shoaling fish, as well as krill, apparently adjusting its diet to regional prey abundance (Jonsgård, 1982; Lydersen *et al.*, 1991; Lindstrøm *et al.*, 1997; Neve, 2000; Sigurjónsson *et al.*, 2000; Olsen & Holst, 2001; Haug *et al.*, 1995, 2002; Pierce *et al.*, 2004; see General Introduction). Minke whales also appear to be able to switch between different prey types among years within a region in response to resource availability, e.g. from capelin (*Mallotus villosus*) to krill in the northern Barents Sea (Haug *et al.*, 2002). However, in the southern Barents Sea, they were found to be in poorer body condition during years in which their primary prey, immature herring (*Clupea harengus*), occurred in low abundance and the animals were forced to switch to a broader diet instead (krill, capelin and gadoids; Haug *et al.*, 2002). Moreover, the abundance of whales in the study area was higher in 1989, a year with higher herring recruitment than in 1995, when herring was scarce (Schweder *et al.*, 1997). This is consistent with findings by Piatt & Methven (1992), who were able to relate the presence and densities of humpback, minke and fin whales directly to capelin densities in Newfoundland. They identified a prey density threshold, below which it did not seem to be worthwhile for the animals to visit the area in order to exploit the capelin shoals.

In years of low availability of their primary prey, whales have a choice between a) switching to an alternative source of prey, if available, b) exploiting the lower concentrations of prey, which would sustain lower densities of predators and therefore

lead to increased competition amongst them, or c) investing energy into travelling to an alternative, potentially more rewarding, feeding ground. A combination of all three scenarios seems to have applied to the situation in the Barents Sea, due to the availability of alternative prey species in the area, whereas in Newfoundland, capelin represents the key forage species for both cetaceans and several seabird species (Piatt *et al.*, 1989; Davoren & Montevecchi, 2003), likely resulting in more extreme differences in baleen whale sighting rates between good and poor capelin years compared with the Barents Sea.

Both of the studies mentioned above were able to relate minke whale distribution and abundance directly to available prey, determined from stomach contents in the case of the Barents Sea, and sampled directly in the field during hydroacoustic surveys in Newfoundland. In most cases, however, the prey distribution and abundance cannot be sampled simultaneously during cetacean surveys due to resource or logistical constraints. To overcome this problem, prey distribution to some extent can be inferred from the spatial and temporal distribution of the study species with respect to environmental parameters, whilst other taxa known to feed on the same resource within an area can help shed light on interannual differences in its abundance.

Distribution

Physical habitat characteristics likely to influence resource distribution for cetaceans are constant variables such as water depth, bottom topography and sediment type, as well as temporally variable parameters such as currents (i.e. mainly tides in the coastal environment) and water temperature which may determine changes in local prey distribution and abundance. A preference for particular depths can reflect the diving abilities of a species as a response to certain dietary specializations. Around the British Isles, cetaceans can successfully be classified into three distinct groups according to their different bathymetric preferences (coastal, offshore shelf, and oceanic; Anderwald, 2002). Variable seafloor topography, especially when combined with strong currents, causes increased vertical mixing of water masses (Pingree & Griffiths, 1978). Bringing nutrient-rich cold bottom water into the photic zone, these upwellings facilitate phytoplankton growth (e.g. Valiela, 1995: p.79ff.). The most productive areas are therefore often the edges of the continental shelf (which seem to play an important role in the distribution of species like the fin whale in the Eastern North Atlantic (Evans, 1990) and Risso's dolphins in the Gulf of Mexico (Baumgartner, 1997)), shallow banks or sea mounts, and

the waters surrounding headlands (which are known to be preferred feeding sites for example for bottlenose dolphins; Lewis & Evans, 1993; Mendes *et al.*, 2002; Hastie *et al.*, 2004). Tidal currents through deep channels can have the effect of concentrating prey, and in Shetland and West Wales, harbour porpoises appear to adjust their foraging behaviour according to the tidal cycle in these areas (Evans & Borges, 1996; Pierpoint, 2008). Similarly, tidal currents influence capelin distribution in the St. Lawrence Estuary, concentrating the fish at the head of the Laurentian Channel at certain states of the tidal cycle, and these dynamics match the local fin and minke whale distributions (Simard *et al.*, 2001). Bottom sediment type is expected to influence the distribution particularly of benthic fish species, but it has also been found to determine summer distribution of pelagic species such as herring in the northern North Sea; Maravelias (1999) related the presence of herring shoals to gravel / sand substrates, intermediate water depths (70-150m) and high zooplankton abundance. Sandeels (*Ammodytes marinus*) show a preference for areas with coarse or medium sandy substrates with low silt content, shallow waters (30-70m) and strong bottom currents (Wright *et al.*, 1998; 2000; Holland *et al.*, 2005). Both herring and sandeels have been identified as important prey for several cetacean species, including minke whales (see General Introduction), so it is likely that the same environmental parameters dictating the distribution of these species are also important in determining the distribution of their predators. Finally, different fish species show preferences for particular temperature ranges, reflecting either their own physiological adaptations or the occurrence of their zooplankton prey. For example, long-term alternations between herring and pilchard (*Sardina pilchardus*) abundance off south-west England have been related to water temperatures and the associated dominance of warm and cold-water plankton species respectively (the 'Russell Cycle'; Southward *et al.*, 1988). In the Bristol Channel, sole (*Solea solea*) abundance was strongly correlated with a positive trend in the North Atlantic Oscillation (NAO; Visbeck *et al.*, 2001), thought to be due to increased primary and secondary production and enhanced juvenile growth during years of higher water temperatures in the south-west of Britain (Henderson & Seaby, 2005).

Where data on the biotic variables determining cetacean distribution (fish and zooplankton distribution and abundance, which are in turn dependent on phytoplankton concentrations) are not readily available, remotely sensed chlorophyll concentrations can serve as a good proxy for primary productivity. High chlorophyll concentrations (with the exception of those caused by harmful algal blooms such as some dinoflagellates) can

generally be used as an indirect indicator of favourable feeding conditions for baleen whales (e.g. Smith *et al.*, 1986; Thiele *et al.*, 2000), although possible time-lags between a phytoplankton bloom and high zooplankton and fish concentrations may need to be taken into account (e.g. Panigada *et al.*, 2008).

Almost all environmental parameters discussed above have been found to influence minke whale distribution in one way or another, but different studies have focused on different subsets of variables: Naud *et al.* (2003) identified underwater sand dunes as an important feature of minke whale summer habitat in the Mingan Islands, Eastern Canada, whereas no obvious trend was observed for a relationship with bathymetry or topography. By contrast, Ingram *et al.* (2007) found a positive relationship between minke whale sighting rates and depth, as well as benthic slope, in the Bay of Fundy. In their study, sightings were concentrated in areas subject to strong tidal currents off two islands, although no relationship was found between minke whale distribution and the state of the tidal cycle. Concentrating on temporally variable parameters, Tetley *et al.* (2008) correlated monthly changes in minke whale numbers in the Moray Firth with sea surface temperature and chlorophyll-a concentration: the whales were more abundant during months when a warm water plume dominated in the area, which was also related to higher phytoplankton concentrations, than during those periods when a cold current was dominant. These features showed little variation between years. Both Naud *et al.* (2003) and Tetley *et al.* (2008) discussed their findings in the light of the distribution of most likely minke whale prey in their respective areas (capelin in the Mingan Islands, sandeels in the Moray Firth). In the absence of direct evidence for minke whale diet on the west coast of Scotland, Macleod *et al.* (2004) attributed an observed change in preference for different bottom sediment types in the vicinity of the Isle of Mull between spring and autumn to minke whales feeding on sandeel early in the summer, and pre-spawning herring later in the season. Temporally variable environmental parameters were not included in their study.

So far, the only direct evidence of minke whale diet around Scotland has been derived from the stomach contents of 10 individuals sampled between 1992-2002 (Pierce *et al.*, 2004). Only three of these animals were from the west coast, of which two had stranded in winter. The most important prey item from these samples over the whole of Scotland was sandeels (two-thirds), followed by clupeids (herring and sprat (*Sprattus sprattus*); ca. one-third). Olsen & Holst (2001) also reported sandeels as the most important prey (86.7% by weight) in the North Sea. However, direct data on the diet

composition of minke whales on the west coast of Scotland during summer are still unavailable. Sandeel stocks on the west coast of the UK appear to be more patchily distributed and less extensive than in the North Sea, where they are known to form the most important food source for seabirds during the breeding season (Harris & Wanless, 1985, 1997; Monaghan, 1992; Wanless *et al.*, 1998, 2004, 2005; Frederiksen *et al.*, 2005, 2006; Daunt, 2008) and support a large-scale industrial fishery. Given the lower density of sandeels on the west coast compared to the North Sea (Frederiksen *et al.*, 2005), it is likely that other fish species, such as clupeids, have a relatively higher importance in the diet of both cetaceans and seabirds by comparison to the east coast of Scotland.

The aim of this study is to identify both physical and biological parameters relevant in determining the spatial and temporal distribution of minke whales around the Hebrides on the west coast of Scotland. Macleod *et al.*'s (2004) hypothesis of a switch in prey between early and late season is investigated in more detail by including modelling results of the likelihood of sandeel presence in minke whale habitat models. In addition, direct, opportunistic prey sampling was carried out in the months of August and September. Both physical and biological variables may be relevant at different spatial scales. This issue is addressed here by examining minke distribution over both the entire Hebrides and at a finer scale within a core study area benefiting from extended spatial and temporal coverage.

Interannual changes in abundance

Habitat models alone can only account for interannual differences in abundance of the study species if they include temporally variable relevant physical and biological parameters. Where a significant relationship with these variables is found in a model, it is often worth examining the patterns further with respect to general applicability to the ecosystem, ideally by investigating organisms known to feed on the same prey as the study species or at lower trophic levels. Human overexploitation of certain fish species such as herring and mackerel (*Scomber scombrus*) may lead to increases in numbers of small, faster growing species such as sandeel and sprat through relaxation of competition and predation pressure (Sherman, 1981). An increase in sprat and sandeels in turn would improve feeding conditions for seabirds and some cetaceans feeding on small shoaling fish. Indeed, an increase in minke whale sighting rates in west Scotland during the 1990's (Evans *et al.*, 2003) followed a depletion of the herring stock through overfishing in the

1970's (ICES, 2007) and a shift in migration patterns of predatory mackerel in the 1980's (Walsh & Martin, 1986). The changes in mackerel migration routes on the west coast in turn coincided with distributional changes of white-beaked dolphins (known to feed on mackerel; Evans, 1987), probably following their prey northwards (Evans *et al.*, 2003; Evans, *personal communication*). Two cetacean species feeding at different trophic levels thus have shown opposite trends in their distribution and abundance on the west coast of Scotland as a likely response to changes in prey availability. Similarly, Payne *et al.* (1990) detected opposite trends in interannual abundance of sandeels and the copepod *Calanus finmarchicus* in the Gulf of Maine. These changes were mirrored by the changes in relative abundance of the piscivorous humpback and fin whales versus the planktivorous right and sei whales in the area.

In the Hebrides, the minke whale is the only common baleen whale species. A comparison with other related, easily observable, species feeding at the same or lower trophic levels, as in Payne *et al.* (1990), is therefore not possible. However, during the summer months, basking sharks (*Cetorhinus maximus*) are common in the area. Due to their habit of often swimming directly under the surface while feeding (with dorsal fin showing above the water), they are easily detected from a boat. Their main prey appears to be copepods, namely *Calanus helgolandicus* (Sims & Merrett, 1997). Studies in the Baltic have indicated that calanoid copepods are also important prey for both sprat and herring (Casini *et al.*, 2004; Möllman *et al.*, 2004), whereas sandeel larvae feed on copepod eggs and nauplii (Economou, 1991). It could therefore be assumed that in years of low abundance of planktivorous small shoaling fish and thus low food availability for minke whales, basking sharks should be found in higher abundance in the area. Conversely, a number of seabird species, such as auks (common guillemots (*Uria aalge*), razorbills (*Alca torda*) and puffins (*Fratercula arctica*)), kittiwakes (*Rissa tridactyla*), *Larus* gulls and Manx shearwaters (*Puffinus puffinus*), which all breed in the Hebrides, share the same diet with minke whales (see Table 3.1, Chapter 3). A positive relationship between numbers at sea and breeding success of these seabird species and minke whale abundance in the same area within a given year might thus be predicted.

In this chapter, the results of the minke whale habitat models are investigated further with respect to the temporally variable parameter phytoplankton concentration. By comparing relative abundance of different Hebridean vertebrate taxa between years of intensive study, the effects of changes in primary productivity are examined at two different trophic levels.

METHODS

Study area

Hebrides

The Hebrides are a group of over 200 islands located on the west coast of Scotland, consisting of the Western Isles or Outer Hebrides (Lewis, Harris, North and South Uist, Barra, etc.) and Inner Hebrides (Skye, Rhum, Eigg, Mull, Coll, Tiree, etc.; Figure 2.1). Despite frequent gales, the study area is protected from the open Atlantic by the Outer Hebrides. Strong currents of >2kn at spring tides run through the narrower channels, but the spring tide average over the whole region is between 0.5-1kn, with an average tidal range of 4m (Bryan, 1994). Upwellings around islands and headlands provide nutrient-rich conditions for phytoplankton growth and thus favourable feeding conditions for zooplankton, fish, marine mammals and seabirds. The area shows a varied topography, with a maximum depth of ca. 300m, but an average bathymetry of ca. 80m. The predominant bottom sediment type in the deeper areas is mud, whereas the shallower parts are often covered by sand and gravel (British Geological Survey, 1997). Typical water temperatures in summer (July) reach between 12°C towards the Outer Hebrides and 16°C close to the mainland. Winter water temperatures (February) are between 7°C in the west and 3°C near the mainland coast (Bryan, 1994). Due to the dominance of Atlantic water in the region, the difference between summer and winter temperatures is limited.

The numerous sea lochs are important nursery areas for herring and sprat. Other notable fish species in the region include mackerel, cod (*Gadus morhua*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*; Bryan, 1994). A limited sprat fishery exists in the region between October and January (Lee & Ramster, 1981; P. Fernandes, *personal communication*). Sandeels have also been fished on a small scale commercially since 1981, with a peak in 1986, followed by a decline in both effort and landings since then (ICES, 2003). By contrast to the North Sea, the Hebrides are overall poorly surveyed for abundance of different fish species. Long-term time series on zooplankton are also unavailable for the region, since only two samples exist from the Continuous Plankton Recorder (CPR; D. Johns, SAHFOS, *personal communication*). Eleven cetacean species were recorded during systematic surveys across the region during the 1990s, with harbour porpoise and minke whale

accounting for the majority of sightings (Boran *et al.*, 1999). Risso's, common, bottlenose and white-beaked dolphin, as well as killer whale, are also regularly seen (Evans *et al.*, 1993; Evans, 1997; Boran *et al.*, 1999; P. Evans, R. Dyer, C. Swann, *personal communication*).

Small Isles

Located south of the Isle of Skye, the Small Isles consist of four islands – Eigg, Rhum, Muck and Canna (Figure 2.1). This area was chosen as the core study area, enabling detailed spatial and temporal coverage of effort. The island of Rhum, which comprises up to 30% of the world breeding population of Manx shearwaters, is managed as a National Nature Reserve by Scottish Natural Heritage (SNH). Canna holds breeding colonies of kittiwakes and common guillemots.

The area is generally shallower by comparison to the wider study area, with a varied topography including some shallow banks, and an average bathymetry of 30-50m. A deeper channel (70-80m) originates in the Sound of Sleat and, at the Point of Sleat, splits into a north-west and a southerly component, the latter running between Oberon Bank (15m; Figure 2.1) and the mainland. A larger shallow bank (Maxwell Bank; 14m) is located south-east of Eigg. The predominant bottom sediment type in this area is sandy mud (Bryan, 1994).

The fishing port of Mallaig is also the main ferry terminal in the region, from where Caledonian McBrayne operates ferry routes to Armadale on Skye and to the Small Isles.

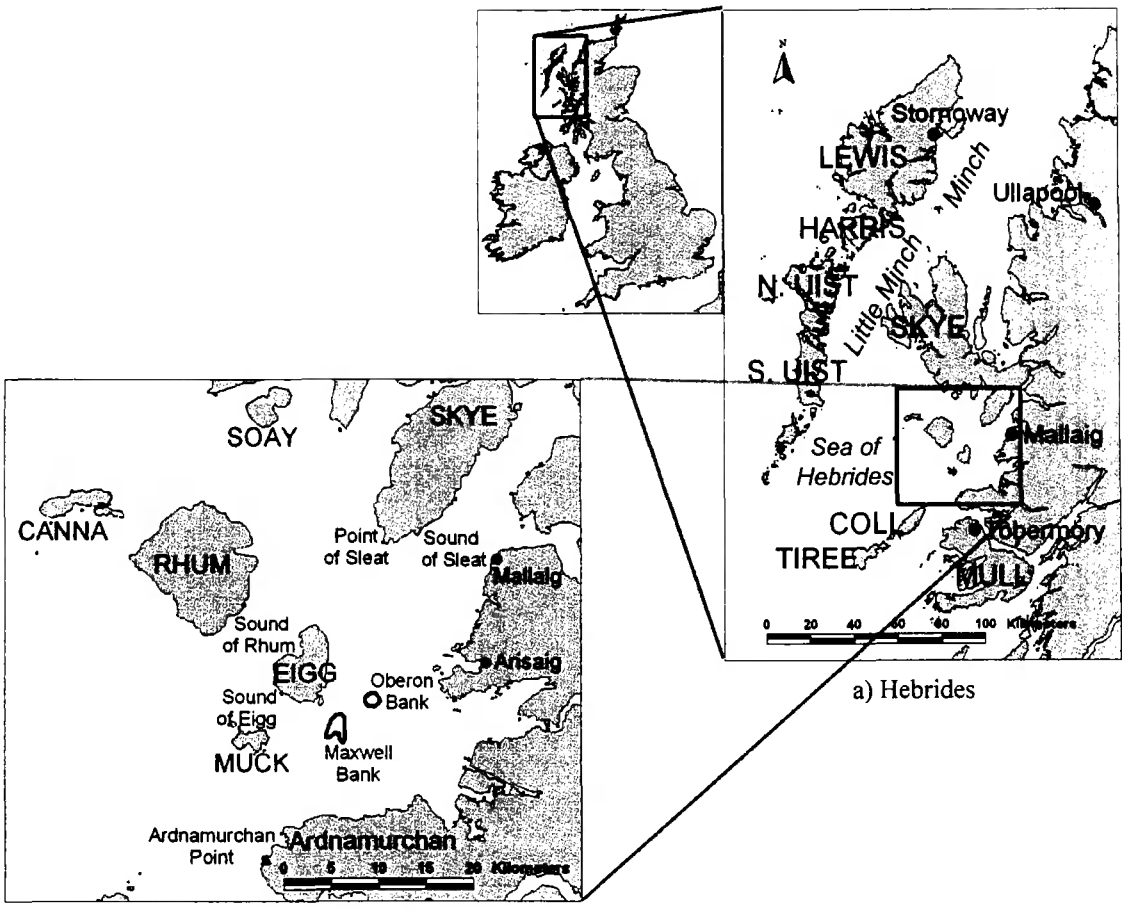


Figure 2.1. Study area over the entire Hebrides (1993-2002), and core study area around the Small Isles (1998-2007).

Habitat models

Survey data

A) Entire Hebrides

These data were kindly made available by Dr. Peter Evans, Sea Watch Foundation. Line-transect and *ad libitum* surveys for cetaceans were conducted from the ketch *Marguerite Explorer* (Table 2.1) over the whole of the Hebrides during summer months between 1992 and 2002 in a collaboration between the Sea Watch Foundation and Western Isles Sailing and Exploration Company. Surveys lasted between 5 and 20 days, depending on funding, availability of the boat, and weather conditions. Over the 11 years, all summer months from June to September were covered, although no month received coverage in

every year. Although a number of surveys were combined with commercial trips and passengers could participate, at least two experienced observers (either P. Evans or J. Heimlich-Boran with the skipper Christopher Swann) and a trained volunteer were on watch at all times.

Effort was noted on pre-printed recording forms every 15-30min and at every change in direction, speed or environmental conditions. Effort records consisted of time, date, position (latitude / longitude), vessel speed and direction, and environmental conditions (sea state, swell height, wind force and direction, visibility and precipitation). At each cetacean sighting, species, group size, time, position, distance and direction to animal(s), their behaviour, as well as associated environmental conditions were recorded. All effort and sightings data were then coded onto a spreadsheet and, after independent verification against the originals, integrated in the National Cetacean Sightings Scheme administered by Sea Watch Foundation, from which they were accessed.

Between 1998 and 2001, emphasis during fieldwork from the *Marguerite Explorer* in some months was placed more on photo-identification studies and/or biopsy-sampling, resulting in lower spatial coverage and more time spent in areas where minke whale numbers were known to be high, especially around the Small Isles. Inspection of the survey tracks for each month and year revealed that this applied to August 1998, and September 1999, 2000 and 2001. These years and months were therefore less representative for an analysis over the entire Hebrides and were excluded. Where appropriate, however, they were included in the fine-scale analysis around the Small Isles (see below). Since no sea surface temperature data could be obtained prior to July 1993, records from 1992 were not considered in the analysis.

B) Small Isles

Over the last ten years, Sea Watch Foundation's minke whale fieldwork has mainly been concentrated around the Small Isles in order to obtain better coverage of a smaller, high-density area for minke whales (identified during the *Marguerite Explorer* surveys 1992–1997), and to enable fine-scale analyses of habitat use.

Data from several vessels were combined for this analysis, while making sure that appropriate correction factors were applied for each platform (see below). Only data collected after August 1997 were considered, so as to enable inclusion of chlorophyll-a data as an explanatory variable, which was unavailable for earlier years.

Marguerite Explorer: For the fine-scale analysis around the Small Isles, only months and years with a minimum total coverage of 10h within the study area were considered. This condition applied to August 1998, September 1999, July 2001 and August 2002 (combined with *MV Sheerwater*). The main focus during these years was photo-identification of minke whales. In addition, biopsy-samples were taken during August 1998 and September 1999. The protocol for recording effort and sightings remained the same as during line-transect surveys in earlier years.

Own fieldwork: Following on from earlier work by Sea Watch Foundation, fieldwork around the Small Isles was intensified as part of this thesis between 2003 and 2007, using mainly smaller vessels (Table 2.1). Although additional methods were incorporated (photo-identification, focal sampling of individual whales, prey sampling; see Chapter 3), the fieldwork protocol with respect to effort and sightings recording followed the same methodology as from the *Marguerite Explorer* in earlier years. Fieldwork activities could be divided into four categories: 1) searching, 2) with feeding group of whales (photo-ID, prey sampling, counting seabirds), 3) with seabird group, without whales present (counting seabirds, prey sampling), and 4) focal follow of an individual whale (photo-ID, recording of surfacing times and positions, prey sampling). During searching (at 6-10kn) and when with a seabird group without a whale, a minimum of two observers were on watch at all times. When an individual whale was sighted, focal sampling and photo-ID were conducted for as long as possible, with at least one person on dedicated watch and one recording. Any sightings of cetaceans other than the focal individual also continued to be recorded during focal sampling. If a (feeding) group of whales was encountered, the boat stayed with it until the animals dispersed and one individual was then selected for focal sampling.

Although a small study area has the advantage of achieving more detailed coverage than surveys over a wider area, there is a danger of recording the same individuals more than once, leading to inflated sighting rates, as well as possible autocorrelation in a statistical model on habitat use. Every effort was therefore taken in the field to flag up any repeat sightings of the same individual(s) for later exclusion from the analysis. In addition, photo-identification from both *Marguerite Explorer* and during fieldwork seasons 2003-07, as well as focal sampling of individual whales during the latter period, helped to alleviate the problem of duplicate counting of the same individuals within a restricted time and area. Photo-ID images were taken whenever possible, linked

to sightings and analysed prior to determining sighting rates. Only the first sighting of each individual within an encounter was considered in the analysis. An encounter was defined as a sighting of one or more whales, which were observed until the animals were lost or left. Additional whales joining a group were recorded as new sightings at the time they were first seen. Encounters with the same individuals on different days were counted separately, so that the sighting rates (expressed as number of individuals per hour) used in this analysis do not represent absolute counts of individuals in the study area within a month and year. Given the high mobility and relatively low site fidelity of minke whales in the small study area (see Chapter 3), the ranges of individual whales likely extended far beyond the Small Isles. Re-sightings of the same individuals on different days could therefore be treated as essentially independent of each other and were only ever observed during periods of high feeding activity, thus reflecting real habitat preferences. This definition of sighting rates within the study area was therefore considered more appropriate for an analysis of habitat use than attempts to estimate the absolute numbers of whales in a month.

MV Sheerwater: Due to funding constraints, intensive fieldwork could only be conducted for a limited number of weeks each season. In order to obtain representative temporal coverage of the study area over the entire season, sightings data were therefore kindly collected systematically by the skipper and crew of the ferry *MV Sheerwater* from September 2003 onwards. The ferry operates from Easter to mid- to end September between Arisaig, Eigg, Muck, Rhum and Soay (Figure 2.2).

During one week in August 2002 and two weeks in August 2003, I accompanied the daily sailings, taking 5min recordings of the position of the vessel on each route in order to assess average journey time to specific waypoints used later to calculate temporal coverage. The routes normally covered within a week were (Figure 2.2):

1) Arisaig – Eigg – Muck – Eigg – Arisaig (every second day)
2) Arisaig – Eigg – Rhum – Eigg – Arisaig (every second day)
3) Arisaig – Rhum – Soay – Rhum – Arisaig (Thursdays)

Minor deviations from this schedule could occur subject to demand. The main observer onboard was the skipper Ronnie Dyer, a keen naturalist with over 30 years sea-watching experience and a special interest in cetaceans and seabirds. Although the ferry operates

according to a fixed schedule, sailings are simultaneously advertised as wildlife watching trips, and time is allowed for cetacean watching on route.

Recording forms were customised for use by the skipper and crew, taking into account the limited time available for note-taking during their work on board. Effort was recorded as departure and arrival time at each harbour, from which time to specific way-points could later be calculated based on the detailed effort data collected in 2002 and 2003 (Figure 2.2). All sightings of cetaceans and basking sharks were recorded, with species, group size, time, GPS position, feeding activity, associated seabirds and sea state all noted. In order to reconstruct the routes as precisely as possible, the times and positions of any sightings were used as additional waypoints for each day. When no sightings occurred, a straight line was assumed between waypoints.

Although there was temporal overlap and communication with *MV Sheerwater* during the weeks of concentrated fieldwork, the two vessels operated independently of each other. On the few occasions ($n \leq 10$) when both vessels were watching the same individual or group of animals at the same time, the sighting was flagged up as a duplicate on the fieldwork recording form, together with a note of which boat was present with the animals first. The sighting by the second boat was subsequently excluded from the analysis. Before pooling the data collected from *MV Sheerwater* with those obtained during one's own fieldwork for the spatial analysis, correlations in sighting rates between the two independent datasets were tested in a Spearman correlation for general applicability of the trends observed along the ferry route over the whole study area around the Small Isles.

Table 2.1. Description of all observer platforms from which data were collected for the present analysis. Vessel type: Ww = whale-watching vessel. IB = inboard, OB = outboard motor. Speeds are indicated as average during searching.

Vessel name	Vessel type	Length (m)	Sail / IB / OB (speed)	Eye height (m)	Skipper	Years covered
Marguerite Explorer	gaff-rigged ketch (ww)	20.3	Sail / IB (5-8kn)	4 (bow)	Christopher Swann	1993 - 2002
MV Sheerwater	ferry (89 passengers)	14	IB (10kn)	3.5 (bridge)	Ronnie Dyer	2002 - 2007
Gwen	motor boat	5	OB (60hp) (6-8kn)	2	fieldwork assistants	2003 - 2005
Wild Free	fishing boat (ww)	ca. 15	IB (ca. 8kn)	4.5 (roof)	James Fairbairns	2004
Alpha Beta	motor boat (ww)	12	IB (6-9kn)	4.5 (roof)	Brennen Fairbairns	2006
Mairi Grace	motor cruiser	16.7	IB (8-10kn)	4.5 (bridge)	Angus John MacLellan	2006
Durham boat	Dell Quay Dory	5.15	OB (75hp) (6-8kn)	2	fieldwork assistants	2006
Wave	fishing boat	10.9	IB (5-7kn)	4 (roof)	Colin MacEwan	2007

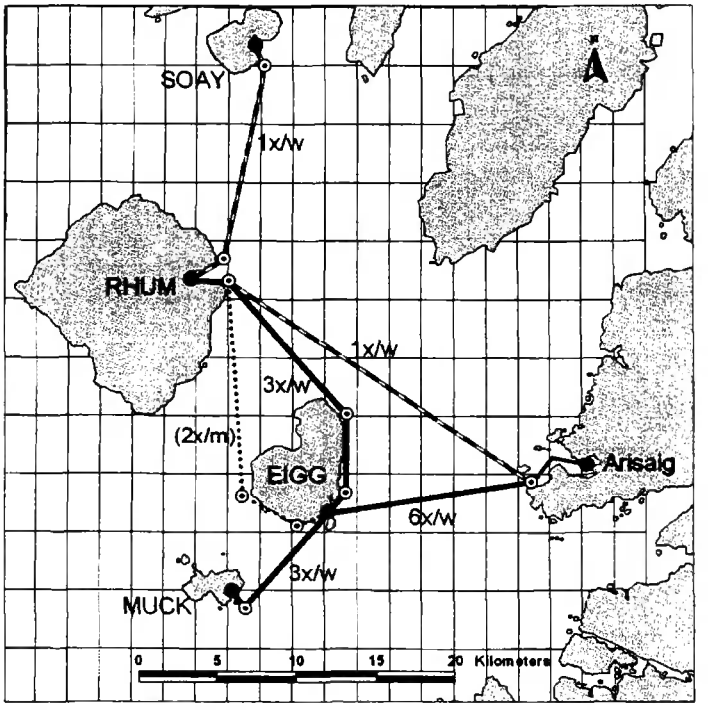


Figure 2.2. Normal weekly route of MV Sheerwater between Arisaig and the Small Isles and Soay. The dotted line through the Sounds of Eigg and Rhum indicates a route which was taken ca. 2x / month on average and therefore received too little coverage to be included in the analysis. The solid lines represent the routes most regularly covered (3 days a week, return journey each day). Waypoints are indicated by encircled points. Grid cells in the background represent the 2min cells on which the analysis was based.

Sea state correction

Sighting efficiencies for marine mammals at sea depend on a variety of factors, including the behaviour of the animals (group size, positive or negative response to observation platform), environmental conditions (swell height, sea state, cloud cover, precipitation, atmospheric conditions etc.), platform characteristics (observer height and field of view), as well as observer experience and efficiency. Whereas the behaviour of the animals cannot be controlled for, correction factors can be derived for certain environmental and platform characteristics.

Amongst the environmental variables mentioned above, the most important parameter influencing sighting efficiency is known to be sea state, and is thus the only one for which routine corrections are made (Buckland *et al.*, 1993; Hammond *et al.*, 2002; Reid *et al.*, 2003; Evans & Hammond, 2004; Marubini *et al.*, 2009). For all cetaceans which do not show an obvious high blow during surfacing (i.e. dolphins and smaller whales), sighting efficiency decreases with increasing wave height. This effect is most pronounced when observing from low platforms. The most common approaches to correcting sighting efficiency are either to include Beaufort sea state directly as a factor in the statistical model (e.g. Marubini *et al.*, 2009) or to calculate a correction factor for time or distance travelled, based on the sighting rates for the species at different sea states (e.g. Evans & Wang, 2002). For the present analysis, the latter method was chosen, which made it possible to sum total effort per cell directly as sea state corrected time spent in that cell. Correction factors were calculated separately for each of the three main vessels used (*Marguerite Explorer*, *MV Sheerwater* and *Gwen*), thus taking into account the expected interaction between sea state and the different platform heights on observer efficiency. Assuming that sighting efficiency was highest at sea state 0, correction factors were calculated as percentages by dividing the sighting rates at each higher sea state by the sighting rate at sea state 0. Due to low effort in adverse conditions, data for the highest sea state categories were pooled for each vessel. Time spent on the additional boats around the Small Isles during fieldwork seasons 2004-07 was too short to arrive at reliable sea state correction factors. Due to their similar observer heights (Table 2.1), the same correction factors as calculated for *MV Sheerwater* were also applied to *MV Wildfree*, *Alpha Beta*, *Mairi Grace* and *Wave*, whereas the correction factors calculated for *Gwen* were applied to the similar-sized *Durham boat* used in 2006.

Cell data

The study area was divided into grid cells at two different spatial scales: 4min resolution for analysis of the *Marguerite Explorer* data over the entire Hebrides (Figure 2.3d), and 2min for analysis of the distributional data around the Small Isles only (Figure 2.2). A previous analysis of the *Marguerite Explorer* data based on a grid size of 2min for the entire Hebrides had resulted in too low coverage of each cell and thus inflated sighting rates. Therefore, the division into 2min cells was reserved for the core study area around the Small Isles which had greater coverage. The choice of larger cell sizes also decreased the risk of spatial auto-correlation, which can be a problem especially for fine-scale analyses. Moreover, the 2min cells for the Small Isles allowed for some deviation from the normal straight route by *MV Sheerwater*, which would otherwise have resulted in erroneous assignment of some survey segments to cells at a finer resolution (such as 1min).

The two cell themes were created in ArcView 3.3 using the extension cr_tools. Cell areas were calculated using the XTools extension. Areas covered by land were excluded from each cell by combining cell and land polygons and subsequently deleting all land fragments from the total cell area. A British National Grid Transverse Mercator projection, centred on the study area (57°N, 6°W) and with chart datum set to WGS84 (as on the GPS) was used for all calculations within ArcView. Both map and distance units were set to metres.

For each vessel and year, effort records were linked with sightings and subsequently cut into segments of 1min duration using an Excel macro provided by Mick Baines, Sea Watch Foundation. The same macro also calculated the length (in km) of each segment. This allowed for automatic calculation of the mid-point of each 1min segment, based on speed and direction during each effort leg calculated from its start and end times and positions. Based on the position of its mid-point, each 1min segment could then be assigned to its corresponding 4min or 2min cell by using an additional macro.

Explanatory variables

BATHYMETRY AND TOPOGRAPHY

Bathymetric data for the larger study area were derived from the British Geological Survey's Digbath250 CD for the Northwest Scotland sector, which contained contour

lines at a resolution of 1:250,000 (10m contours from 0-200m, 20m contours from 200-400m, 100m contours for >400m). The 0-contour of this dataset was also used to adjust the coastline of the landmask for the entire Hebrides to enable a more accurate calculation of cell areas covered by sea. For the core study area around the Small Isles, however, these bathymetric data were inadequate since they did not take into account important smaller features such as Oberon Bank (Figure 2.1). The bathymetry data for the Small Isles were therefore combined with a further 6800 depth soundings taken either directly from the research vessel between 2003 and 2005, or extracted by hand from Jeppesen Marine's C-Map World electronic chart (www.c-map.com). Using the ArcView extensions 3D-Analyst and Spatial Analyst 3.3, a Triangular Integrated Network (TIN) was created from the combined depth data and subsequently converted into a raster. A resolution of 0.0019deg (ca. 200m) was chosen for the 4min cells covering the whole of the Hebrides (Figure 2.3a), and 0.00064deg (ca. 70m) for the 2min cells restricted to the area around the Small Isles with finer-scale bathymetry data available. Slope (in degrees) was then derived from the depth rasters at the same resolutions (Figure 2.3b), and values of all rasters summarised per cell for the four cell themes.

Bathymetry and topography data considered in the exploratory analyses included:

- Depth: mean, maximum and minimum, range (max-min), standard deviation.
- Topography: mean, maximum and minimum slope, range of slope (max-min) and standard deviation of slope.

Two additional measures for seabed topography were calculated from the bathymetry data for each cell: a contour index (CI) and average topographic variability (M). The contour index was calculated following Hui (1979) and Watts & Gaskin (1985) as CI = $(D_{max} - D_{min}) / D_{max} * 100$, where D_{max} = maximum depth and D_{min} = minimum depth within the cell. The average topographic variability was calculated as M = standard deviation / mean depth x 100 (Cañadas, 2006).

SEA SURFACE TEMPERATURE AND CHLOROPHYLL-A

Both sea surface temperature (SST) and chlorophyll a (Chl-a) remote sensing data were obtained as monthly csv files from the NERC Earth Observation Data Acquisition and Analysis Centre (NEODAAS) at Plymouth. Monthly composites were chosen in

preference to weekly files since the latter contained too high proportions of missing data due to cloud cover. This problem was still present for the monthly composites, but greatly reduced by comparison.

Sea Surface Temperature: The monthly SST composites were based on NOAA Advanced Very High Resolution Radiometer (AVHRR) satellite imagery, and were available at a resolution of $1.1km^2$ over the entire west coast of Scotland for all months of effort from July 1993 onwards (Figure 2.3c). However, due to cloud cover, spatial coverage for the month of July was inadequate for most years and areas with survey data. SST therefore had to be excluded as an explanatory variable from the models for July, both for the entire Hebrides and the Small Isles alone.

Chlorophyll-a: Monthly Chl-a composites were derived from NASA's Sea-viewing Wide Field-of-view ocean colour sensor (SeaWifs) over the whole study area from September 1997 to September 2004, and from the Moderate Resolution Imaging Spectroradiometer (MODIS Aqua) at a resolution of $1.1km^2$ for May 2005 to September 2007. No Chl-a data were available at an appropriate resolution prior to September 1997. This parameter could therefore not be included in the models based on the *Marguerite Explorer* data over the entire Hebrides, but only for the newer data around the Small Isles.

A matrix of latitude and longitude for each data point was created in Excel from the positional data supplied in separate files by NEODAAS, and the numerical arrays from the monthly csv files were imported. Using a macro provided by Mick Baines (Sea Watch Foundation), all SST and Chl-a data points were then linked with their respective positions in column format. All values depicting land or no data were deleted and the remaining data transformed to real-world values using the formulae provided by NEODAAS:

SST (deg C) = (DN * 0.1) + 5

and

Chl-a (mg/m^3) = 10^(DN*0.015 - 2),

where DN = digital number from file.

All mid-points of the 1min survey segments were then linked with their nearest SST and Chl-a data points for their corresponding year and month using the spatial join function in ArcView.

For Chl-a, some extreme values of up to 64mg/m^3 were detected. Such high concentrations may sometimes occur during dinoflagellate blooms e.g. in the Western Approaches to the British Isles during April and May, but would be very unusual in the Hebrides, where values of <4mg/m^3 dominate during summer (Edwards & John, 1997; Prof. P.M. Holligan, *personal communication*). Closer inspection of the monthly datasets linked with the 1min segments revealed gaps in represented values between lower concentrations of up to 6mg/m^3 and higher values. Moreover, concentrations of 6mg/m^3 or higher occurred mostly as isolated points amongst cells with much lower values and in close proximity to land (ca. 1-2miles). The most likely cause for extreme values was therefore sedimentation close to land causing an incorrect signal, a common problem associated with remote sensing data for Chl-a in coastal waters. All values above a concentration of 6mg/m^3 in the dataset were therefore substituted with the average of their surrounding data points.

TIDES

Tidal data for the *Marguerite Explorer* records over the entire Hebrides were obtained from a total of 22 representative ports and 26 tidal diamonds using the tidal prediction software *TotalTide* (http://www.ukho.gov.uk/amd/TotalTideSDK.asp), provided by the UK Hydrographic Office (UKHO). Using the spatial join function in ArcView, each effort record was linked with the nearest harbour that contained tidal information. The state of the tidal cycle (hours after local high water) was determined for the mid-point in time of all effort records, as well as information on whether the survey date fell into a period of spring or neap tides. After cutting the effort records into 1min survey segments, these were then linked with the appropriate tidal stream information of the nearest tidal diamond for that hour, taking into account spring and neap tides. In addition, the difference in water height above chart datum between highest and lowest water per day was determined for each effort record as a measure of the water volume exchanged between high and low tide.

As with the bathymetric data, however, the tidal current information contained in this commercially available software was inadequate for the core study area around the Small Isles. Based on the fine-scale bathymetric data for this region (see above), a customised, fine-scale tidal model was therefore developed and provided for the present study by Dr. Andrew Dale from the Scottish Association of Marine Sciences (SAMS) at Dunstaffnage Marine Laboratories, Oban. The model was based on mean depth velocities over 20 vertical levels from sea floor to surface for each data point, and covered the area between Ardnamurchan Point, Rhum, Soay and the mainland, including the Sound of Sleat (Figure 2.1). For the purpose of this study, a spatial resolution of 0.5min (ca. 520m longitude by 940m latitude) was used, and current strength and direction were provided for each hour of the tidal cycle, i.e. 13 datasets for spring and 13 datasets for neap tides.

The numerical arrays of the eastward (u) and northward (v) velocity component for each data point were linked with their respective coordinates using a matrix and macro in Excel, and both components combined in one file for each hour of the tidal cycle at spring and neap tides, respectively. Current strength at each point was then calculated as $\text{sqrt}(u^2+v^2)$. Based on local high tide at Mallaig, the state of the tidal cycle (hours after high water) was determined for the mid-time of each effort record in the area using the *TotalTide* software (and verified with Mallaig tide tables), noting whether the date fell into a period of spring or neap tides, as previously for the larger study area. Each 1min survey segment was then linked with its nearest fine-scale tidal data point and its corresponding information on current strength for that hour at spring or neap tide. Tidal data for *Marguerite Explorer* records were re-calculated for use with the 2min cells for the fine-scale study area.

SANDEEL OCCURRENCE

Probabilities for sandeel (*Ammodytes marinus*) occurrence were derived from a GAM prediction based on a relationship between measured sandeel densities from trawl data and silt and gravel content of seafloor sediment (Wright *et al.*, 2000), provided by Dr. Peter Wright of Marine Scotland - Science.

For the *Marguerite Explorer* data over the entire Hebrides, all sandeel prediction points within the study area were assigned to the 4min cells. Where more than one prediction point fell within a cell, the maximum probability for sandeel occurrence was selected. Probabilities of occurrence were divided into three categories: $x \leq 0.3$ = sandeel presence unlikely, $0.3 < x \leq 0.7$ = sandeel presence probable, and $x > 0.7$ = sandeel presence

very likely. Cells with no prediction points were assigned to a fourth category (Figure 2.3d).

By comparison to >40 prediction points of "sandeel presence unlikely", only four points of "sandeel presence very likely" and one point of "sandeel presence probable" fell within the small study area around the Small Isles (two on Maxwell Bank, and three at the western edge of the study area; Figure 2.3d). This factor therefore had to be excluded from the fine-scale analysis of this area based on the 2min cells.

CORRECTION FACTORS

Since the sighting rate per cell depends on the amount of time spent watching at different sea states, the sea state corrected time spent on effort (see above for calculation) was included as a correction variable in each model for both 4min and 2min spatial scales. However, if the time spent watching is restricted to a small portion of the cell, the chances of detecting a whale are limited. With the exception of the ferry *MV Sheerwater*, surveys were not conducted at constant speeds (stopping and travelling depending on different activities during fieldwork), so that the spatial coverage per cell was not linear to the time spent watching. The spatial coverage of each cell was expressed as number of km travelled (the total length of all 1min segments in the cell), and was included in each model as a second correction variable. Finally, the same amount of effort with respect to time spent watching and distance travelled in a cell with reduced sea area (i.e. adjoining land) results in better coverage than an equivalent amount of effort in a cell entirely covered by sea. Sea area per cell was therefore included as a third correction parameter.

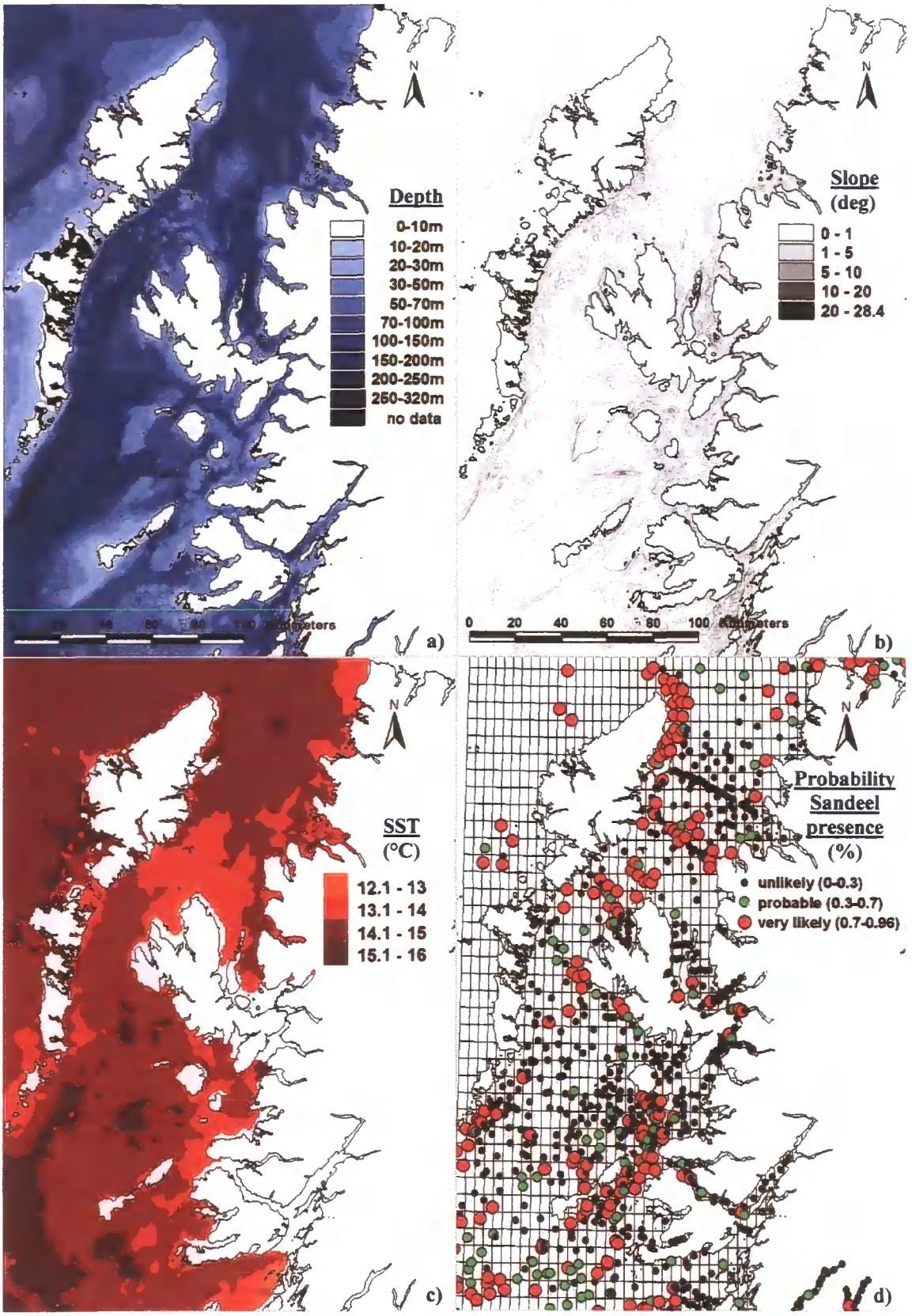


Figure 2.3. Depth, slope, sea surface temperature (example for August 1997) and probabilities for sandeel presence for entire study area. Grid lines in d) represent 4min cells used for the analysis.

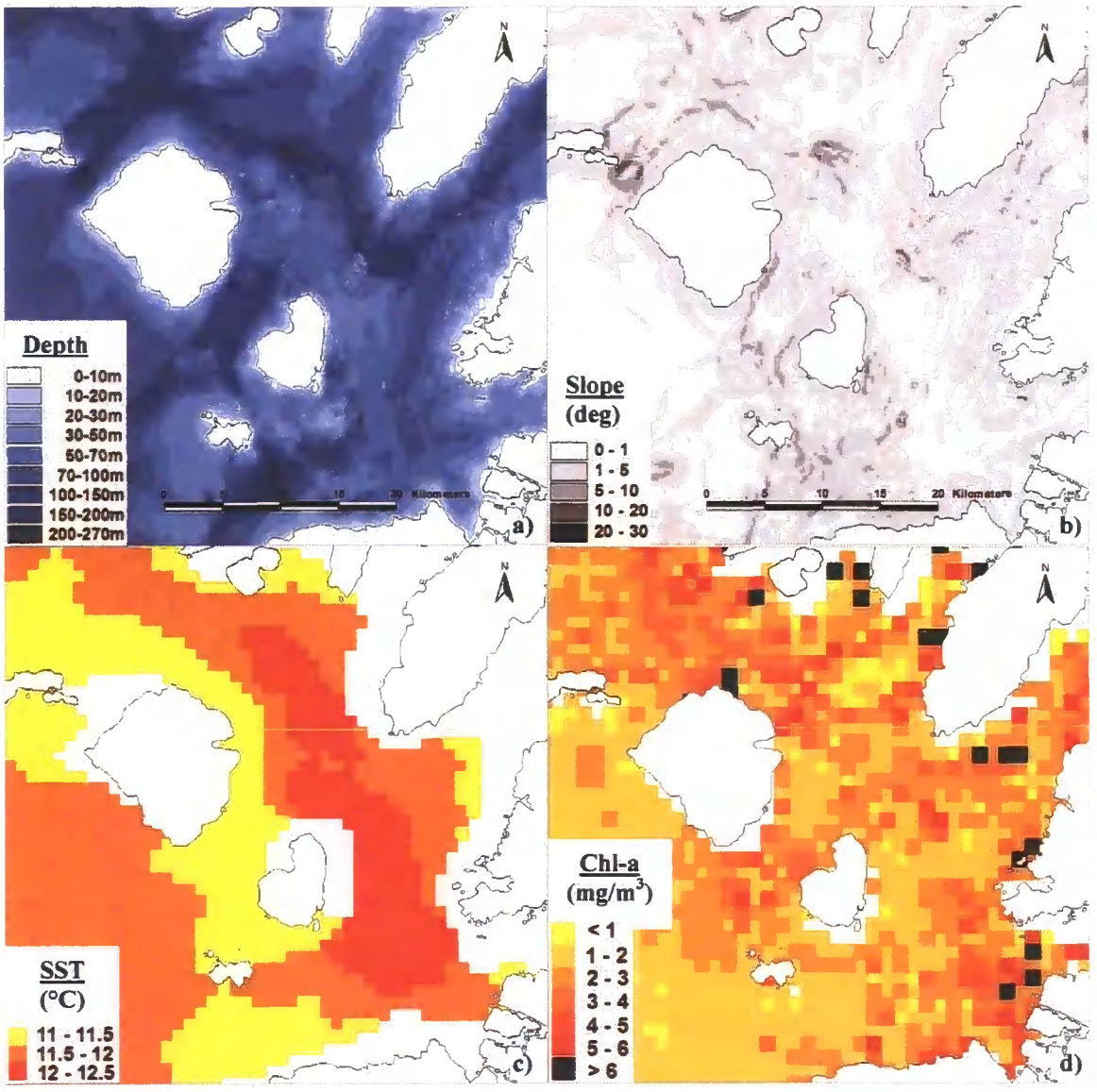


Figure 2.4. Depth, slope, sea surface temperature (example for June 2006) and chlorophyll-a concentration (example for August 2003) for core study area around the Small Isles.

Cell summaries

A) Entire Hebrides

The 4min cell data of effort and sightings from the *Marguerite Explorer* over the whole of the Hebrides were summarised by year, month and spring / neap tide. Since all 1min survey segments were linked with their nearest tidal, SST and Chl-a data points, these cell summaries resulted in mean values for these parameters along the survey track per cell, weighted by the amount of time spent in the proximity of each value. Given the spatial scale of the 4min cells relative to the resolution of the environmental data, this approach

was considered the most accurate representation of these environmental parameters along the survey track in a cell. It was therefore chosen in preference over whole cell summaries, which were applied to the bathymetric and topographic variables. Since the majority of 4min cells was only crossed once per month and year during line-transect and *ad libitum* surveys, an additional division according to hours after high water to take into account the differences in current strength, was considered unnecessary, since temporal coverage of most cells was restricted to only one or sometimes two consecutive hours during the tidal cycle, with almost identical values for tidal current (usually ±0.1-0.3kn). If the same cell was crossed again a few days later, however, a switch from spring to neap tide (or vice versa) was conceivable, with a difference in current strength of up to 2x or more. The dataset was therefore divided into spring and neap tides, in addition to month and year.

B) SMALL ISLES

In contrast to the monthly coverage of the entire Hebrides, the 2min cells around the Small Isles were crossed repeatedly at different states of the tidal cycle. For accurate representation of current strength, the cell data therefore had to be divided according to each hour of the tidal cycle, as well as spring and neap tides, in addition to month and year.

In a second step, summaries were re-calculated for all parameters without the sub-division according to the 2x13 hours of the tidal cycle in order to achieve better coverage and thus more representative sighting rates per cell, and to alleviate the problem of zero-inflation. This resulted in the same division as for the 4min cells: by year, month and spring / neap tide. Since the 2min cells were crossed at different tidal states, the inclusion of current strength and direction in these new models made no sense anymore. However, the division into spring / neap tides was retained, in order to investigate whether the animals showed a preference for the study area around the Small Isles at these two different states of the lunar cycle (as subjectively perceived during fieldwork).

Macleod *et al.* (2004) found differences in habitat use of minke whales between early and late season, and sighting rates are known to increase on the west coast of Scotland from May onwards with a peak usually around August (Evans *et al.*, 2003). In order to avoid missing possible changes in habitat preference through the season, as well as a bias towards August, the month with most survey effort, the season was divided into early

(May & June), mid (July) and late (August & September) periods for both the entire Hebrides and the study area around the Small Isles. This resulted in six separate models – three for the entire Hebrides and three for the Small Isles. Visual inspection of sightings plots yielded no qualitative differences in minke distribution between May and June, or August and September. These months were therefore included in the same models for early and late season, respectively, but a correction for month was applied.

In order to arrive at representative sighting rates (number of individuals / h) per cell without inflation due to low temporal coverage, only 4min cells with a minimum coverage of an equivalent of 20min at sea state 0 (i.e. using the sea state corrected time) per spring / neap tide per month per year were considered for the analysis in models for the entire Hebrides. For the 2min cells around the Small Isles, this limit was set at a minimum of 10min at sea state 0. In order to avoid inclusion of narrow sea lochs (which were sometimes used as anchorage by the *Marguerite Explorer*) and very shallow areas close to the coast unsuitable as minke whale habitat, cells with a maximum depth of less than 20m or mean depth of less than 10m were excluded from models at both spatial scales.

Statistical analysis

Pair-plots were produced for each of the six models to check for co-linearity between continuous explanatory variables and to examine their relationship with minke whale sighting rates (expressed as number of individuals seen per hour). In combination with Spearman's correlation coefficients between all continuous explanatory variables, the pair-plots were used to decide upon which parameters to exclude from the models due to co-linearity.

Minke whale sighting rates per cell were then modelled using Generalised Additive Models (GAMs; Hastie & Tibshirani, 1990), implemented in the mgcv library (Wood, 2004; 2006) in the freeware R (R Development Core Team, 2006). By comparison to parametric linear or Generalised Linear Models (GLMs), GAMs have the advantage of letting the data dictate how the shape of the dependent variable is affected by each covariate by fitting non-parametric smoother terms. They have therefore been widely applied, especially in fisheries (Augustin *et al.*, 1998; Maravelias, 1999; Beare *et al.*, 2002), and more recently in marine mammal studies (Bradshaw *et al.*, 2004; Hastie *et al.*, 2005) for modelling species distribution and habitat preferences, where the relationship between explanatory and dependent variables is not expected to be linear.

Due to an excess of zero values in the dependent variable, overdispersion in the residuals was detected in four of the six separate analyses when applying models with a Poisson distribution (which assumes that the variances are equal to the means). The overdispersion in the residuals was accounted for by applying a quasi-Poisson GAM, in which the dispersion parameter was estimated automatically and the standard errors of the coefficients of the explanatory variables multiplied by its square root. While this technique does not change the estimates for the means by comparison to a Poisson distribution, it provides more realistic estimates of the variance and thus significance of each smoother in the model. The residuals of the two spring models showed minimal overdispersion, (dispersion parameter <1.1; Zuur *et al.*, 2009), and minke whale sighting rates at both spatial scales for spring were therefore re-fitted with a Poisson distribution. Thin plate regression splines were used as penalised regression smoothers for all models. The amount of smoothing (i.e. the degrees of freedom) for each continuous explanatory variable was estimated automatically using generalised cross-validation (GCV). However, in order to avoid over-fitting, the maximum degrees of freedom used for a single parameter was set to 4. Model selection was performed in a stepwise backward procedure by minimising the UBRE score (for Poisson models) and GCV score (for quasi-Poisson models), respectively (Craven & Wahba, 1979; Wood, 2006). UBRE and GCV scores are the mgcv equivalents to Akaike's Information Criterion (AIC), which measures the goodness of fit of the model, penalised by the number of parameters included. For quasi-Poisson models, the deviance explained was used for model selection in addition to the GCV score. Non-significant variables were retained in the model if they contributed to minimizing the UBRE/GCV score and (in the latter case) increased the deviance explained. Residuals of the final models were plotted against each explanatory variable to check for residual patterns. Since the data were divided into three separate models per season, the significance values of each explanatory variable in the final models were Bonferroni-corrected, with a new p-value of 0.0167.

Prey sampling

A total of 23 prey samples were taken on an opportunistic basis, either from feeding locations of minke whales (n=13) or from the centre of seabird feeding aggregations (n=10) in 2003 (n=17) and 2004 (n=6). No surface feeding was observed in 2005 and 2006, and no fish or scales were found at the surface in 2007, so no prey sampling could

be conducted in those years. Most samples consisted of scales floating in the water. Only once in 2003 and twice in 2004 could whole fish be retrieved. Both scales and whole fish were preserved in 100% ethanol. Three prey samples, all consisting of whole fish, had been taken from the same area earlier, in September 2001, of which two had been identified as sprat and one as juvenile herring by the relative position of the base of the ventral fins to the base of the dorsal fin (Muus & Dahlstrøm, 1974).

Scales taken from 20 frozen sprat (7.5 – 11cm in length) and 30 juvenile herring (7.2 – 10cm in length) caught on the coast of Northeast England, as well as from the identified whole fish in 2003 and 2004, were used as a reference collection to which all scale samples were compared under the microscope at a magnification of 4x and 10x. All scales were taken from the upper sides or back of the fish, within the area of dark pigmentation. These appeared to be the areas from which the scales became detached most easily and thus the most likely origin of loose scales found floating in the water. Scales in direct proximity to the dorsal fin, which in herring showed an elongated shape and different structure to the remainder of the scales, were omitted.

The juvenile herring in the reference sample were slightly smaller than the sprat. Therefore, scales of six adult Northeast Atlantic herring (ca. 24cm in length) obtained from a local supermarket were also examined. Sandeels have been reported as important minke whale prey in various parts of the North Atlantic, including the North Sea and Scottish waters (Olsen & Holst, 2001; Pierce *et al.*, 2004). For this reason, the scales of a reference sample of sandeels caught around the Farne Islands off Northeast England were also examined under the microscope.

Yearly comparisons with other taxa

Focusing on the years with the best temporal coverage only, annual trends in sighting numbers of minke whales around the Small Isles were compared with 1) temporal variability in chlorophyll-a concentration, 2) sprat catch statistics for the west coast of Scotland, 3) basking shark numbers, and 4) breeding success and numbers of seabirds in the area using Spearman correlations where applicable or qualitative assessment of comparative plots.

Sprat catch statistics for the west coast of Scotland were obtained from the Fisheries Management Database and were provided by Dr. Paul Fernandes, FRS Marine Laboratory, Aberdeen.

The comparison with basking sharks was based on data collected from *MV Sheerwater* between 2004 and 2008. Since the data were collected from the same vessel within the small study area, no correction for effort was necessary, and no bias was introduced due to possible interannual sampling differences of regions with known high basking shark densities, such as the Cairns of Coll or Hyskeir (P.G.H. Evans, *personal communication*).

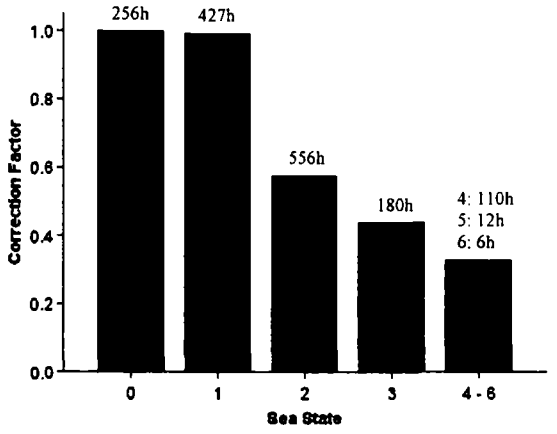
Minke whale sighting rates were compared to both annual breeding success of seabirds at local colonies, and numbers counted at sea during fieldwork seasons 2003-07 (see Chapter 3 for methodology). The comparison with bird numbers at sea counted simultaneously to minke whale observations was included in order to take account of the time lag between seabird breeding in spring and peak minke whale numbers in summer. Data on seabird breeding success were kindly provided by R.L. Swann, and by R. Mavor, Joint Nature Conservation Council (JNCC).

RESULTS

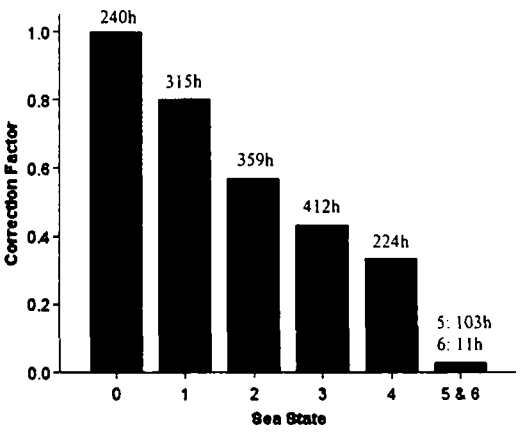
Habitat models

Sea state correction

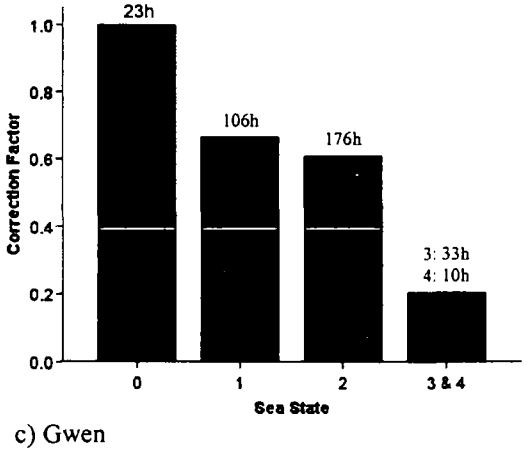
As expected, sighting efficiency for minke whales decreased with increasing sea state, but differences were found between the three platforms with sufficient survey effort, and this could mainly be attributed to observer height. The derived correction factors for each of the three main vessels are shown in Figure 2.5. Whereas the sighting efficiency at sea state 1 remained almost as high as for sea state 0 for the *Marguerite Explorer* (Figure 2.4a), it decreased to 80% for *MV Sheerwater* (Figure 2.4b) and ca. 65% for *Gwen* (Figure 2.4c), which had the lowest observer height. On the other hand, sighting efficiency at sea state 2 was almost identical (at ca. 60%) for all three vessels. At higher sea states (3 and 4), the steepest drop was noted for *Gwen*, whereas by comparison, the sighting efficiency for both *Marguerite Explorer* and *MV Sheerwater* at around 40% was almost twice as high probably due to their increased observer height by comparison to *Gwen*. Amongst the three vessels, *MV Sheerwater* showed the most regular decrease in sighting efficiency with increasing sea state.



a) Marguerite Explorer



b) MV Sheerwater



c) Gwen

Figure 2.5. Sea state correction for the three main observer platforms. Figures above the bars indicate the number of hours spent watching at each sea state.

Sightings and Effort

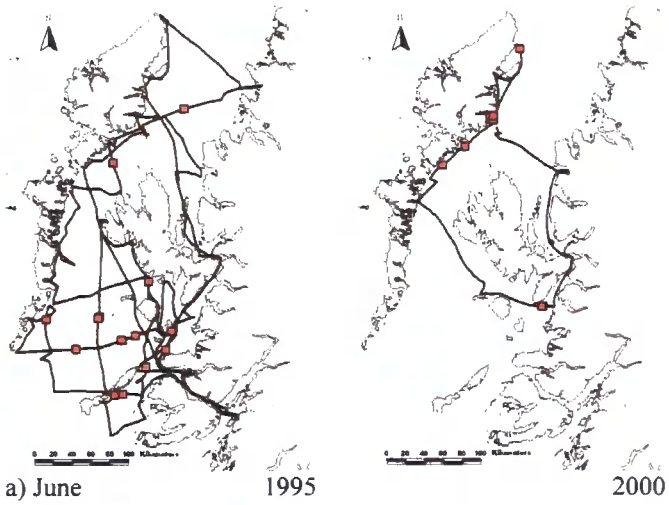
A) Entire Hebrides

A total of 356 minke whale sightings (comprising 409 individuals) during 1515 hours of survey effort were included in the analysis from the *Marguerite Explorer* data over the entire Hebrides between 1993-2002 (Table 2.2, Figure 2.6). A general increase in numbers of sightings per unit effort was observed over the study period (as reported in Evans *et al.* (2003), using other datasets in addition to this one), at least for the month of August with the best temporal coverage. Numbers of sightings per hour were lower in June and September by comparison to July and August (except for 1994). Minke whales were not randomly distributed over the study area, but sightings were clustered in particular regions. These were not consistent between years or months, however, except

for a reliable presence of animals in the vicinity of the Small Isles for those months with sufficient coverage in that area (Figure 2.6). The Little Minch (Figure 2.1) represented another potentially high density area in some years, but the centre of the distribution appeared to be variable, shifting north (August 1997) or south (September 1994) in some months.

Table 2.2. Yearly and monthly summaries for Marguerite data over entire Hebrides.

Year	Month	No. days (fieldwork dates)	No. hours (No. sea state corrected hours)	km travelled	No. sightings (no. individuals)
1993	July	15 (17.-31.)	136 (108)	770	22 (24)
	August	19 (1.-20.)	165 (139)	929	11 (12)
1994	July	9 (23.-31.)	66 (43)	359	13 (13)
	August	17 (1.-12 & 27.-31)	170 (121)	859	39 (50)
	September	20 (1.-22.)	163 (105)	902	55 (65)
1995	June	19 (10.-30.)	207 (140)	1122	15 (15)
1996	August	14 (10.-23.)	137 (105)	803	50 (56)
	September	7 (14.-20)	64 (46)	349	5 (5)
1997	August	14 (9.-22. & 30.-31.)	148 (122)	840	79 (89)
	September	12 (1.-12.)	83 (41)	432	2 (2)
1998	July	7 (25.-31.)	72 (56)	400	39 (46)
2000	June	5 (15.-16 & 19.-21.)	52 (39)	281	7 (7)
2002	August	7 (24.-30.)	52 (35)	245	19 (25)
Total		**165**	**1515 (1100)**	**8291**	**356 (409)**



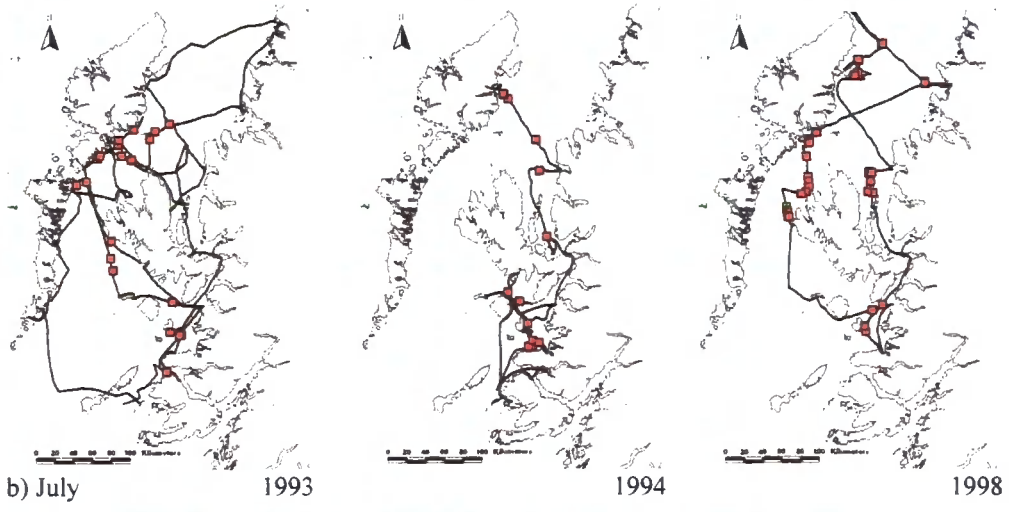
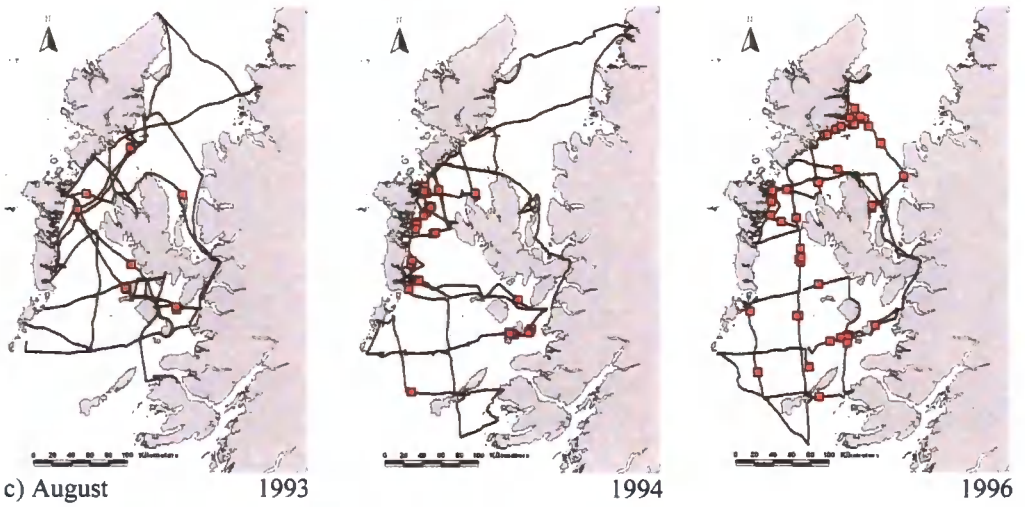


Figure 2.6. Track lines by month from Marguerite Explorer between July 1993 and August 2002 used for spatial models. Red squares represent minke whale sightings, grid lines in the background represent the 4min cells on which the analysis was based. The scale bar indicates a distance of 100km.



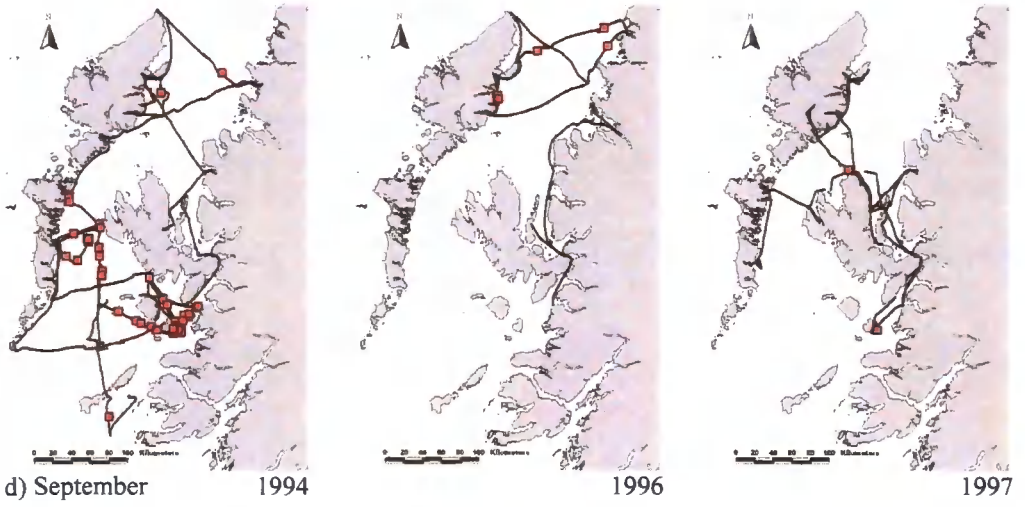


Figure 2.6, continued. August – September. Track lines by month from Marguerite Explorer between July 1993 and August 2002 used for spatial models. Red squares represent minke whale sightings, grid lines in the background represent the 4min cells on which the analysis was based. The scale bar indicates a distance of 100km.

B) SMALL ISLES

Survey effort around the Small Isles amounted to a total of 2326 hours with 765 minke whale sightings between 1998 and 2007 (Table 2.3, Figure 2.7). Of these, data from *MV Sheerwater* between 2003-07 contributed 1688h (72.5%) with 376 (49%) sightings; my own fieldwork 2003-07, 572h (24.5%) with 342 (45%) sightings; and *Marguerite Explorer* between 1998-2002, 66h (3%) with 47 (6%) sightings. By contrast to the fixed route by *MV Sheerwater*, effort during my own fieldwork and from *Marguerite Explorer* was targeted towards high density areas, which accounts for the comparatively higher sighting rates.

As with the seasonal trend over the entire Hebrides, an increase in numbers of sightings was observed between spring and summer, with peak numbers occurring in July or August (Table 2.3, Figure 2.7). Peak minke whale activity in the area occurred in summer 2004 (July – September), when groups of up to 10 individuals were feeding mainly between Arisaig and Eigg, as well as at the entrance to the Sound of Sleat (Figure 2.7). However, this was followed by a sharp decline in numbers of sightings throughout the whole season of 2005, with only slow recovery since then. Of the total number of sightings, only 22% (171) occurred between May 2005 and September 2007, despite 63% (1476h) of total survey effort during this period.

Changes in the distribution of the animals were observed mainly between the years 2003 and 2004 during the month of August. Whereas high numbers of whales were seen per unit effort south of Eigg (around Maxwell Bank) during my own fieldwork in 2003, sighting rates in that area were close to zero from 2004 onwards (Figure 2.1). By contrast, the deep channel (ca. 70m depth; Figure 2.4a) and its margins between the Isle of Eigg and Arisaig consistently yielded sightings in all months and years. Amongst the years that it received coverage, the entrance to the Sound of Sleat was particularly important in August 2004 and July 2007, whereas no whales were found in that area in August 2003 or July and August 2005.

Table 2.3. Yearly and monthly summaries for Small Isles data. Marguerite = *Marguerite Explorer*, DB = *Durham boat*. The different vessels are described in Table 2.1.

Year	Month	Vessel name	No. days (fieldwork dates)	No. hours (No. sea state corrected hours)	km travelled	No. sightings (no. individuals)
1998	August	Marguerite	7 (1.-7.)	28 (16)	150	23 (33)
1999	September	Marguerite	4 (6, 7, 11, 18)	15 (11)	77	14 (19)
2001	July	Marguerite	2 (28, 31)	15 (11)	73	6 (6)
2002	August	Marguerite	2 (24, 30)	8 (4)	38	4 (7)
		Sheerwater	4 (26.-29.)	15 (8)	114	12 (15)
2003	August	Gwen	11 (4.-15.)	103 (66)	430	101 (111)
		Sheerwater	16 (3, 16.-31.)	64 (37)	537	76 (84)
	September	Sheerwater	20 (1.-28.)	59 (30)	534	27 (40)
2004	May	Sheerwater	23 (4.-31.)	73 (51)	715	9 (10)
	June	Sheerwater	19 (1.-30.)	63 (31)	617	7 (7)
	July	Sheerwater	25 (1.-31.)	91 (50)	827	45 (101)
	August	Gwen	6 (17.-31.)	53 (33)	227	52 (77)
		Sheerwater	29 (1.-31.)	107 (68)	942	74 (163)
	September	Gwen	7 (1.-10.)	51 (29)	216	55 (73)
		Wild Free	5 (6.-10.)	56 (41)	207	68 (108)
		Sheerwater	16 (2.-29.)	49 (25)	428	21 (57)
2005	May	Sheerwater	25 (1.-31.)	73 (44)	740	3 (3)
	June	Sheerwater	28 (1.-30)	92 (52)	889	5 (5)
	July	Gwen	6 (24.-30.)	34 (18)	178	0
		Sheerwater	29 (1.-31.)	94 (44)	934	2 (3)
	August	Gwen	13 (1.-20., 31)	79 (48)	378	11 (12)
		Sheerwater	28 (1.-31.)	90 (48)	877	5 (6)
	September	Gwen	6 (2.-12.)	32 (20)	191	3 (3)
		Sheerwater	15 (1.-20.)	37 (20)	376	1 (1)
2006	May	Sheerwater	18 (1.-31.)	51 (36)	525	1 (1)
	June	Sheerwater	24 (1.-30.)	77 (48)	742	10 (11)
	July	Sheerwater	29 (2.-31.)	97 (66)	921	14 (23)
	August	Alpha Beta	2 (2.-3.)	12 (6)	62	6 (7)
		MairiGrace	5 (6.-12.)	43 (23)	242	6 (6)
		DB	9 (15.-30.)	55 (35)	211	6 (6)
		Sheerwater	30 (1.-31.)	101 (50)	989	5 (5)
	September	DB	2 (2.-3.)	4 (2)	25	0
		Sheerwater	20 (2.-24)	53 (30)	526	4 (4)
2007	May	Sheerwater	22 (1.-31.)	76 (38)	762	4 (4)
	June	Sheerwater	26 (1.-30.)	93 (66)	915	11 (13)
	July	Wave	6 (20.-24., 29)	50 (35)	206	34 (61)
		Sheerwater	29 (1.-31.)	99 (59)	907	29 (35)
	August	Sheerwater	26 (1.-31.)	85 (40)	797	7 (10)
	September	Sheerwater	17 (1.-19.)	49 (23)	459	4 (5)
Total			**533**	**2326 (1362)**	**18984**	**765 (1135)**

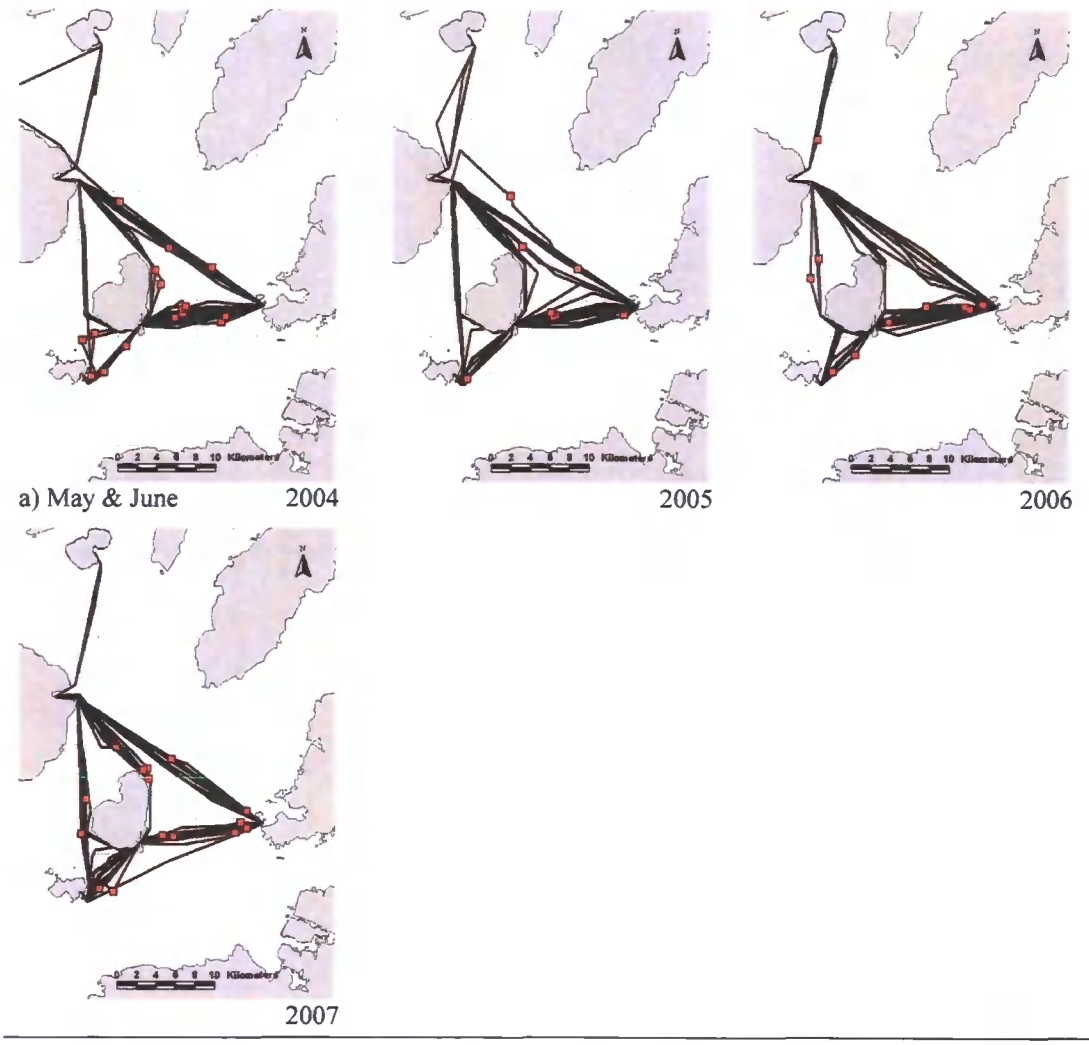
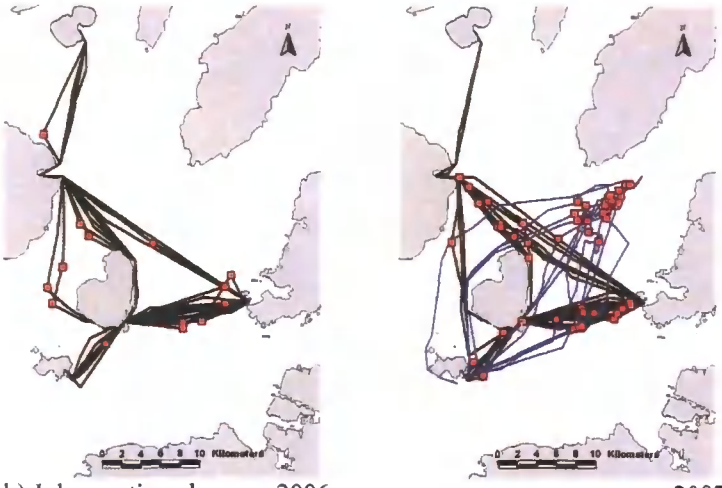
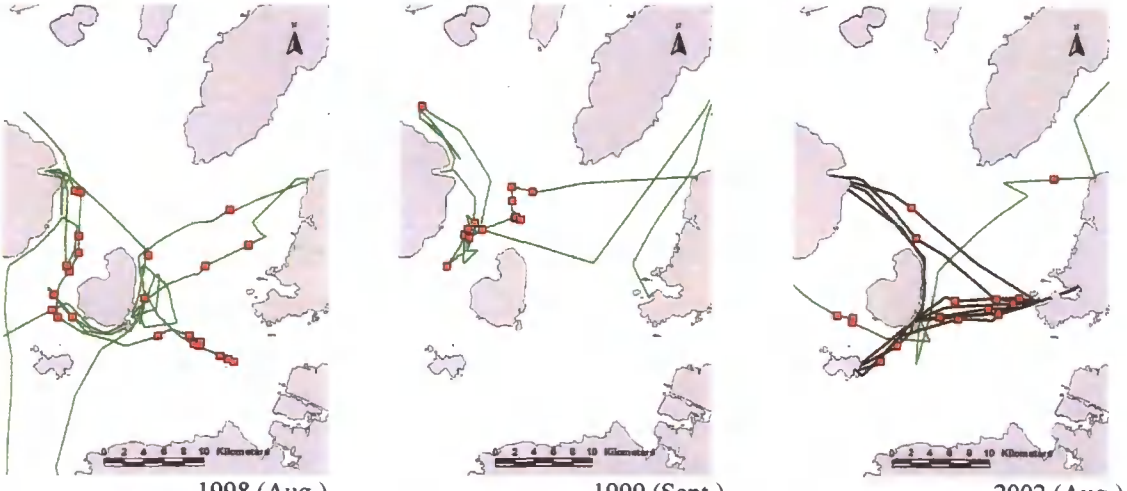


Figure 2.7. Track lines by month for the core study area around the Small Isles used for spatial models. Red squares represent minke whale sightings, grid lines in the background represent the 2min cells on which the analysis was based. The scale bar indicates a distance of 10km. Green = track of *Marguerite Explorer*, blue = own fieldwork, black = *MV Sheerwater*.

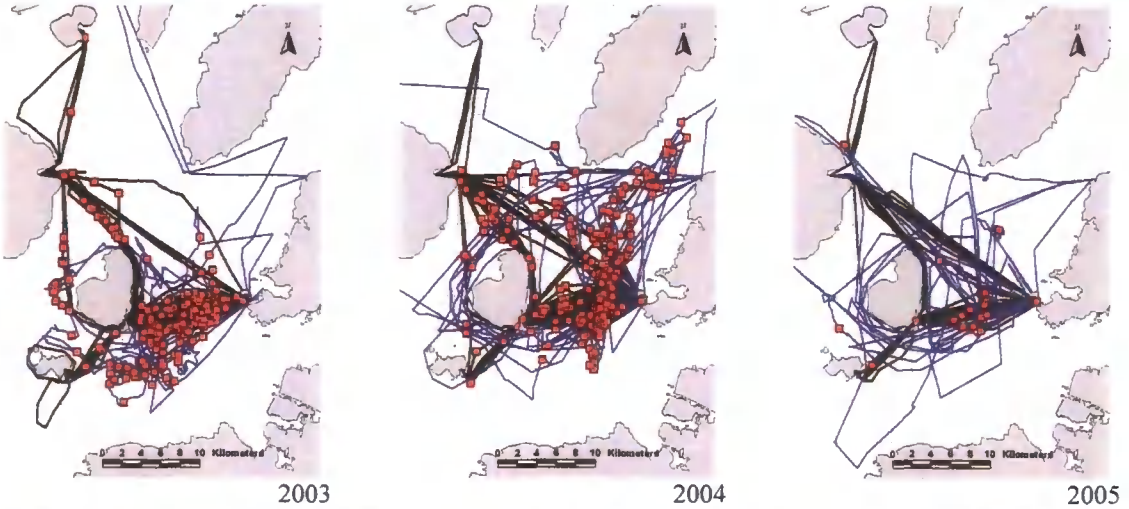


b) July, continued 2006 2007



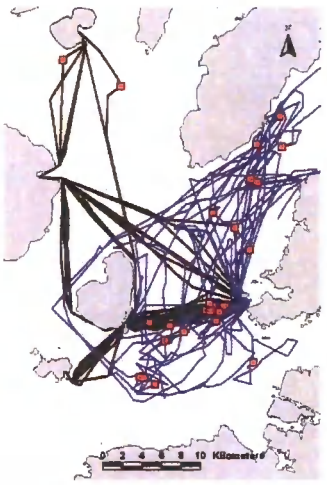
1998 (Aug.) 1999 (Sept.) 2002 (Aug.)

c) August & September



2003 2004 2005

Figure 2.7, continued. Track lines by month for the core study area around the Small Isles used for spatial models. Red squares represent minke whale sightings, grid lines in the background represent the 2min cells on which the analysis was based. The scale bar indicates a distance of 10km. Green = track of *Marguerite Explorer*, blue = own fieldwork, black = *MV Sheerwater*.



2006

2007

c) August & September, cont.

Figure 2.7, continued. Track lines by month for the core study area around the Small Isles used for spatial models. Red squares represent minke whale sightings, grid lines in the background represent the 2min cells on which the analysis was based. The scale bar indicates a distance of 10km. Green = track of *Marguerite Explorer*, blue = own fieldwork, black = *MV Sheerwater*.

Exploratory Analysis

A) Entire Hebrides

Strong correlations were found within explanatory variables for both bathymetry and topography. Amongst the different candidate variables for bathymetry, mean depth showed the clearest relationship with minke whale sighting rates per cell in the pairplots and was therefore included in the models. For topography, mean slope best explained differences in sighting rates between cells (data not shown). No strong correlations were found between mean depth and mean slope (Spearman's $r<0.2$), or any of the other selected explanatory variables ($r<0.6$).

B) Small Isles

For months with coverage of the study area by both *MV Sheerwater* and my own fieldwork, minke whale sighting rates from the two independent sources were positively correlated (Spearman correlation: number of sightings / hour: $r=0.803$, $p=0.009$; number of sightings / hour, sea state corrected: $r=0.787$, $p=0.012$; number of individuals / hour: $r=0.745$, $p=0.021$; number of individuals / hour, sea state corrected: $r=0.795$, $p=0.01$; $n=9$). Data collected along the ferry route could therefore be viewed as representative of the whole study area around the Small Isles, and so the data from *MV Sheerwater* and my

own fieldwork were combined for the analysis. In addition, the good correlation between sighting rates along the ferry route - where individual minke whales are likely to be counted only once during a crossing due to its speed and direct line of travel - and the fieldwork data with more targeted effort in high density areas, served as a control that individuals had not been over-recorded during the latter.

In the initial approach of dividing cell data according to each hour of the tidal cycle, the three seasonal models were examined particularly with respect to the relevance of tidal currents in determining minke whale occurrence. However, sighting rates around the Small Isles were found to be independent of this parameter (Figure 2.8). The additional division according to the 2x13 hours of the tidal cycle, which had been included for accuracy of the tidal data, was therefore abandoned. Instead, summaries of cell data were re-calculated according to year, month and spring/neap tide only. Due to the resulting improvement of temporal coverage per cell, sighting rates became more representative, and the percentage of zero observations was reduced, which resulted in a decrease of the dispersion parameter in the models (Table 2.4).

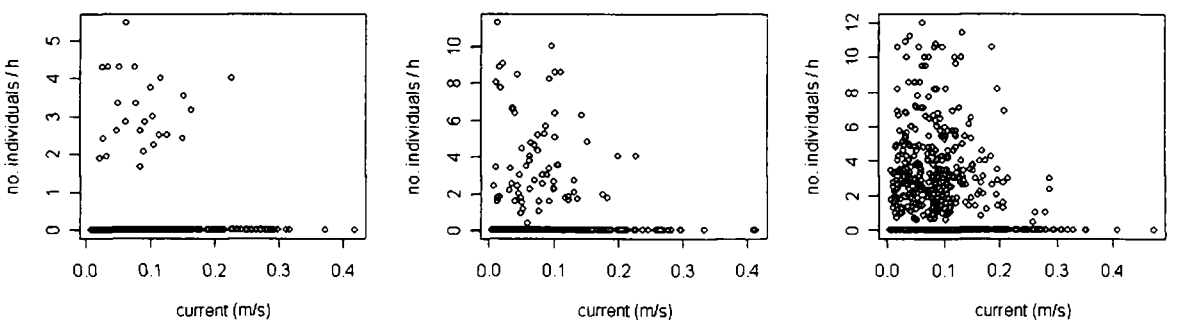
As with the 4min cells over the entire Hebrides, candidate explanatory variables for bathymetry and topography were strongly correlated with each other within the two categories. For bathymetry, mean depth showed the strongest relationship with minke whale sighting rates per cell; for topography, maximum slope better explained sighting rates than mean slope. Inclusion of the *MV Sheerwater* data resulted in strong correlations (Spearman's r: $0.788<r<0.927$) between the correction variables 'number of hours (sea-state corrected)' and 'distance travelled' per cell. The two variables could therefore not be included in the same model. The decision on which parameter to include was based on which improved the model the best (i.e. led to a greater decrease in the GCV/UBRE score and increase in explained deviance). For the May - June and August – September models, this was the number of sea-state corrected hours; for the July model, it was the distance travelled per cell.

The full models for the entire Hebrides and the Small Isles were thus of the form:

Dependent variable: number of individuals per hour

Explanatory variables (*italics* = only for 4min cells; * = only for 2min cells):

- factors: - year (2 – 8 categories)
  - month (for May / June and August / September models; 2 categories)
  - spring / neap tide (2 categories)
  - *sandeel category (4 categories: unlikely, probable, very likely, no data).*
- smooth terms:
  - SST (deg); excluded from models for July
  - CHL* (mg/m^3)
  - mean depth (m)
  - *mean slope* (deg); maximum slope* (deg)
  - *tidal current (kn)*
  - *mean difference between high and low water at nearest harbour (m)*
  - sea state corrected time spent per cell (min)
  - length of survey track per cell (km)
  - area per cell covered by sea (ha)



a) May & June b) July c) August & September

Figure 2.8. Relationship between minke whale sighting rates per cell and tidal currents around the Small Isles when the data were sub-divided according to each hour of the tidal cycle to achieve accurate representation of current strength.

Model results

A) ENTIRE HEBRIDES

A common feature between all three seasonal models for the entire Hebrides was that none of the three tidal parameters (the factor 'spring vs. neap', as well as the smoothers for current strength and difference in tidal height) was relevant in determining minke whale sighting rates per cell (Table 2.4). Although retained in some models for better fit, they were never significant when corrected for the other explanatory variables. For the August/September model, 'month' was significant, with lower sighting rates in September by comparison to August. The factor 'year' was significant for both the June and August/September models, with later years showing higher sighting rates compared to the first year of the study for that part of the season. On the other hand, year did not play a role for the July models. In June, minke whale sighting rates were significantly higher in cells with probable and very likely sandeel occurrence, compared to cells with unlikely sandeel presence (Table 2.4a), whereas there was no difference between cells with unlikely sandeel occurrence and no prediction points. For July, sandeel occurrence was still retained in the model for better fit, even though it was not significant anymore (Table 2.4b), and for August/September, this factor was removed from the model altogether (Table 2.4c).

Smooth terms also showed differences in the relevance of continuous explanatory variables between months. For June and July, correction terms were retained in the model, but were not significant, whereas for August/September, minke whale sighting rates were positively correlated with the sea state corrected time spent per cell (Table 2.4c, Figure 2.9c). Seafloor topography only played a role for the month of June, with whales showing a preference for intermediate slopes of around 2-2.5deg (Figure 2.9a). During summer and autumn, however, depth better explained minke whale distribution. Sighting rates increased with water depth (from 50-60m and above, reaching a plateau at 110-120m; Figure 2.9b) in July, when depth was the only significant continuous variable in the model. During August/September, the smoothing curve for depth was of an overall bell-shaped form, with a broad preference for waters of 50-150m deep (Figure 2.9c). Sea surface temperature was important in explaining minke whale distribution during both June and August/September. During June, the animals showed a preference for temperatures at the higher end of the scale at around 11.5-12°C (Figure 2.9a), and in August/September for intermediate values between 13°C and 14°C (Figure 2.9c).

The model which best explained minke whale distribution over the whole of the Hebrides was for June, accounting for 64.2% of the deviance (Table 2.4a). The models for July and August/September, on the other hand, only explained 26.1% and 29.1% of the deviance, respectively, despite the high number of explanatory variables retained in the latter (Tables 2.4b, c).

Table 2.4. Summaries for GAM final models for *Marguerite Explorer* data; 4min cells over entire study area. * = significant after Bonferroni-correction.

a) June 1995 & 2000 (n=174):

Parametric coefficients:

	Estimate (± std. error)	p
Intercept:	-6.283 (± 1.031)	<0.001*
Year2000 (vs. 1995):	3.860 (± 1.465)	0.008*
Sandeel.cat2 (vs. cat.1):	3.091 (± 0.839)	<0.001*
Sandeel.cat3 (vs. cat.1):	2.777 (± 0.778)	<0.001*
Sandeel.cat4 (vs. cat.1):	0.661 (± 0.868)	0.447
Spring tide vs. neap:	0.803 (± 0.610)	0.188

Smooth terms:

	edf	X^2	
s(SST):	3.81	15.507	0.003*
s(km travelled/cell):	1.82	2.265	0.286
s(cell area):	2.48	3.566	0.235
s(mean slope):	3.77	15.875	0.002*

Deviance explained: 64.2%
UBRE score: -0.287

b) July 1993, 1994 & 1998 (n=212), without SST:

Parametric coefficients:

	Estimate (± std. error)	p
Intercept:	-1.629 (± 0.360)	<0.001*
Sandeel.cat2 (vs. cat.1):	-8.654 (± 52.14)	0.868
Sandeel.cat3 (vs. cat.1):	-0.284 (± 0.500)	0.571
Sandeel.cat4 (vs. cat.1):	0.116 (± 0.311)	0.709
Spring tide vs. neap:	0.449 (± 0.554)	0.418

Smooth terms:

	edf	X^2	
s(km travelled/cell):	2.95	5.552	0.135
s(sea state corr. duration):	2.41	6.545	0.058
s(cell area):	1	0.896	0.345
s(diff. tidal height):	2.51	6.111	0.077
s(mean depth):	1.91	10.320	0.006*

Dispersion parameter: 1.451
Deviance explained: 26.1%
GCV score: 1.568

c) August – September 1993, 1994, 1996, 1997 & 2002 (n=738):

Parametric coefficients:

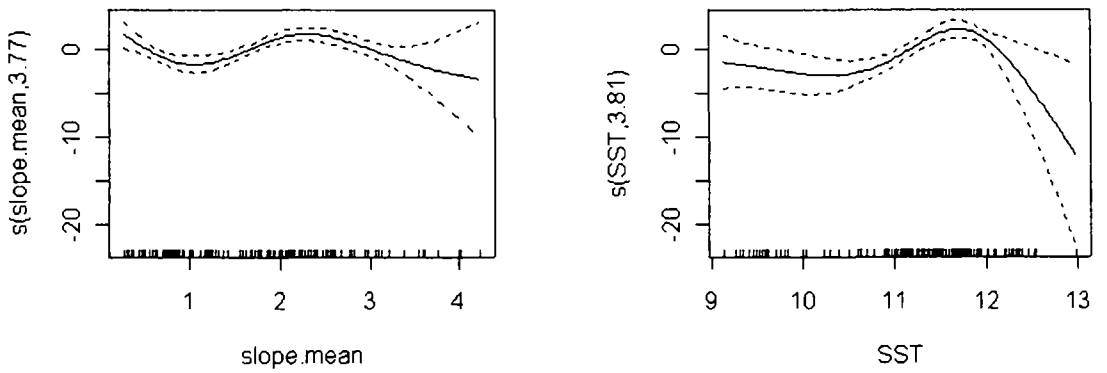
	Estimate (± std. error)	p
Intercept:	-2.625 (± 0.459)	<0.001*
September vs. August:	-0.611 (± 0.254)	0.016*
Year1994 (vs. 1993):	1.614 (± 0.461)	<0.001*
Year1996 (vs. 1993):	1.680 (± 0.454)	<0.001*
Year1997 (vs. 1993):	2.021 (± 0.481)	<0.001*
Year2002 (vs. 1993):	1.856 (± 0.554)	<0.001*
Spring tide vs. neap:	-0.828 (± 0.377)	0.028

Smooth terms:

	edf	X^2	
s(SST):	3.83	21.343	<0.001*
s(km travelled/cell):	1.49	3.302	0.125
s(sea state corr. duration):	2.42	31.523	<0.001*
s(diff.tidal.height):	1.82	4.127	0.110
s(mean depth):	3.68	20.084	<0.001*
s(mean slope):	3.70	9.959	0.034
s(current):	2.58	1.546	0.590

Dispersion parameter: 1.585
Deviance explained: 29.1%
GCV score: 1.644

a) June



b) July

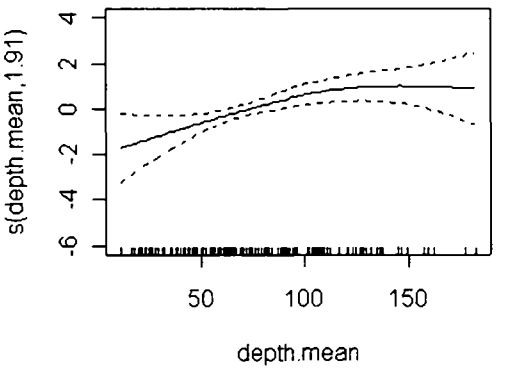


Figure 2.9. GAM smoothing curves for significant parameters (after Bonferroni-correction) on the sighting rates (no. individuals / hour) per cell for the three seasonal models over the entire Hebrides. Broken lines represent 2-SE ranges around the main effects. The degrees of freedom for each smoothing curve are indicated on the y-axis. Vertical dashes on the x-axis represent the distribution of the explanatory variable.

c) August & September

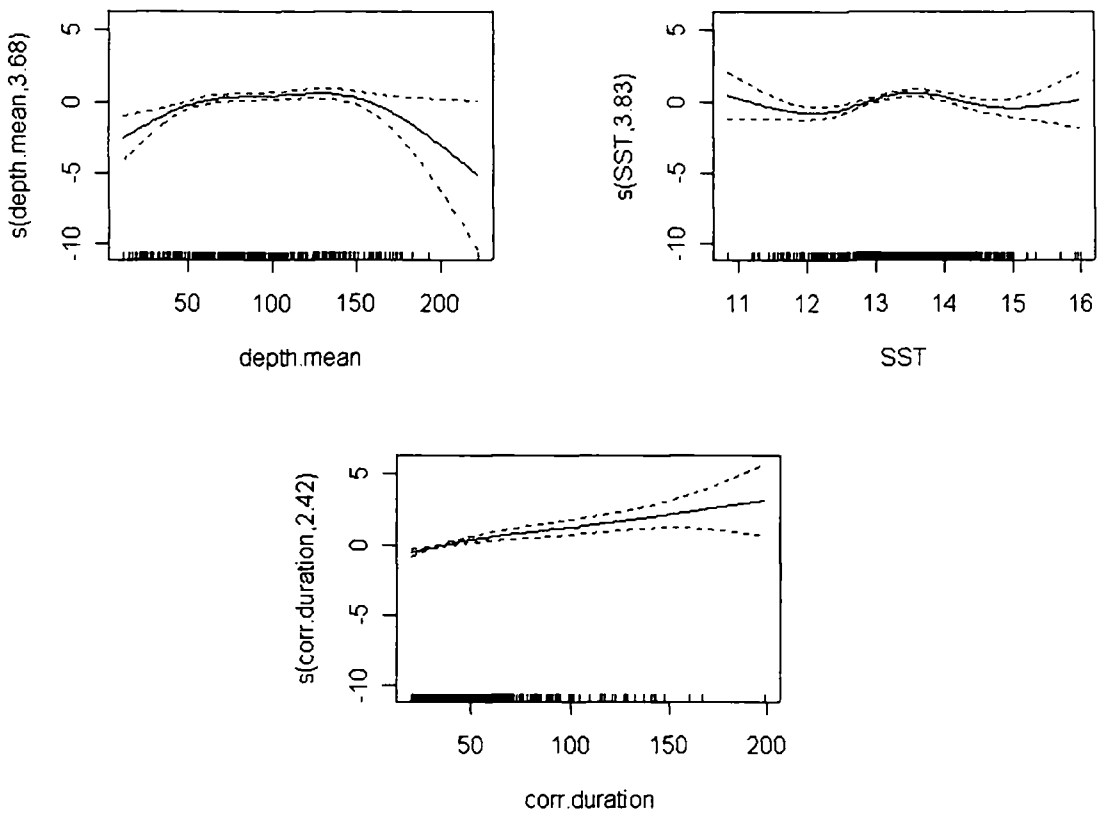


Figure 2.9, continued. GAM smoothing curves for significant parameters (after Bonferroni-correction) on the sighting rates (no. individuals / hour) per cell for the three seasonal models over the entire Hebrides. Broken lines represent 2-SE ranges around the main effects. The degrees of freedom for each smoothing curve are indicated on the y-axis. Vertical dashes on the x-axis represent the distribution of the explanatory variable.

B) SMALL ISLES

As in the models for the entire Hebrides, minke whale sighting rates did not show a significant relationship with the tidal factor 'spring vs. neap' around the Small Isles (Table 2.5), although it was retained in the August/September model for better fit. Another parallel amongst factors for the models covering the core study area vs. the whole of the Hebrides was the significantly lower sighting rates in September by comparison to the month of August (Table 2.5c), suggesting that this decreasing trend towards the end of the summer has applied throughout the region for most of the 15 years covered by this study. On the other hand, no difference was apparent between sighting rates for May and June for the area around the Small Isles, resulting in 'month' being excluded from the spring model (Table 2.5a). The factor 'year' was also irrelevant for spring, whereas it showed a highly significant effect on sighting rates during July and August/September (Tables 2.5b, c): significantly more whales were seen per unit effort in the month of July 2004 and 2007 by comparison to 2001 and 2005 (and to a lesser extent 2006). By contrast, there was a large and significant drop in sighting rates during August/September for the years 2005-07, compared to all the previous years included in the model since 1998 (Table 2.5c).

Correction terms were not significant in the May/June model (although the sea state corrected time spent per cell was retained for better fit), but they were for July and August/September. In July, a negative linear relationship was detected between minke whale sighting rates and km travelled per cell, when corrected for all other explanatory variables in the model (Table 2.5b, Figure 2.10b). This counter-intuitive result was caused by a combination of a) a number of encounters with relatively large groups of minke whales from *MV Sheerwater* in cells with low coverage (<1h), particularly in 2004; and b) consistent targeted effort in cells with particularly high whale densities around the entrance to the Sound of Sleat during the six days of fieldwork in July 2007 (Figure 2.7b). This resulted in high temporal coverage of cells with minke whales present, combined with small distances travelled, since the boat was either stationary or moving slowly in the presence of whales. For August/September, minke whale sighting rates showed a positive linear relationship with sea state corrected time spent per cell, again caused by targeted effort towards some high density areas during my own fieldwork (see distribution of time spent per cell in Figure 2.10c).

The smoothing curve for depth in July showed the same shape as for the same month in the model for the entire Hebrides, except that around the Small Isles, sighting

rates began to increase at slightly shallower depths of ca. 40m (compared to 50-60m for the whole region); both reached a plateau at around 100m (Figure 2.10b). For August/September, the shape of the depth curve was similar, but reached a peak at 70-80m, remaining level up to 100m (Figure 2.10c). This depth range coincides with the deep channel between Arisaig and the Isle of Eigg (Figure 2.4). Topography was only relevant in determining minke whale sighting rates during the month of July, with maximum slope showing a bell-shaped form around a peak of 15-17deg (Figure 2.10b).

Both temporally variable continuous parameters (SST and CHL) were highly important predictors of relative minke whale abundance. SST was the only significant variable in the May/June model, with whales showing a preference for water temperatures around 11°C (Table 2.5a, Figure 2.10a). This result was consistent with the June model for the entire Hebrides (Figure 2.9a), which showed a preference for temperatures around 11.5°C - 12°C. The slightly lower value for the Small Isles was probably caused by inclusion of the month of May (which was not covered in the wider Hebrides). By contrast to the entire Hebrides, however, SST was not significant in the Small Isles model for August/September. Instead, chlorophyll concentration (data for which had not been available for the earlier years of coverage) played a highly significant role in determining minke whale sighting rates during the later part of the season (Table 2.5c): numbers of whales per unit effort showed a steady increase from a chlorophyll-a concentration of 1mg/m^3 to a peak at 3mg/m^3, and a subsequent decline from ca. 3.5mg/m^3 onwards (Figure 2.10c). On the other hand, chlorophyll concentration was not a significant variable in determining minke whale sighting rates during May/June (when SST was important instead) or July.

The explanatory power of the three seasonal models was reversed for the Small Isles by comparison to the entire Hebrides. The spring model, with SST as the only significant variable, explained only 14.9% of the deviance (Table 2.5a), making it the poorest of all six models. On the other hand, both the July and August/September models performed better for the Small Isles than for the whole area, with 46.3% of the deviance explained for July and 41.6% for August/September, respectively (Table 2.5b, c).

Table 2.5. Summaries for GAM final models for Small Isles, based on 2min cells. * = significant after Bonferroni-correction.

a) May & June 2004 – 2007 (n=440):

Parametric coefficients:

	Estimate (± std. error)	p
Intercept:	-2.688 (± 0.211)	<0.001*

Smooth terms:

	edf	X^2	
s(SST):	2.71	11.942	0.006*
s(CHL):	1	0.395	0.530
s(sea state corr. duration):	2.47	2.385	0.396
s(mean depth):	3.17	6.627	0.096
s(max. slope):	1.50	1.211	0.414

Deviance explained: 14.9%
UBRE score: 0.059

b) July 2001 & 2004 – 2007 (n=305):

Parametric coefficients:

	Estimate (± std. error)	p
Intercept:	-2.954 (± 0.694)	<0.001*
Year 2004 (vs. 2001):	2.767 (± 0.696)	<0.001*
Year 2005 (vs. 2001):	-0.733 (± 1.116)	0.512
Year 2006 (vs. 2001):	1.716 (± 0.718)	0.017
Year 2007 (vs. 2001):	1.742 (± 0.699)	0.013*

Smooth terms:

	edf	X^2	
s(km.travelled):	1	7.391	0.007*
s(cell area):	3.51	8.157	0.065
s(mean depth):	2.28	29.879	<0.001*
s(max. slope):	2.43	16.497	<0.001*

Dispersion parameter: 2.712
Deviance explained: 46.3%
GCV score: 2.844

c) August - September 1998 – 1999, 2002 - 2007 (n=814):

Parametric coefficients:

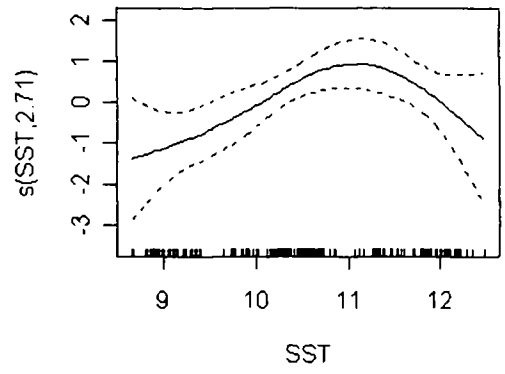
	Estimate (± std. error)	p
Intercept:	-0.035 (± 0.297)	0.905
September vs. August:	-0.772 (± 0.222)	0.001*
Year 1999 (vs. 1998):	1.017 (± 0.444)	0.022
Year 2002 (vs. 1998):	-0.045 (± 0.399)	0.911
Year 2003 (vs. 1998):	-0.209 (± 0.421)	0.619
Year 2004 (vs. 1998):	0.096 (± 0.301)	0.749
Year 2005 (vs. 1998):	-2.504 (± 0.575)	<0.001*
Year 2006 (vs. 1998):	-2.524 (± 0.510)	<0.001*
Year 2007 (vs. 1998):	-2.607 (± 0.684)	<0.001*
Spring tide vs. neap:	0.165 (± 0.143)	0.246

Smooth terms:

	edf	X^2	
s(SST):	1	0.768	0.381
s(CHL):	3.306	16.455	0.001*
s(sea state corr. duration):	1	11.859	0.001*
s(mean depth):	2.662	32.181	<0.001*
s(max. slope):	1	5.123	0.024

Dispersion parameter: 2.275
Deviance explained: 41.6%
GCV score: 2.329

a) May & June



b) July

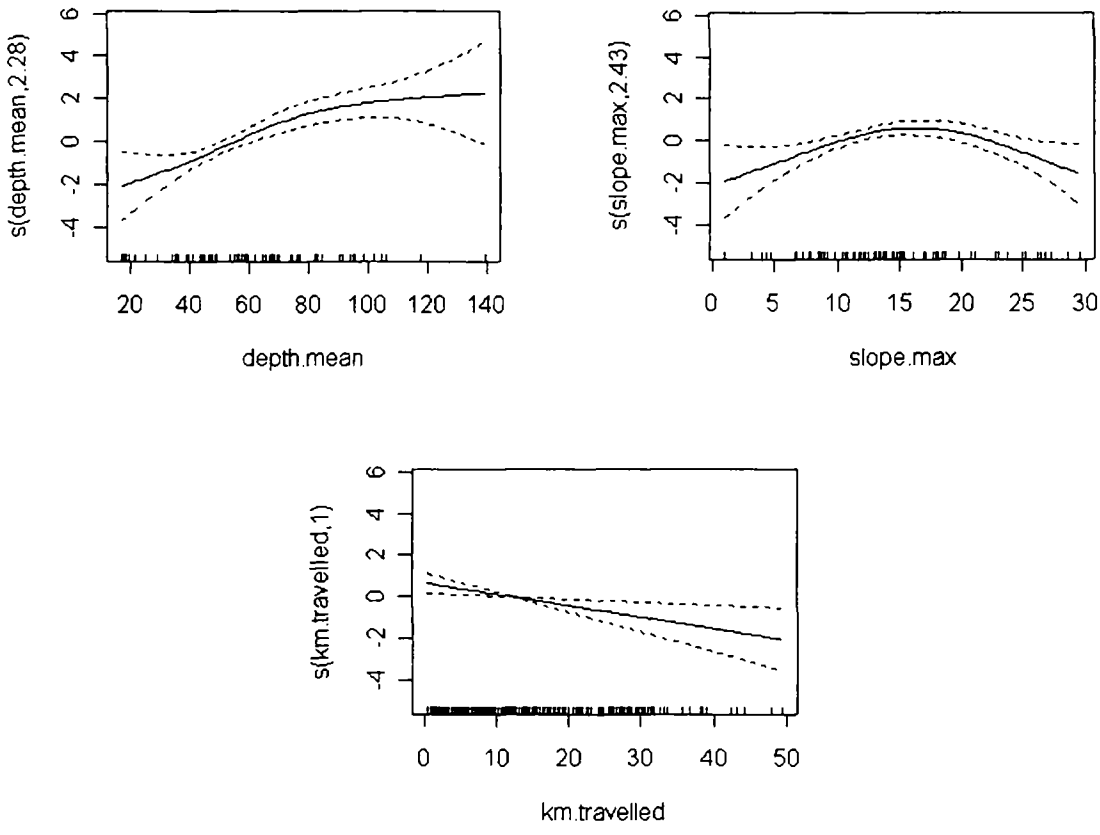


Figure 2.10. GAM smoothing curves for significant parameters (after Bonferroni-correction) on the sighting rates (no. individuals / hour) per cell for the three seasonal models around the Small Isles. Broken lines represent 2-SE ranges around the main effects. The degrees of freedom for each smoothing curve are indicated on the y-axis. Vertical dashes on the x-axis represent the distribution of the explanatory variable.

c) August & September

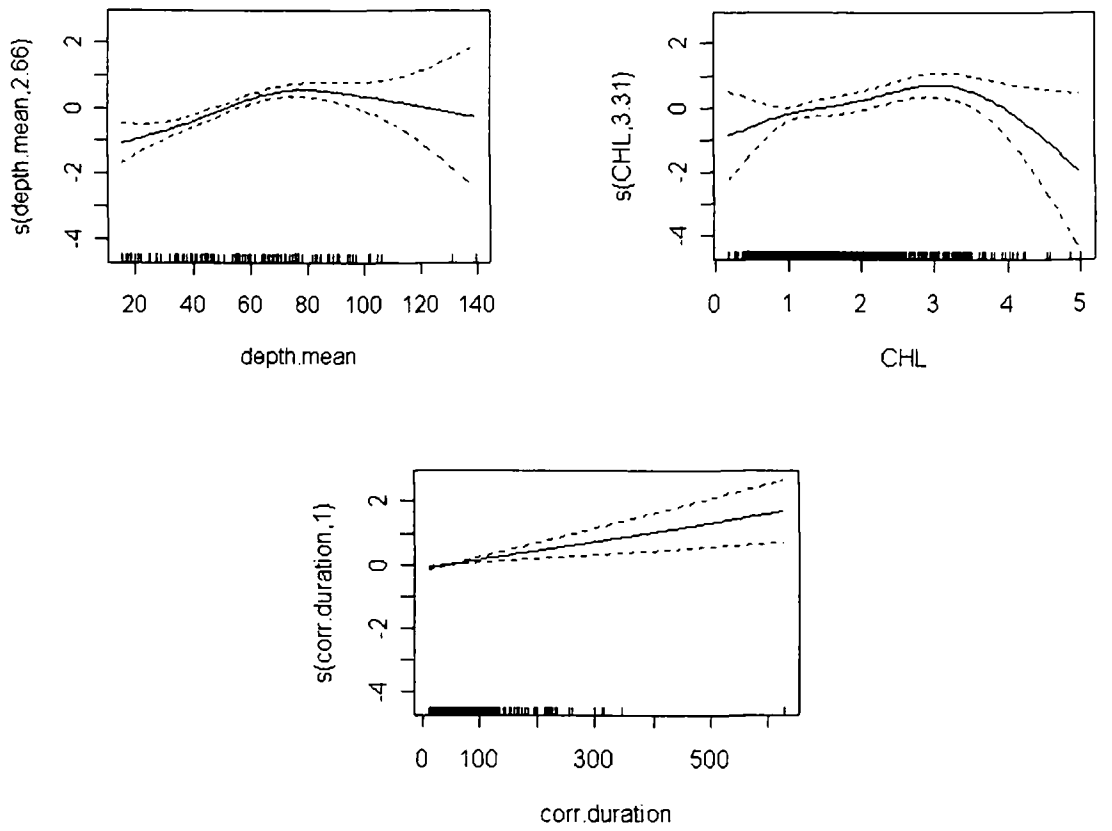


Figure 2.10, continued. GAM smoothing curves for significant parameters (after Bonferroni-correction) on the sighting rates (no. individuals / hour) per cell for the three seasonal models around the Small Isles. Broken lines represent 2-SE ranges around the main effects. The degrees of freedom for each smoothing curve are indicated on the y-axis. Vertical dashes on the x-axis represent the distribution of the explanatory variable.

Prey sampling

All samples of whole fish collected from feeding locations of minke whales and seabirds (one in 2003, consisting of five individuals; and two in 2004, consisting of three individuals) were identified by the relative position of the base of their ventral fins relative to the dorsal fin as sprat. The five individuals caught in 2003 were between 6.85cm and 7.5cm long; the three individuals caught in 2004 measured between 7.5cm and 8.5cm.

As expected, the scales of herring and sprat in the reference collection were very similar. However, some subtle differences could be detected, which together were sufficient to distinguish the two species reliably by the microscopic structure of their scales in the reference sample:

Scale shape: Although there was a small amount of overlap, the shape of the sprat scale was rounded or wider than its length (length : width ratio = 0.64–1.1), whereas the juvenile herring scale was either rounded or longer than its width (length : width ratio = 1.05–1.45).

Scale structure: The anterior part of the scale without growth layers was proportionately smaller in sprat than in juvenile herring. Although the ratio in length between the anterior part and the overall scale did not differ between the two species (sprat: 0.31 – 0.58, herring: 0.29–0.67), in sprat, this base was more embedded in the part of the scale containing growth layers, which resulted in a smaller ratio in width between the anterior part and the overall scale (0.44–0.85). In juvenile herring, it was approximately as wide as the part containing the growth layers (width ratio = 0.91–1). In sprat, the scales tended to become detached more easily, thus yielding a smoother anterior edge compared with herring, all specimens of which showed a ragged anterior edge to their scales. Taken together, these features gave the sprat scale a somewhat "neater" appearance than the juvenile herring scale (Figure 2.11).

The scales of adult herring were easily distinguishable from those of sprat. Besides the difference in size (4-7mm in length vs. 1.5-2mm in sprat), 90% of adult herring scales lacked the clear division line between the anterior part without and the posterior part with growth layers, which was present in both sprat and juvenile herring. Sandeel scales showed a very different structure from clupeid scales (Figure 2.11), and could therefore be excluded as a possibility for any of the prey samples.

Based on these criteria, all scale samples taken around the Small Isles in 2003 (August) and 2004 (August and September) were identified as sprat (Table 2.6, Figure 2.12), although the possibility of mixed shoals containing both sprat and juvenile herring cannot entirely be excluded.

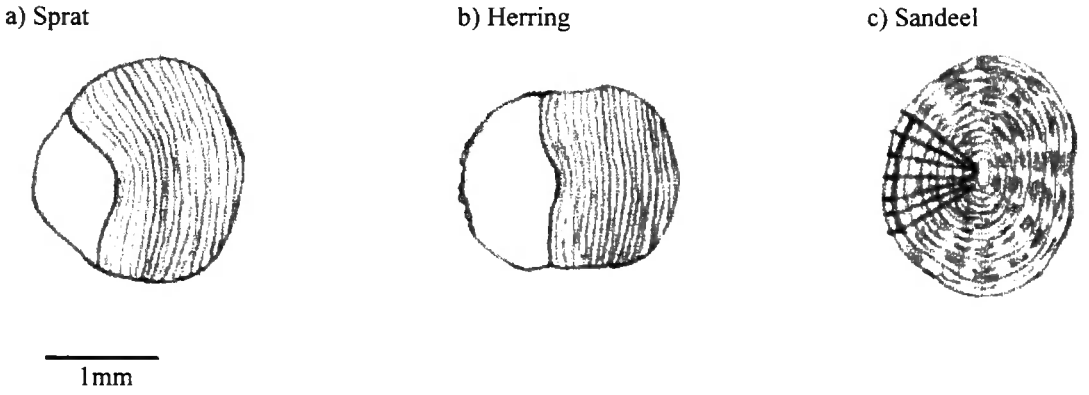


Figure 2.11. Schematic drawings of a) sprat, b) juvenile herring, and c) sandeel scales. The lines in a) and b) represent growth layers (reduced in number for these drawings), probably all within years. Year-rings could not be detected in these samples.

Table 2.6. Prey sample details. Presence of: MW = minke whale, HW = humpback whale, HP = harbour porpoise. AU = auks (dominated by common guillemots), KIT = kittiwakes, GU = *Larus* gulls (dominated by herring gulls), SG = shags, MS = Manx shearwaters, GAN = gannets.

Date	Time	Sample	Species	MW	HW	HP	seabirds
18.09.2001	08:10	whole fish	sprat				AU, GU
20.09.2001	14:45	whole fish	sprat	x			AU, KIT, GU
22.09.2001	17:39	whole fish	herring				AU, KIT, GU
04.08.2003	17:35	scales	sprat				GU, MS
05.08.2003	11:10	scales	sprat				AU, GU, SG, MS
06.08.2003	21:04	scales	sprat				AU, GU
10.08.2003	11:09	whole fish	sprat				AU, KIT, GU
11.08.2003	12:56	scales	sprat	x			-
11.08.2003	15:55	scales	sprat	x			-
11.08.2003	17:59	scales	sprat	x			AU, KIT, MS
11.08.2003	18:16	scales	sprat	x			-
11.08.2003	18:21	scales	sprat	x			AU,GU,GAN,MS
12.08.2003	10:51	scales	sprat	x			AU, GU
12.08.2003	12:25	scales	sprat				AU
12.08.2003	14:23	scales	sprat	x			AU, GU
12.08.2003	16:10	scales	sprat			x	AU, KIT, MS
14.08.2003	08:42	scales	sprat			x	AU,KIT,GU,MS
14.08.2003	15:53	scales	sprat				AU,KIT,GU,MS
15.08.2003	15:24	scales	sprat				AU, KIT, GU
15.08.2003	17:30	scales	sprat				AU,KIT,GU,MS
17.08.2004	15:16	scales	sprat	x	x		AU, KIT, GU
17.08.2004	15:59	whole fish	sprat	x			AU, KIT, GU
22.08.2004	11:06	scales	sprat	x			AU,KIT,GU,GAN
22.08.2004	11:20	scales	sprat	x			KIT, GU
06.09.2004	19:14	whole fish	sprat	x			AU, GU, MS
07.09.2004	16:57	scales	sprat	x			AU, KIT, MS

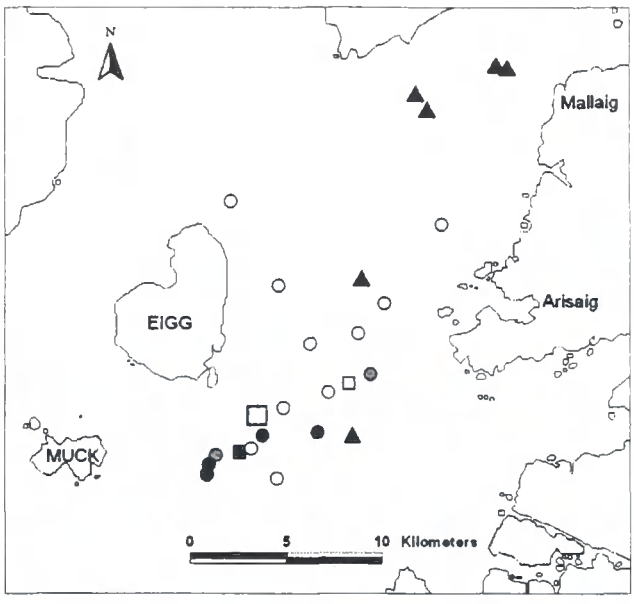


Figure 2.12. Prey sampling locations. Squares represent samples taken in 2001, circles in 2003, and triangles in 2004. Black = minke whale(s) & birds present; white = birds only, no whale; grey = minke whale only, no birds. The larger open square SSE of Eigg indicates the sample of juvenile herring taken in 2001. All other samples consisted of sprat.

Interannual changes in abundance and comparisons with other taxa

The habitat models for the Small Isles showed a steep decline in minke whale sighting rates for the years 2005-07 by comparison to earlier years. This decline was most pronounced during the month of August (by a factor of ≥10), when minke whale numbers had normally reached a peak in the area during previous years (see Tables 2.2 & 2.3). Figure 2.13 illustrates the interannual changes in overall monthly sighting rates from *MV Sheerwater* for the years 2002 (August only) to 2007. Sighting rates in spring were generally not a good indicator of minke whale abundance during summer and autumn, although the year 2005 proved to be poor for sightings in all months, whereas minke numbers in May showed a peak in 2004, along with sighting rates for July – September. During the years of 2006 and 2007, peak sighting rates occurred earlier in the year, i.e. in July instead of August, with a steep drop-off (by a factor of ≥3) for the remainder of the season (Figure 2.13).

Primary productivity: Amongst the two temporally variable parameters included in the Small Isles habitat model for August/September, primary productivity (expressed as

chlorophyll-a concentration) was found to play a significant role in determining minke whale sighting rates per cell, corrected for the other parameters including year. A comparison between interannual differences in overall minke whale sighting rates from *MV Sheerwater* in August and September (Figure 2.13) and average chlorophyll-a concentration along the survey route during the same months (Figure 2.14) indicated annual co-variation between relative minke whale abundance and primary productivity, although the relationship was only significant for August (Spearman's r=0.975, p=0.005; September: r=0.8, p=0.052, n=5). Chlorophyll-a plots for the whole study area (Appendix 2.1) show that the reduction in primary productivity during August and September 2005-07 was not a local phenomenon around the Small Isles, but applied to the entire Hebrides. Exceptionally low chlorophyll concentrations over the whole area were also apparent in May 2005 (Appendix 2.1).

Sprat landings: Following mainly high yields since the 1997/98 winter sprat fisheries season (except for 2001/02), landings data for the species for West Scotland indicated a decline in catches from the 2004/05 season onwards, with almost complete failures (<20t) each year since 2006/07 (Figure 2.15). With the exception of the 2004 season, this pattern paralleled the sharp decrease in relative minke whale abundance around the Small Isles during August and September 2005-07 by comparison to earlier years.

Basking sharks: Basking shark numbers around the Small Isles tend to be highest in June, whereas minke whale numbers peak later in the summer. A comparison between numbers of minke whales and basking sharks seen from *MV Sheerwater* per year showed no correlation (r=-0.3, p=0.624; Figure 2.16a). When only data for May and June were considered, the correlation coefficient increased, but the relationship was not significant (r=-0.718, p=0.172). Based on the limited number of years available (n=5), there was thus no clear correlation between numbers of minke whales and basking sharks in the study area around the Small Isles (Figure 2.16b), although basking sharks were the only taxon to show a negative correlation coefficient in comparisons with numbers of minke whales.

Seabird breeding success: Positive, although non-significant, correlations were found between overall minke whale sighting rates around the Small Isles during summer (July-September) and seabird breeding success at the local colonies, as well as at the distant larger colonies on Handa Island (Figure 2.17; Canna kittiwakes: r=0.8, p=0.104; Rhum

Manx shearwaters: r=0.6, p=0.285; Handa kittiwakes: r=0.667, p=0.219; Handa common guillemots: r=0.6, p=0.285). Although the correlations were not linear, years of good breeding success for common guillemots, kittiwakes and Manx shearwaters in spring coincided with years of high sighting rates of minke whales during summer (2003-04), whereas 2005-07 were poor years for both taxa (Figure 2.17). This relationship between breeding success and relative minke whale abundance around the Small Isles not only applied to the local kittiwake and guillemot colonies on Canna (Figures 2.17b, c), but also to distant Handa Island, ca. 160km to the north (Figures 2.17e, f).

Seabird counts at sea: Minke whale sighting rates during fieldwork 2003-07 showed a positive relationship with average group sizes of auks (r=0.9, p=0.037), kittiwakes (r=0.8, p=0.104) and *Larus* gulls (r=0.8, p=0.104) counted at sea during the same time, whereas no correlation was found with group sizes of Manx shearwaters (r=-0.1, p=0.873; Figure 2.18). While Manx shearwaters showed a steady increase in numbers between 2003 and 2007 (Figure 2.18e), average kittiwake (Figure 2.18c) and *Larus* gull (Figure 2.18d) group sizes were close to zero during the fieldwork seasons of 2005-07. Yearly average auk group sizes (Figure 2.18b) followed the same pattern as overall minke whale sighting rates during the period 2003-07 (Figure 2.18a) and were thus the only seabird taxon whose numbers showed a significant correlation (although not Bonferroni-corrected) with minke whale sighting rates, given the low sample size of n=5.

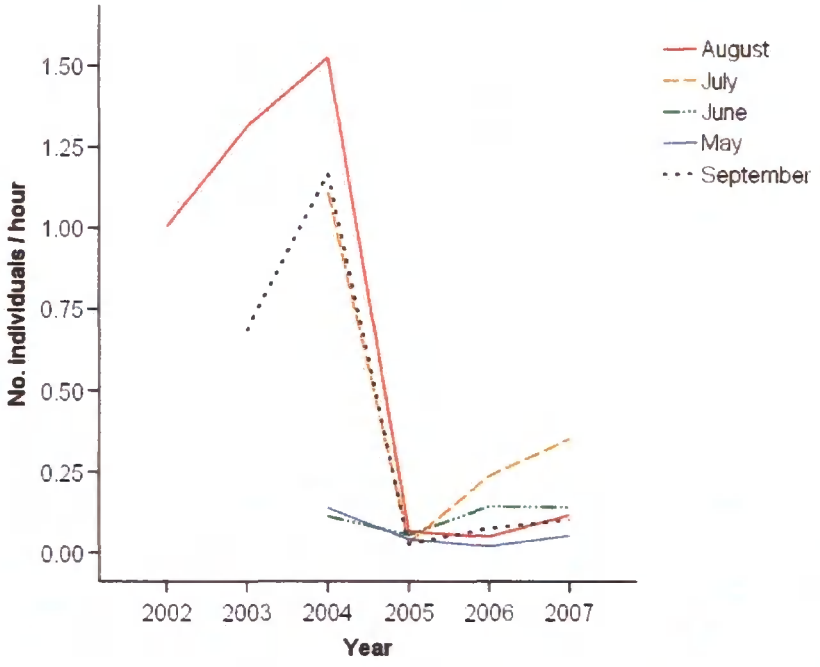


Figure 2.13. Changes in yearly minke whale sighting rates (as number of individuals per hour) from *MV Sheerwater* around the Small Isles.

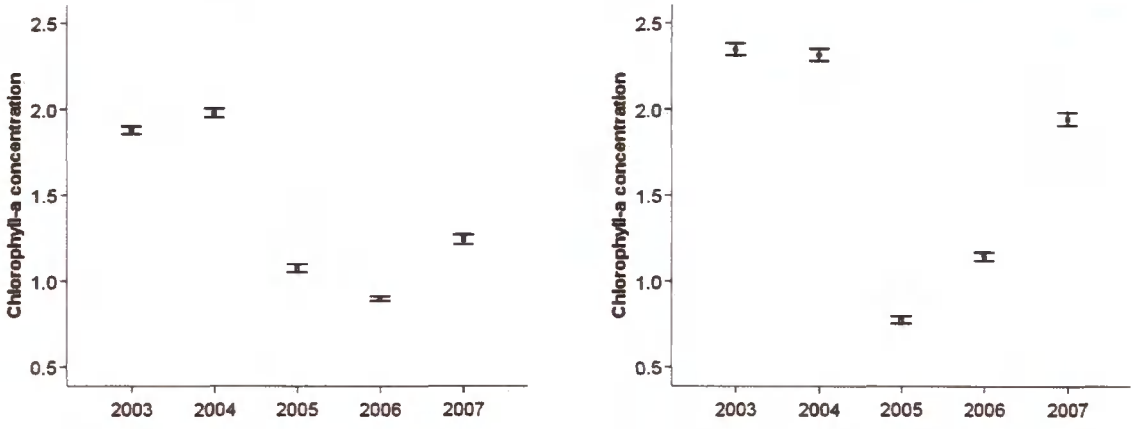


Figure 2.14. Average chlorophyll-a concentration / min (mg/m^3; ± 95% CI) along the route of *MV Sheerwater* for August and September 2003-07.

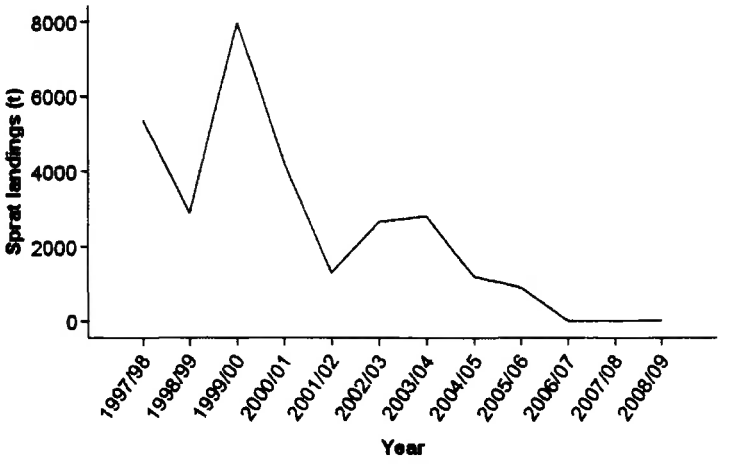


Figure 2.15. Sprat landings on the west coast of Scotland between September and March 1997/98 – 2008/09. Fishing effort in most years was concentrated between October and December.

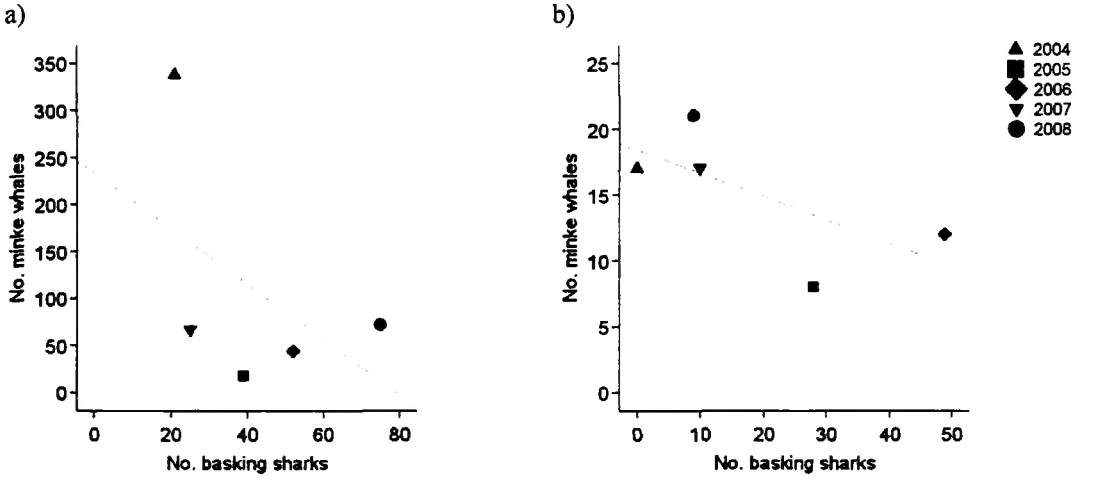
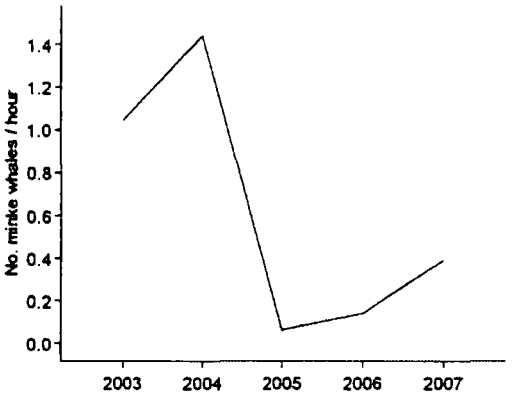
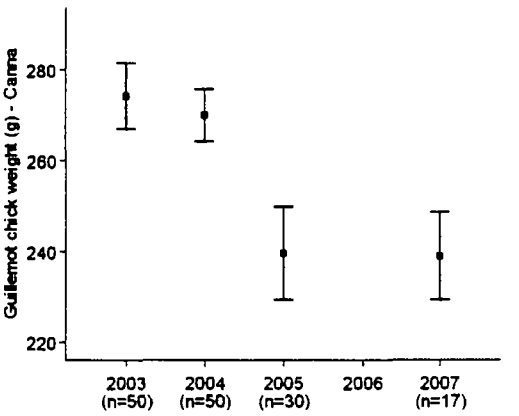


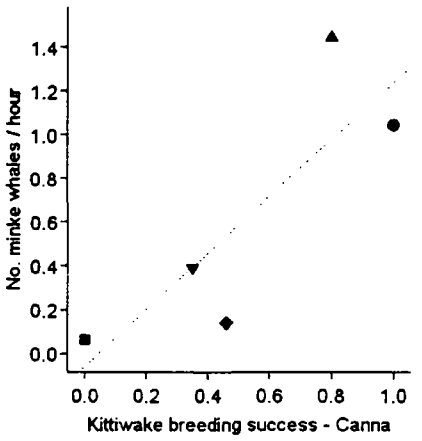
Figure 2.16. Comparison of total number of minke whales and basking sharks seen from *MV Sheerwater* 2004-08, a) per year (May-September), and b) in spring (May – June) only.



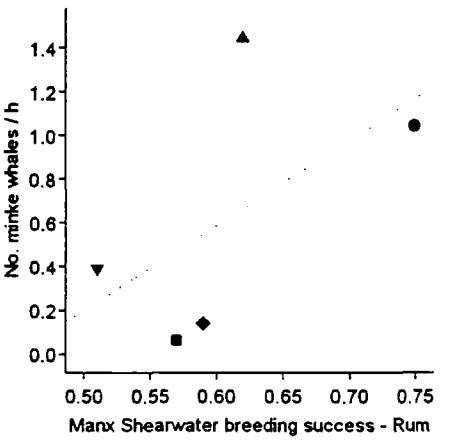
a) Small Isles - Minke whale sighting rates



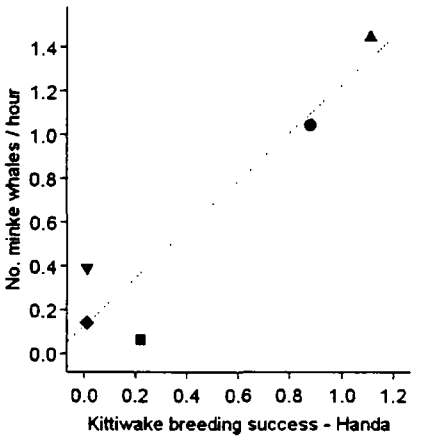
b) Canna - Guillemots (chick weights)



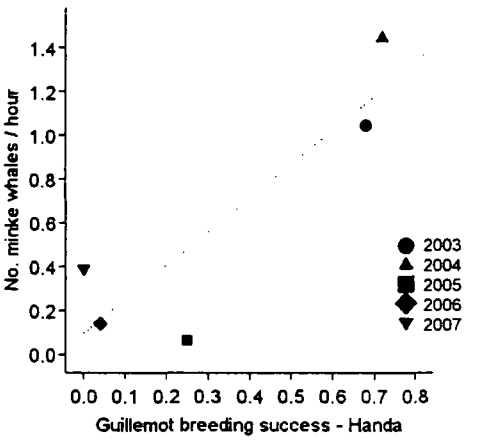
c) Canna - Kittiwakes



d) Rhum - Manx Shearwaters

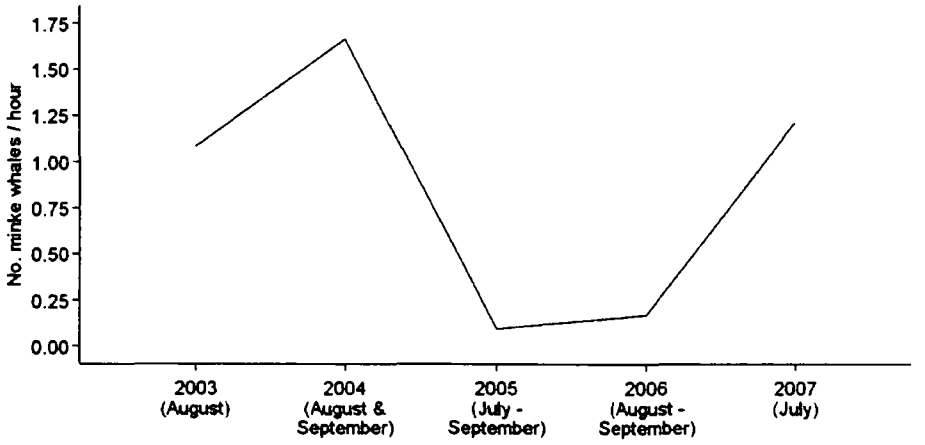


e) Handa - Kittiwakes

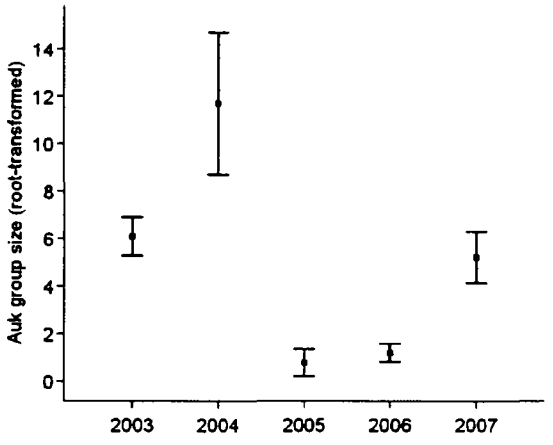


f) Handa – Guillemots

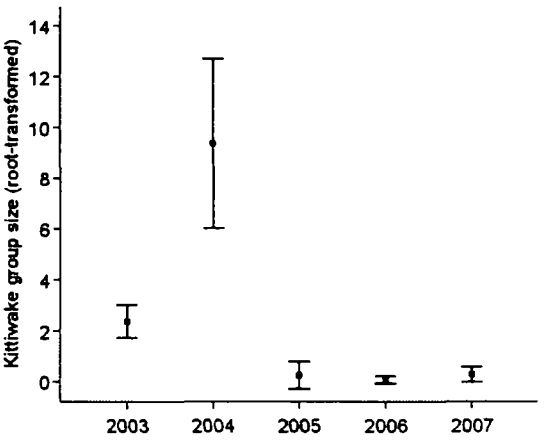
Figure 2.17. Overall minke whale sighting rates (a; as number of individuals per hour) around Small Isles from *MV Sheerwater* and own fieldwork during July – September (August – September for 2003), compared to breeding success of seabirds (b–f) on neighbouring Canna and Rhum, as well as distant Handa Island (ca. 160km to the north). Yearly breeding success of common guillemots on Canna in b) is expressed as weights of chicks with a wing span of at least 60cm (data kindly provided by R.L. Swann; no data are available for 2006). Breeding success for kittiwakes on x-axes in c) and e) is expressed as numbers of chicks fledged per apparently occupied nest; for Manx shearwaters in d) as young fledged per burrow with egg; and for guillemots on Handa Island as mean number of young per active and regular site (JNCC Seabird Monitoring Programme).



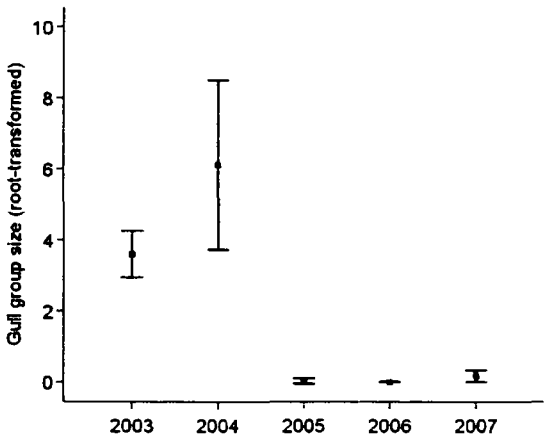
a) Minke whale sighting rates



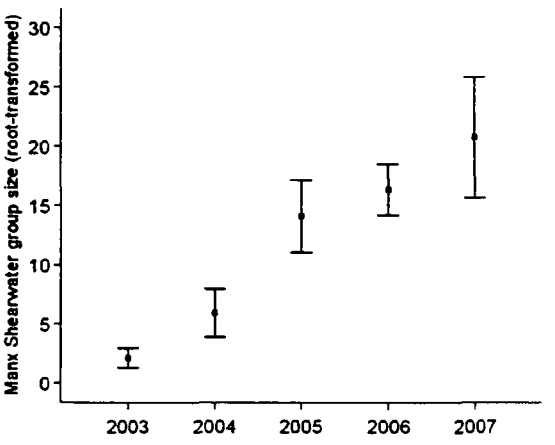
b) Auk group sizes



c) Kittiwake group sizes



d) Gull group sizes



e) Manx Shearwater group sizes

Figure 2.18. Overall yearly minke whale sighting rates (as number of individuals per hour) during fieldwork seasons 2003-07 (excluding sightings from *MV Sheerwater*), compared to average group sizes (root-transformed) of four seabird guilds counted at sea from the same boat around the Small Isles during the same time periods. Auks = common guillemot (76.9%), razorbill (23%) and puffin (0.1%); Gulls = herring gull (92.3%), greater (7.1%) and lesser black-backed gull (0.6%). Numbers of bird groups counted: 2003: n=137; 2004: n=45; 2005: n=27; 2006: n=68; and 2007: n=51.

DISCUSSION

The aim of this study was to relate minke whale distribution on the west coast of Scotland to relevant physical and biological characteristics of their habitat, both over the entire Hebrides and in a smaller core study area, in order to shed some light on recent observed changes in the relative abundance of the animals. The findings indicate that the distribution of whales is influenced by a number of different environmental variables, both fixed and temporally variable, but that their relative importance changes through the season.

Amongst the fixed physical parameters (depth and topography), depth was the more important in determining minke whale distribution during July and August/September at both spatial scales. During July, sighting rates increased with water depth from 40-50m to 100-120m, whereas in August/September a plateau was reached from ca. 70m on. These results were consistent between the 2min cells for the core study area around the Small Isles and the 4min cells over the entire Hebrides, covering an earlier study period. Depth did not play an important role in habitat choice during spring, but was replaced by slope for the 4min cells during June. Where significant relationships were found between minke whale sighting rates and slope, the animals preferred areas of intermediate topography at both spatial scales. All models during all parts of the season and at both spatial scales failed to detect any relationship between minke whale sighting rates and any of the tidal parameters. This result was somewhat surprising, especially for the area around the Small Isles, for which high resolution tidal data had been incorporated in the models. It also appears to be in contradiction to the general view that minke whales are associated with tidally active areas (Evans, 1990; Johnston *et al.*, 2005; Ingram *et al.*, 2007). However, given the extreme variations in current strength in one and the same location throughout the tidal cycle, it would be expected that this parameter is more likely to influence minke whale behaviour in a particular area rather than their overall distribution itself (see Chapter 3). Where relationships between cetacean distribution and tidal current are found, it is not necessarily the current strength itself which makes an area important, but its interaction with bathymetric features which in combination have the potential to concentrate prey (Simard *et al.*, 2001). An apparent preference for deeper areas by the whales during July and August/September may be linked to greater efficiency in catching prey. It is possible that small shoaling fish become more

concentrated in deeper areas, depending on the currents. The deep channels around the Point of Sleat and between Arisaig and the Isle of Eigg in the core study area (Figures 2.1, 2.4) might have the potential for concentrating small fish along them. The largest seabird feeding aggregations encountered during the study period were concentrated generally along these channels (Figure 3.17; Chapter 3), and the deep area between Arisaig and the Isle of Eigg consistently showed some of the highest probabilities of whale encounters (Figure 2.7).

Amongst the temporally variable parameters (SST and chlorophyll concentration, which showed no co-linearity ($r<0.3$)), SST was particularly important in spring, with highest minke sighting rates occurring around the higher temperature ranges of 11-12°C. This relationship was also highly consistent between the model for the entire Hebrides and the one for the Small Isles when the inclusion of May (with lower SST values) in the latter was taken into account. While a preference for intermediate temperature ranges (13-14°C) was detected for the entire study area during August/September, this effect was replaced by the importance of chlorophyll concentration for the model around the Small Isles during this part of the season (chlorophyll concentration could not be included in the models over the whole study area as such data did not exist for all of the study period).

Despite the differences in spatial scale (4min vs. 2min), coverage (large area with relatively little temporal coverage, and Small Isles with extensive temporal coverage) and study period (large area 1993-2002; Small Isles 1998-2007, but mainly 2003-07), the GAM results for each part of the season were surprisingly consistent between the entire Hebrides and the core study area around the Small Isles. This suggests general applicability of the findings on minke whale habitat use within a comparatively small, but high-density area for the species to the entire west coast of Scotland, and over an extended time period (15 years).

Based on sightings data collected from a whale-watch operation on the Isle of Mull, Leaper *et al.* (1997) and Macleod *et al.* (2004) detected a general northward movement of minke whales from the Ardnamurchan / Coll area in spring to the region around the Small Isles in August and September, which coincided with a peak in seasonal abundance. This pattern was consistent between years and was associated with a change in minke habitat preferences with respect to seabed sediment type and water depth: during spring, whales were associated predominantly with depths of <60m in areas of gravelly sand type sediment, whereas their distribution during summer and autumn was more widespread,

and deeper waters were preferred (the latter of which is consistent with the present results). Macleod *et al.* (2004) attributed these changes in habitat preferences through the season to a switch in diet from sandeel during spring to pre-spawning herring in autumn by overlaying minke whale distributions with maps of likely sandeel and herring occurrence, based on habitat information from the literature. However, direct data on diet were not available for the region. The results from the present study support both the increase in minke numbers around the Small Isles and the hypothesis of a change in diet between early and late season, based on the changes in relative importance of the different explanatory variables between the three seasonal models. However, Macleod *et al.*'s (2004) inference of pre-spawning herring being the main prey during August and September appears to be incorrect, at least for the area around the Small Isles in 2003 and 2004: all prey samples taken in August and September of these two years consisted of sprat, upon which both whales and seabirds were feeding. During summer and autumn, the great majority of minke whale surface feeding activity in the area occurs in the presence of multi-species flocks of seabirds apparently taking the same prey as the whales (auks, kittiwakes, *Larus* gulls and Manx shearwaters; see Chapter 3). Pre-spawning (i.e. adult) herring would be too large for any of these bird species to catch, and scales compatible with the size of adult herring were never found in either whale or seabird feeding locations. Juvenile herring were sampled once as seabird prey in 2001, but sprat appeared to be the dominant prey for both minke whales and birds around the Small Isles during August and September 2003 and 2004.

On the other hand, Macleod *et al.*'s (2004) hypothesis of sandeels being the most important prey item for the whales during spring was strongly supported by the GAM results in this study. The qualitative seabed sediment type categories, upon which sandeel presence was inferred in their study, were substituted by the results of a GAM for probability of sandeel occurrence (based on sandeel density information from trawls vs. silt and gravel content of the seafloor sediment) in the present analysis, in order to incorporate more quantitative information on actual likelihood of sandeel presence. Over the whole of the Hebrides during June 1995 and 2000, sighting rates of minke whales were significantly higher in 4min cells with probable or very likely sandeel occurrence by comparison to cells where sandeel presence was unlikely. By contrast, this relationship did not apply later in the season (during July or August/September), suggesting that sandeels are important in minke whale diet only during spring, as suggested by Macleod *et al.* (2004). This result was further supported by the important contribution of SST

towards explaining relative minke whale abundance during spring, both for the Small Isles (where it was the only significant parameter for May/June) and the entire Hebrides. Minke whale sighting rates showed a peak towards the higher end of the spring temperature scale at around 11-12°C. Winslade (1974) demonstrated in laboratory experiments that swimming activity of sandeels increased with temperature (5°C < 10°C < 15°C), thus making them more readily available to predators at higher temperatures than when the fish are inactive and buried in the sand. After July, sandeels enter their overwintering stage, during which they bury in the sand again and become unavailable to the whales. The observed temperature preferences of minke whales during spring would therefore be consistent with those water temperatures in which sandeels are more active during this time of year, even when allowing for the fact that sea surface temperature (as measured here) is somewhat higher than seafloor temperature (relevant for sandeel activity), if the water is stratified. Around the Dogger Bank in the North Sea, average differences between surface and seafloor temperatures up to ca. 60m depth were mostly below 0.5°C, and the greatest difference between seafloor temperatures at depths of 10-60m during spring was <3°C (van der Kooij *et al.*, 2008). The highest likelihood of sandeel presence in their study occurred at bottom temperatures of 8.5-9.5°C. This range is 2.5°C below the preferred surface temperatures found for minke whales in the Hebrides and thus is largely consistent with the present results, allowing for a water temperature difference between surface and seafloor greater than van der Kooij *et al.*'s (2008) average measurements. A positive correlation between minke whale sighting rates and water temperature was also found in the Moray Firth on the east coast of Scotland (Tetley *et al.*, 2008), where one of the main prey for the animals appears to be sandeel (Pierce *et al.*, 2004). In the Moray Firth study, temperature was interpreted as having a positive effect on sandeel and thus minke whale feeding conditions through the increase in phytoplankton (and thus zooplankton) concentration at higher temperatures. Around the Small Isles, however, temperature was found to be more relevant in determining minke whale sighting rates in spring than chlorophyll concentration itself, and the relative importance of the two parameters was reversed in August/September.

A recent dietary study of common guillemots on the west coast of Scotland during the breeding season (Anderson, 2008) identified sandeels as the main prey being fed to chicks at some of the major auk colonies: Handa (100%), Lunga (100%) and Colonsay (99%). Given the current importance of this species to seabirds in spring, it is not surprising that it also appears to be the main prey for minke whales at this time of year.

Since sandeel presence is unlikely over most of the core study area around the Small Isles (Figure 2.3d), this could explain the low numbers of minke whale sightings in this region during spring, followed by a movement into the area only later on, when the whales appear to be feeding mainly on sprat. Indeed, the model for May/June for the Small Isles explained only 14.9% of the deviance (making it the poorest model of all), by comparison to 64.2% of the deviance explained for the entire Hebrides, which included the likelihood of sandeel presence as an explanatory variable. It is possible that minke whales can use water temperature to assess where and when an area is likely to be productive for sandeels in the water column, which would explain why the relative abundance of minkes around the Small Isles in spring seemed to be dictated entirely by SST.

The same seasonal changes in distribution with respect to sandeel occurrence as identified here for minke whales have been found for common guillemots across Scotland (Wright & Begg, 1997). The spatial parameter 'sandeel presence' had a significant effect in a GAM on guillemot distribution, but only during the breeding season (April – June) and not at other times of the year. It is notable that during the 1990s and early 2000s, guillemot chick diet on Canna (one of the Small Isles, where longterm seabird breeding studies have been conducted) consisted mostly of sprat (ca. 50%), with sandeels (ca. 25%) and gadoids (ca. 25%) being of comparatively less importance (Swann *et al.*, 2008). Assuming that guillemots forage in the vicinity of their colony and take sprat and sandeels in proportion to their relative availability, this could be interpreted as a further indication that the Small Isles are more important habitat for sprat than for sandeels. Both fish species have high calorific content (Hislop *et al.*, 1991), so that guillemots tied to their colony on Canna during the breeding season would not be expected to show a preference for either, but would take whichever is more abundant in close proximity to the colony. However, if sandeels show an overall higher (and more predictable) abundance than sprat in most other areas within the Hebrides during spring, it would make sense for the more freely mobile whales to seek locations with high likelihood of sandeel occurrence and presumably higher overall prey densities than around the Small Isles at this time of year. Sprat concentrations, on the other hand, probably build up throughout the study area during the summer, before the fish aggregate into their overwintering concentrations in coastal waters in October and November, during which time they cease feeding (Lee & Ramster, 1981). Both whales and seabirds would therefore be expected to profit from this energy rich food source, available in high concentrations in the study area during late summer and early autumn. A dependence on

sprat in August/September would also explain the significant effect of phytoplankton concentration in the GAM for the area around the Small Isles that occurred precisely during this part of the season. Since late summer and early autumn appear to be a crucial time for sprat to increase their fat reserves before the winter fast, it would make sense for them to aggregate in areas of high phytoplankton and thus presumably high copepod abundance.

Minke whale sighting rates increased with chlorophyll concentration up to $3mg/m^3$. This is at the very high end of concentrations reported for most of the study area during summer by Edwards & John (1997), apart from exceptionally large blooms in some sea lochs. The decrease in sighting rates indicated by the smoothing curve for concentrations above 3.5-4 mg/m^3 may be an indication that these high values were caused by suspended sediments rather than actual chlorophyll concentrations (see Methods).

The relationship between minke whale sighting rates and chlorophyll concentration was corrected for year and month in the GAM (both remained highly significant factors in the model), and therefore incorporated the spatial effect of the parameter. Further examination specifically of interannual changes revealed a highly significant co-variation between relative minke whale abundance and chlorophyll concentration within the core study area around the Small Isles for the month of August. Compared to 2003 and 2004, phytoplankton concentration over the whole of the Hebrides was greatly reduced during August and September of 2005-07 (Appendix 2.1). Although a decline in winter sprat landings was already noticeable in the 2004/05 season (the causes for which are unknown), complete failures in the fisheries have only occurred since 2006/07 (Figure 2.15). Low primary (and thus presumably secondary) productivity throughout the Hebrides during late summer since 2005 might have resulted in low food availability for sprat at the crucial time of year before the onset of their winter fast, and thus poorer body condition of adults, possibly resulting in low winter survival and/or subsequent egg production. This might have contributed to recruitment failures for the species since 2005, and thus a further decline. In turn, minke whales, guillemots, kittiwakes and *Larus* gulls were almost absent from the study area during the fieldwork seasons of August and September 2005-06 (Figure 2.18; fieldwork in 2007 took place only in July, so no data on seabird numbers at sea are available for August/September of that year). In parallel to the failures in the sprat fisheries (Figure 2.15), minke whale numbers around the Small Isles have also reached their peaks earlier in the season (in

July) since 2006, with a steep decline in sighting rates during August and September (Figure 2.13), when they are thought to be feeding mainly on sprat. This trend continued into the season of 2008 (based on *MV Sheerwater* data), along with the continued failure in the sprat fisheries during winter of the same year. These patterns further highlight the apparent importance of sprat to both minke whales and seabirds in the study area during the months of August and September.

The steep declines in minke whale numbers during the summers of 2005 and 2006 were observed not only around the Small Isles, but were reported over the entire Hebrides by whale-watch operations from Mull (see Stevick, 2007; B. & R. Fairbairns, *personal communication*) to Gairloch (I. Birks, *personal communication*). Given that the decrease in chlorophyll concentration applied to the whole area, these large-scale parallels with both sprat landings and relative minke abundance would thus be expected if there is indeed a direct link.

Amongst the seabird groups counted at sea simultaneously to minke whale observations from 2003-07, auk numbers showed the strongest (and only significant) correlation with interannual sighting rates of minke whales around the Small Isles. Although the sharp decline in numbers between 2003/04 and 2005/06 also applied to kittiwakes and *Larus* gulls, in contrast to minke whales and auks, numbers of these taxa remained very low during the fieldwork season of July 2007. This was probably due to a combination of two reasons: a) both kittiwakes and the larger gulls depend on the availability of sufficient concentrations of small fish close to the surface and are therefore more sensitive to changes in overall prey concentrations, whereas auks can dive for fish; b) in years of low prey availability, kittiwakes and larger gulls can leave the area of the colony immediately after the breeding season in search of more productive regions, whereas guillemots and razorbills (at least the fathers) leading their flightless chicks, remain tied to the general area in the vicinity of the breeding colony.

The notable exception for observed changes in seabird numbers at sea during the summer was the Manx shearwater. In sharp contrast to minke whale, auk, kittiwake and *Larus* gull numbers all collapsing between 2004 and 2005, shearwater numbers at sea showed a steady increase between 2003 and 2007. This was also consistent with numbers of adults counted at the colony on Rhum (JNCC Seabird Monitoring Programme), but not with their breeding success. High recruitment of young from previous, successful breeding seasons may have caused the increase in numbers of adults at the colony and

surrounding waters. However, their breeding success generally showed the same overall pattern as for the other seabirds, i.e. a sharp decline in 2005-07 (Figure 2.17).

Since breeding success of kittiwakes and guillemots is determined by feeding conditions during spring and early summer, the widespread failures in 2005-07 cannot be attributed to the low phytoplankton concentrations during August and September in those years, even though they also coincided with low minke numbers during summer. The parallels between good and poor years of seabird breeding success and minke whale numbers during summer and autumn must therefore at least in part be related to processes affecting the entire season from May to September.

It is clear from Figure 2.13 that in 2005, minke whale sighting rates around the Small Isles were exceptionally low not only during August and September, but also from May to July, whereas all other years showed higher variability between months. Although no overall relationship was found between minke whale sighting rates and chlorophyll concentration during spring, Appendix 2.1 shows exceptionally low phytoplankton concentrations during May 2005, suggesting that the spring bloom, upon which feeding conditions for fish, seabirds and cetaceans depend, failed that year. These low phytoplankton concentrations measured in May persisted for the entire season of 2005. The coincidence of low sighting rates of minke whales in August and September with years of low breeding success of kittiwakes and guillemots in spring may thus be explained by a combination of both the extent of the spring phytoplankton bloom and the weather conditions during summer: high concentrations of phytoplankton can only form or be maintained during extended periods (i.e. several days) of calm, sunny conditions following periods of vertical mixing of the water column through tides and / or wind force (Pingree *et al.*, 1968). Although the spring bloom is a pre-condition for favourable feeding conditions later on in summer, sunny and calm periods are still necessary at this time for high primary productivity. Indeed, the fieldwork seasons during August and early September of both 2005 and 2006 conspicuously lacked such periods, with wet and windy conditions predominating. By contrast, August 2003, August and beginning of September 2004, as well as July 2007, all included calm and sunny spells persisting for several days, and this coincided with high numbers of whales in the area.

In the two years of lowest minke whale abundance in the Hebrides (i.e. the summers of 2005 and 2006), unusually large numbers of animals were reported from the Pentland Firth off the north coast of Scotland during June and July (Sea Watch Foundation, *unpubl.*

data), suggesting the possibility that whales from the west coast might at least temporarily have moved further north to find better feeding conditions there.

Although a period of only five years is too short to adequately assess relationships of relative abundance involving three trophic levels, the present study fell within a time period of substantial interannual changes in the abundance of two of the top predator taxa along the west coast of Scotland - minke whales and a number of seabird species. Despite little or no information on zooplankton or the fish stocks most relevant to these taxa in the area, minke whale habitat models, combined with interspecific comparisons of relative abundance, have provided insights into plausible interactions between the different trophic levels. The most important mechanism to affect numbers of minke whales and seabirds in the study area appears to be bottom-up control of planktivorous fish through the environmental effects upon phytoplankton and thus zooplankton concentrations. Data collection on minke whales, basking sharks and seabird breeding success around the Small Isles continues, and with an increasing length of time series available, both the trophic relationships and the possible reasons for changes in relative abundance of both whales and seabirds in this area should become clearer.

CHAPTER 3:

BEHAVIOURAL ASPECTS OF MINKE WHALE FORAGING AROUND THE SMALL ISLES, WEST SCOTLAND

INTRODUCTION

According to optimal foraging theory, an animal should maximize its energy gain per unit time (MacArthur & Pianka, 1966; Emlen, 1966; Stephens & Krebs, 1986). For organisms undergoing seasonal migrations between spatially separated breeding and feeding habitats, opportunities for food intake and stocking up on fat reserves are concentrated within a limited time period, followed by migration and reproduction, during which feeding is greatly reduced or in some cases may cease altogether. The survival of these migratory animals will therefore depend crucially on optimizing their feeding efficiency while in a suitable habitat, even more so than for organisms which are able to feed throughout the year. Besides physiological adaptations, it would be expected that organisms with such a life cycle also adjust their foraging behaviour adaptively to maximize energy gain within a short space of time. A wide range of behavioural adaptations to optimize feeding efficiency are plausible. These may include interannual site fidelity to a particular feeding ground that has a predictable food source, associated with learning how to exploit local conditions for finding prey. Depending on the local abundance and predictability of resources, it may pay to either specialize on the most energy-rich food or that which can be handled most efficiently, or to be more generalist and opportunistically take a variety of prey. Adaptation to a particular feeding ground and / or prey species can in turn lead to the evolution of differential foraging techniques

within species. Besides increasing the feeding efficiency of individuals, these may also serve in partitioning local resources and thus reduce intra-specific competition.

Amongst animals undergoing seasonal migrations between feeding and breeding grounds involving periods of fasting or reduced food intake, the best-known examples are a large number of pelagic marine fish (e.g. mackerel, herring, cod, bass, etc.) and most species of baleen whales. Surface-feeding baleen whales are well suited as subjects for study with respect to behavioural adaptations to optimal foraging on the summer feeding grounds, particularly those species in which individuals can readily be identified. The best example is probably the humpback whale due to easy and reliable individual identification by fluke photographs (Katona & Whitehead, 1981). Although minke whales are less well marked than humpbacks, a number of individuals can be identified by marks on their dorsal fins or backs, and they commonly engage in conspicuous surface feeding activity. This enables direct observation of feeding events, as well as prey sampling from the surface (see Chapter 2). Although the winter distribution and extent of seasonal migrations in minke whales is poorly understood, the species appears to follow the same pattern as most other baleen whales, with feeding activity concentrated mainly during the summer months (April – October) in temperate to sub-arctic regions (Stewart & Leatherwood, 1985; Perrin & Brownell, 2002).

The aim of this chapter is to investigate some behavioural aspects of minke whale feeding ecology within a local summer feeding ground. I will concentrate on site fidelity and foraging strategies involving interactions with both biotic and abiotic factors of the local environment within my study area around the Small Isles, which is part of the species' summer feeding ground extending along the entire west coast of Scotland.

Site fidelity

If resources are predictable within a localized area, individual minke whales would be expected to show a high degree of interannual and seasonal site fidelity to a particular summer feeding ground. On the other hand, unpredictability in spatial prey distribution would be expected to result in a large home range over the course of the summer and little site fidelity between years.

Minke whales can be individually identified by naturally occurring markings on the dorsal fin and back using photo-identification techniques (Dorsey, 1983; Dorsey *et al.*, 1990; Joyce and Dorsey, 1990; Stern *et al.*, 1990; Gill *et al.*, 1995), and within the

North Atlantic, ID-catalogues for the species now exist for the west coast of Scotland (ca. 80 individuals since 1990; Gill *et al.*, 1995), the Gulf of St. Lawrence, Canada (ca. 250 individuals since 1995; Tscherter & Morris, 2007), the outer Moray Firth, Scotland (ca. 30 individuals since 2001; Baumgartner *et al.*, 2007) and Iceland (ca. 60 individuals in 2007; C. Bertulli, *personal communication*). So far, no evidence exists for matches between regions. However, in all areas where catalogues have been in existence for more than a year, some well-marked individuals have been seen between different years, and re-sightings within seasons are common in all locations. In the San Juan Islands, Washington State, long-term site fidelity was observed at a very fine scale between adjoining areas, which were separated only by a few kilometres. These areas were characterized by differences in their physical environment, and individual minke whales adjusted their foraging strategies according to these fine-scale habitat characteristics (Dorsey, 1983; Hoelzel *et al.*, 1989): over shallow banks and seamounts, minkes were usually observed "bird-association feeding", i.e. taking advantage of fish-shoals close to the surface which had been driven together by predatory fish or auks. By contrast, the main strategy used by individuals in deep open bays was "lunge-feeding", during which the whale would corral fish against the surface without seabirds associated, and then consume the fish-shoal in a vertical lunge. Similar small-scale site fidelity has been observed between adjacent areas in Monterey Bay, California (Dorsey *et al.*, 1990), as well as in the Gulf of St.Lawrence (Tscherter & Morris, 2007).

On the west coast of Scotland, photo-identification of individual minke whales has taken place on an opportunistic basis over a large area mainly from whale-watching vessels (see, for example, Gill *et al.*, 1995). In order to examine fine-scale site fidelity in Hebridean minke whales, photo-identification was conducted within the study area around the Small Isles over the course of the 5-year fieldwork period. High degrees of interannual and seasonal site fidelity to this relatively small area would be indicative of a predictable localized resource, whereas only short visits to the region would indicate that resources are widely distributed and less predictable, thus forcing the animals to cover wider distances in search of prey.

Diving behaviour and use of the physical environment for foraging

In the past, studies on the diving behaviour of minke whales have been conducted with the aim of correcting for the sightability of animals in order to optimize abundance

estimates from line-transect surveys (Gunnlaugsson, 1989; Joyce *et al.*, 1990), for inference of energy expenditure during swimming (Blix & Folkow, 1995) or to examine diurnal and seasonal patterns in dive times (Stockin *et al.*, 2001). Diving behaviour in relation to physical environmental parameters has not been examined in any detail so far for this species, but can be helpful in drawing conclusions about its habitat use. Depending on the type of prey and where in the water column a whale forages, for example, dive times might be expected to increase with depth, or longer dives may occur in areas with low chlorophyll concentrations, which could be indicative of lower prey abundance. Hoelzel *et al.* (1989) found that dive times can also vary with different feeding strategies: the dive before a feeding event lasted longer in lunge-feeding individuals hunting in deep water than in whales specializing in bird-association feeding over shallow banks. Investigating dive times with respect to environmental variables could therefore give a useful insight into behavioural adjustments to local conditions.

Just as in land animals, different daily activities (e.g. travelling, foraging, sleeping) in cetaceans may also be linked to certain characteristics of the environment. Harbour porpoises, for example, are known to favour tidally active areas for feeding, where they commonly forage against the current (Pierpoint, 1993; 2008; Evans & Borges, 1996). It would be expected that foraging activity of minke whales is closely correlated with their overall distribution while on the summer feeding grounds. Comparing fine-scale habitat use specifically during foraging to habitat use during other types of behaviour can thus give an independent estimate to distribution models of which environmental conditions are important characteristics of their preferred feeding habitat, and to elucidate which parameters are used by the animals to locate their prey.

Feeding strategies and interactions with seabirds

Feeding and foraging strategies of cetaceans can in most cases only be studied from the surface, but the most important types of behaviour associated with these activities occur underwater and are thus invisible to the observer. In some cases, however, other taxa can help to give an insight into some of these crucial behavioural strategies. Associations between a wide range of seabirds and marine mammals are well documented and are generally linked to feeding activities (e.g. Harrison, 1979; Evans, 1982; Duffy, 1983; Skøv *et al.*, 1995; Camphuysen & Webb, 1999). Apart from special cases where seabirds feed directly on cetaceans' skin (Thomas, 1988; Rowntree *et al.*, 1998) or by-products

(Clarke *et al.*, 1981; Clarke & Prince, 1981), such associations appear to be based predominantly on seabirds taking advantage of a temporary food source created by cetaceans (or pinnipeds) trapping live fish or plankton against the surface, or a possibility for the birds to scavenge on injured or dead prey left by feeding cetaceans. On other occasions, birds and cetaceans may simply be attracted to the same resource without interacting with each other, and probably in rarer cases, cetaceans might take advantage of the feeding activities of seabirds, especially for locating prey (Pierotti, 1988).

In UK waters, associations between minke whales and several seabird species, most frequently involving common guillemots (*Uria aalge*), razorbills (*Alca torda*), kittiwakes (*Rissa tridactyla*), herring gulls (*Larus argentatus*) and Manx shearwaters (*Puffinus puffinus*) are commonly observed (Evans, 1982). The relative frequency of these species in feeding groups depends on the distance from breeding colonies. They all share the same diet with minke whales (namely sprat, juvenile herring and sandeels; Table 3.1) and exploit prey of similar size. In accordance with the "Feeding Efficiency Theory" (Sealy, 1973; Diamond, 1981), the birds often occur in multi-species feeding flocks, in which each species or group of species takes on a specific role depending on its feeding strategy (Table 3.1; Camphuysen & Webb, 1999). Auks (guillemots, razorbills and puffins) are pursuit divers and potentially capable of herding fish against the surface, thus making prey available to other species such as gulls. They have therefore been referred to as "initiators" or "producers" by Camphuysen & Webb (1999). Although auks may not necessarily herd fish-shoals co-operatively (which would be indicated by co-ordinated diving and surfacing), common guillemots can reach dive depths of up to 180m (Piatt & Nettleship, 1985) and seem to have a tendency to approach and attack a fish shoal mainly from beneath or the lower margins, as observed during underwater filming in the study area around the Small Isles in September 2004. This activity is not only likely to induce "balling-up" of small fish, but also to drive the shoal towards the surface. Shoals of bait-fish can also be trapped against the water surface by harbour porpoises, minke whales, seals or predatory fish such as mackerel, or they may simply have followed their plankton prey to shallower depths and in the process have been discovered by seabirds. However, given the diving capabilities of auks, it seems likely that these birds are perfectly capable of bringing shoals of small fish from intermediate depths closer to the surface themselves, even without the activities of predatory fish or marine mammals.

Once the fish have reached the surface, they (and the feeding auks) may then be discovered by searching kittiwakes. Due to their bright white plumage, flocks of kittiwakes are very conspicuous to other birds even from a great distance. Kittiwakes have therefore been characterized as a "nuclear" species (Sealy, 1973) or "catalyst" in the formation of multi-species seabird feeding flocks. By contrast, larger gulls tend to appear last in these aggregations, placing themselves on top of the fish-shoal and thus blocking access to it to the smaller kittiwakes. The larger gulls were therefore identified as "joiners" and "suppressors" by Camphuysen & Webb (1999) due to the tendency of feeding groups to break up soon after the gulls arrived. The role of Manx shearwaters in these aggregations is less clear: like auks, they can hunt fish underwater (by pursuit plunging rather than pursuit diving) and do not depend on direct surface access to the shoal like kittiwakes and larger gulls. However, they do not appear to be able to herd fish themselves or drive them towards the surface in the way that auks do. One reason may be that they appear to attack a fish-shoal mainly from above or the upper sides, as also observed during underwater filming in 2004. This feeding strategy would be likely to cause a fish-shoal to descend to greater depths if no auks or other predators are present from below at the same time to drive it upwards. Manx shearwaters were also classified as "joiners" by Camphuysen & Webb (1999), but with no negative effect on the other species present, in contrast to the large gulls.

Most seabird taxa cannot swap between different feeding strategies according to different situations. It is therefore likely that each group would occupy the same role in association with a whale as in a multi-species feeding aggregation with other birds. Based on the association patterns between minke whales and different seabird taxa, it is thus possible to make predictions about the relationship between whales and seabirds, as well as the whales' foraging strategies:

1) If minke whales predominantly trap fish against the surface and are followed by seabirds taking advantage of this activity, it would be expected that mainly the more mobile species (kittiwakes, large gulls and Manx shearwaters with approximately equal frequencies of occurrence) in the study area would be found in association with whales, since they can follow them around more easily than the less mobile auks. On the other hand, if minke whales were taking advantage of prey located and herded by seabirds, a closer association between whales and auks would be expected.

2) Pierotti (1988) suggested that humpback whales in the Western North Atlantic used conspicuous seabirds such as gulls for visual detection of prey and other feeding humpbacks. If minke whales also relied mainly on visual detection of such a prey patch, a preferred association with kittiwakes (i.e. the "catalyst" species, which other seabirds also appear to rely on for finding a food source; Camphuysen & Webb, 1999) would be expected.

3) Whilst minke whales are often observed lunging in the centre of a seabird aggregation, the whales can also be found in close association with seabirds without showing this surface-feeding behaviour. In these cases, it is unclear whether they are still feeding at greater depths or if the association with the birds is purely coincidental. If the latter applied, the surface-feeding behaviour of an associated whale should be independent of the composition of the bird group. If an association between a minke whale and a seabird group was a relatively reliable sign that the whale was feeding, however, it would be expected that the composition of the bird group would also be an indicator for whether the whale was feeding at or near the surface, or further down in the water column. Surface-feeding behaviour by the whale in this case should occur more frequently if kittiwakes and larger gulls, which both depend on prey close to the surface, are present, whereas it should be independent of the presence of auks and Manx shearwaters, which can also exploit prey at greater depths.

Table 3.1. Diet, feeding strategy and role in multi-species feeding aggregations (after Camphuysen & Webb, 1999) of the main seabird species commonly found in association with minke whales in the study area. For explanation of roles in feeding groups, see text.

	Feeding strategy	Diet	Role in feeding groups	references
Auks: Common guillemot & razorbill	pursuit diving	herring, sprat, sandeel, mackerel, capelin	initiators, producers	Evans, 1990; Hatchwell, 1991; Skøv *et al.*, 2000; Davoren & Montevecchi, 2003
Large gulls: Herring gull, Greater and Lesser black-backed gull	surface seizing	herring, sprat, sandeel, capelin, long-finned squid; catholic diet, including offal	joiners (suppressors, kleptoparasites)	Pierotti, 1988; *personal observations*
Kittiwake	shallow plunging or dipping	herring, sprat, sandeel, mackerel, capelin, zooplankton	catalyst	Evans, 1990; Wanless & Harris, 1992; Skøv *et al.*, 2000; Carscadden *et al.*, 2002
Manx shearwater	Pursuit plunging	herring, sprat, sandeel, sardines, squid	joiner	Brooke, 1990

METHODS

Site fidelity

Fieldwork

Photo-identification of minke whales was conducted in all years with the aim of obtaining photographs of sufficient quality to enable identification of individual animals from natural markings (especially nicks in the dorsal fin, dark or light skin pigmentation on the dorsal fin and/or back, and scars on the back or sides). The data were then used to determine site fidelity of individuals within and between years, and to enable later verification that the same whale had been followed during focal sampling. For the purpose of this study, site fidelity corresponded to re-sighting the same individual(s) on different days within a field season, or return of an individual to the study area in different years. Under permit from Scottish Natural Heritage (licence numbers 4534 (2003), 5397 (2004), 5998 (2005), 7251 (2006) and 7978 (2007)) and following the same field protocol as Dorsey (1983), Hoelzel *et al.* (1989) and Dorsey *et al.* (1990), minke whales were approached on a parallel course approximately at the whale's swimming speed, with the distance then gradually decreased to ca. 30m, the optimal range for acquiring photo-ID data for this species. All cameras used for photo-ID were equipped with a 75-300mm zoom lens with a UV filter. From 2003 to 2005, analogue Canon EOS 5 and EOS 3000 cameras were used with ISO400 slide film, and the slides subsequently scanned for analysis. In 2006 and 2007, the analogue cameras were replaced by a Canon EOS 20D digital camera.

Analysis

All photo-ID images of sufficiently high quality for individual identification were catalogued and sorted into left and right sides. Matching of individuals was carried out using a combination of the programs *Adobe Photoshop 7.0*, *ACDSee 8.0 Pro* and *Adobe Photoshop Album Starter 3.0*. The best pictures of each individual were also compared to photos taken from the *Marguerite Explorer*, a whale-watch vessel operating in the Hebrides between 1992 and 2001, as well as to a minke whale catalogue for the West coast of Scotland administered by the Hebridean Whale and Dolphin Trust (HWDT), operating from Tobermory on the Isle of Mull. This catalogue contained images of 82

minke whales (incl. left and right sides only) taken by the whale-watch company Sea Life Surveys (SLS) and HWDT staff or volunteers between 1990 and 2006.

Diving behaviour and use of the physical environment for foraging

Fieldwork

Upon sighting a minke whale, an individual was followed for as long as possible, recording its surfacing times to the nearest second, surfacing type, direction of travel, position and association with seabirds, as well as film and frame number of ID photos taken (in years when analogue cameras were used). Surfacing types were defined as: NS = normal surfacing (whale swimming at normal or slow speed, usual surface roll); HA = high arch (whale arching its back before diving, indicating a longer dive), and LU = lunge (surface lunge with distended throat grooves, often with fish visible above the surface). Surfacing positions at footprints were taken as often as possible, but at least at every high arch, i.e. before the whale disappeared for a longer dive. Any possibilities of missed surfacings were noted and those dives subsequently excluded from analysis. All whales were followed according to the same protocol as employed for photo-ID, taking care to remain on as constant a course and speed as possible in order not to influence the focal animal's behaviour or dive pattern. Focal follows were stopped when more than one whale was present in the vicinity such that it became unclear which individual was being followed, or when the focal animal was lost, or if it appeared to change its dive pattern in response to the boat. The latter point usually involved a whale becoming "friendly" and inspecting the boat, but once included a juvenile which appeared to increase its swim speed and dive duration, possibly as a negative response to the boat. This whale was left as soon as this change in behaviour was noticed. No focal follows were attempted above sea state 2, and the majority (73%) took place in either sea states 0 or 1.

Analysis

All photo-ID images taken during focal follows were checked in order to verify that a particular individual had been followed throughout. Typical breathing sequences in minke whales consist of three to six short dives followed by one longer dive (e.g. Gunnlaugsson, 1989; Joyce, 1990; Anderwald *et al.*, 2008). However, since breathing patterns are likely to depend on behaviour (e.g. travelling vs. foraging; Curnier, 2005) and are highly

variable between individuals (Hoelzel *et al.*, 1989), only longer dives, which were considered not to be within a breathing sequence, were included in the analysis. The cut-off value between breathing sequences and potential foraging dives was determined by a marked decline in overall frequencies of dive duration. Only focal follows with either a minimum duration of 30min or containing at least ten long dives (i.e. of length above the cut-off value) were included in the analysis. For combination with the environmental parameters, all dive times were assigned to the start position of a long dive.

Explanatory variables:

For a detailed description of sources and processing methods of all environmental data used in this analysis, please refer to Chapter 2 (pp.70-73).

Bathymetry and topography: Bathymetry data were derived from the same sources and following the same methodology as for the 2min cells covering the study area around the Small Isles, and described in Chapter 2. For the dive and behavioural analyses, the study area was divided into 0.5min cells, and cell summaries calculated for depth, slope and aspect. The start positions of all dives above the threshold value were then linked with the appropriate cell-ID's of the 0.5min cells and their corresponding cell summaries. Bathymetry and topography data considered in the exploratory analyses included:

- Depth: mean, maximum and minimum, range (max-min), standard deviation.
- Topography: contour index (CI) and average topographic variability (M; see Chapter 2), mean, maximum and minimum slope, range (max-min) and standard deviation of slope.

Sea surface temperature (SST) and Chlorophyll a (Chl-a): Each start position of a long dive was linked with the nearest SST and Chl-a data point for the appropriate month and year using the spatial join function in ArcView. For those months which included gaps in SST coverage in the vicinity of a focal follow, the assignment of the nearest SST value was checked against modelled data from Maptool plots extracted for the west coast of Scotland (http://www.seaturtle.org/maptool).

Tides: Current strength for the study area around the Small Isles was derived from the same fine-scale model (0.5min) as described in Chapter 2. The state of the tidal cycle (hours after local high water at Mallaig, spring or neap tide) was determined from the

TotalTide software (see Chapter 2), and each start position of a long dive was linked with the nearest tidal data point of the model for the appropriate state of the tide using the spatial join function in ArcView. Tidal data included in the exploratory analyses included current strength (m/s*1000) and state of the tidal cycle: high water (HW; 0-1 & 11-12 hours after HW), ebbing (2-4h after HW), low water (5-7h after HW) and flooding (8-10h after HW).

Light intensity: Due to the decrease in day length during the course of the summer (fieldwork took place between July and September), time of day was standardized as hours after sunrise / before sunset, determined using the *TotalTide* software and rounded to full hours. Daylight hours were divided into three categories: 2h after sunrise or before sunset (low light), morning (9-12 hours before sunset, equivalent to ca. 3-6 hours after sunrise) or afternoon (3-5 hours before sunset; intermediate light intensity), and mid-day (6-8 hours before sunset, i.e. mostly between 12:00–15.00h; high light intensity). No focal follow data were available during the period up to 2h after sunrise, so the low light category applies only to evening hours.

Behaviour: Due to the variability in dive patterns between individuals and the possibility of animals switching between different behaviours during a focal follow, no attempt was made to distinguish between foraging and travelling whales in the field. Instead, foraging or travelling was assigned based on the plotted track-line of each individual. It was assumed that whales which were foraging would on average spend more time in a given area by comparison to animals which were travelling and thus moving in a straighter line. The number of 0.5min cells covered by the track-line of each focal follow was therefore divided by its duration, giving a rate of 'number of cells visited / h'. Whales moving at a rate of less than 5 cells/h were classed as foraging, whereas animals which covered more than 10 cells/h were classed as travelling. The tracks of individuals moving at intermediate rates of 5-10 cells/h were visually inspected for a possible switch between foraging and travelling, based on a change from moving in a straight line to fine-scale use of cells, combined with an abrupt change in the direction of movement. All other tracks within this category were classed as foraging. These assumptions were then verified independently by checking that any surfacings associated with feeding behaviour (namely lunges) only occurred during focal follows classed as foraging.

This interpretation of the whales' behaviour was then included as a factor in the analysis on dive times.

Other: Additional explanatory variables examined in the exploratory analysis were: year (2003 - 2007), month (July – September), and individual ID.

A) DIVING BEHAVIOUR

Pair-plots were produced to check for co-linearity between continuous explanatory variables and to examine their relationship with dive times. In combination with Spearman's correlation coefficients between all continuous explanatory variables, the pair-plots were used to decide on which parameters to exclude from the analysis due to co-linearity. For nominal variables, box-plots combined with Mann-Whitney-U or Kruskal-Wallis tests were used to decide which factors were worth including in the models.

In order to examine the explanatory variables for their relative importance in explaining dive duration when corrected for each other, and to look for possible interactions, a regression tree was constructed. The advantage of regression trees is that they deal better with non-linearity and interactions than Generalized Linear Models. The process involves splitting the data repeatedly into two homogeneous groups, so that between-group variation is as large, and within-group variation as small as possible. The optimal grouping is calculated automatically by the software. The optimal tree size (i.e. the number of splits necessary) is then calculated as a trade-off between the goodness of fit and the complexity of the tree (i.e. number of branches), similar to Akaike's Information Criterion (AIC; Burnham & Anderson, 2002). Using the rpart-library in R, the optimal tree size was selected by cross-validation and application of the one standard deviation rule (Zuur *et al.*, 2007). The regression tree was also used to re-classify the 30 individuals into fewer categories based on similarities in their dive times, in order to save on the degrees of freedom used for the Generalized Linear Model.

Residual plots of a preliminary univariate ANOVA indicated an increase in variance with increasing dive time, even when the response variable was ln-transformed. Since overdispersion of the data was suspected, the relationship between (untransformed) dive time and the selected explanatory variables was examined with a quasi-Poisson Generalized Linear Model (GLM), in which the dispersion parameter was estimated

automatically and the standard errors of the coefficients of the explanatory variables multiplied by its square root. At first, all explanatory variables were included at once, and the optimal model was then selected in a step-wise backward procedure applying the F-test (Zuur *et al.*, 2007). In each step, the least significant parameter was excluded from the model, and the p-value of the F-statistic was Bonferroni-corrected.

B) FORAGING AND TRAVELLING IN RELATION TO ENVIRONMENTAL PARAMETERS

Based on the behavioural interpretations from the track-lines in the dive analysis, foraging and travelling behaviour were investigated further with respect to environmental parameters. Five individuals which had been included in the dive analysis were excluded from the behavioural model due to uncertainty about their classification as travelling or foraging: three individuals classed as travelling based on the high number of cells visited per unit time had been followed for ≤34min, making it difficult to ascertain whether their relatively straight track-lines over this short period of time indeed reflected travelling behaviour or were part of a broad-scale foraging pattern. The tracks of two individuals classed as foraging, but falling into the intermediate category of 5-10 cells visited per hour, showed elements which could be interpreted as both travelling and foraging. This included an individual which followed a relatively straight course overall, but whose track-line showed a sudden sharp turn at the end (resulting in an overall rate of 5.9 cells visited per hour). Another whale seemed to be searching over a wide area (visiting 7 cells per hour on average) and would probably have been classed as travelling if only part of its track had been known.

To reduce the risk of spatial auto-correlation, the analysis was based on grid cells rather than single dives: all long dives of an individual within a 0.5min cell were summarized and the resulting means of the continuous explanatory variables included in the model, so each cell was only represented once per individual per day. Boxplots combined with Mann-Whitney-U tests were used to decide which parameters to include in the model. A univariate ANOVA with "Behaviour" (forage vs. travel) as the explanatory variable was performed for each continuous parameter in turn in order to examine its residual pattern. Where residuals deviated from a normal distribution, a transformation was applied.

In addition to the continuous explanatory variables, the direction of the tidal current, determined from the fine-scale tidal model for the Small Isles in conjunction with the *TotalTide* software (see Chapter 2), was included in the model as a factor.

Foraging versus travelling behaviour was modelled using a Generalized Linear Model assuming a binomial error distribution with logit link function, i.e. a logistic regression. All explanatory variables were included at once, and model selection was performed in a stepwise backward manner using Akaike's Information Criterion (AIC; Burnham & Anderson, 2002) first, and then the deviance test, since the optimal model according to AIC still included non-significant parameters.

Due to auto-correlation, temporal parameters could not be included in the logistic regression. Behaviour with respect to these variables was therefore examined using Chi-square tests based on individual focal follow sequences rather than cells. In this case, light intensity could not be investigated since >50% of categories showed expected frequencies of <5. Instead, foraging and travelling behaviour was tested for diurnal patterns by aggregating time of day (hours before sunset) into three new categories (morning, mid-day and evening). For tidal state (hours after high water), the same categories were applied as previously: high water (HW), ebbing, low water (LW) and flooding.

Statistical analyses on diving behaviour were conducted using the freeware R (R Development Core Team, 2006).

Feeding strategies and interactions with seabirds

Fieldwork

Although the fieldwork was centred upon minke whales, notes were also taken on any other cetacean species and seabird groups encountered. A seabird group was defined as an aggregation of >10 individuals of one or more species, which were clearly separated spatially by other such groups. Larger aggregations could be spread over an area of 2000m^2 or more. Time and position of encounter, species composition and whether a minke whale was associated, were all recorded. Where time allowed, the number of individuals of each species was counted. For large groups, individuals of the same species were counted in groups of 10 up to 50 or 100 within a restricted area, and this number was then extrapolated to the total area occupied by the flock, taking into account differences in densities. If there was insufficient time to approach the birds close enough

for a count, only the presence of each species was recorded. A pilot study using the same methodology had already been conducted in the same area between 17th and 23rd September 2001 (Anderwald *et al.*, 2002), and data from that week were included in the analysis of presence / absence of minke whales with bird groups. If one or more minke whales were associated with the seabird aggregation, the surfacing behaviour of the whales was recorded, as well as whether any surface feeding was observed. Since the surfacing behaviour of minke whales had not been recorded in the pilot study, the 2001 data had to be excluded from this analysis.

Analysis

The seabirds most commonly encountered in the study area were divided into four "functional groups" or guilds, depending on their feeding strategies (Table 3.1): 1) Pursuit divers: auks (common guillemots, razorbills and puffins, but dominated by guillemots), 2) Surface seizers: large gulls (herring gulls, greater and lesser black-backed gulls, but dominated by herring gulls), 3) Dippers: kittiwakes, and 4) Pursuit plungers: Manx shearwaters. Other taxa were encountered too infrequently in aggregations of >10 individuals to be included in the analysis. For each seabird aggregation that had been counted, diversity was expressed as the Simpson's index with respect to the four guilds, calculated as: $D=1/(\sum P_i^2)$, where P = proportion of each guild (after Simpson, 1949; Begon *et al.*, 1986: p. 682). In addition, the dominant guild was determined for each aggregation, defined as the functional group making up >50% of the total number of individuals.

In order to assess the relative importance of the presence and group size of the four seabird guilds in determining the presence of a minke whale with a bird aggregation, three logistic regressions were performed. Each model used the presence or absence of a minke whale (per seabird group) as the dependent variable. The first model included the group sizes of the four seabird guilds, the Simpson's index with respect to these groups, total number of guilds present, and the dominant guild, as explanatory variables. Total number of guilds present and dominant guild were included as categorical variables. Since the overall size of a seabird aggregation is not independent of the numbers of individuals in each guild, a second model used total size of the aggregation only, instead of numbers within each guild, together with the other three variables (Simpson's index, number of guilds present, and dominant guild). The third model included presence /

absence only of each guild, together with total number of guilds present, as the explanatory variables.

The surface feeding behaviour of minke whales associated with a seabird aggregation (with 'surface feeding observed' / 'not observed' as the dependent variable) in dependence of presence / absence of each guild and number of guilds present, was investigated in a fourth logistic regression.

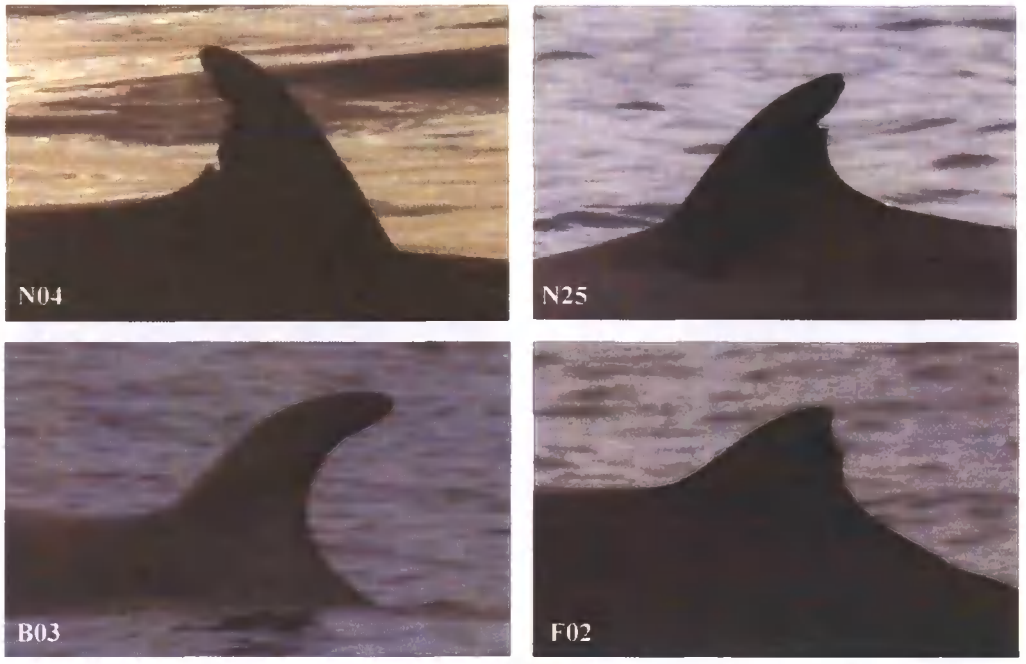
All group sizes were root-transformed in order to fulfil the requirement of Poisson-distributed residuals, and the classification cut-off value was adjusted to the relative frequency of aggregations with minke whales present (or a surface-feeding whale in the case of the fourth model, respectively). Model selection was based on a stepwise backward procedure using the likelihood ratio, and the probability threshold for removal of a parameter was set to 0.05.

Interactions between minke whales and seabirds were analyzed in SPSS v.14 in order to enable a direct comparison with Anderwald *et al.* (2002).

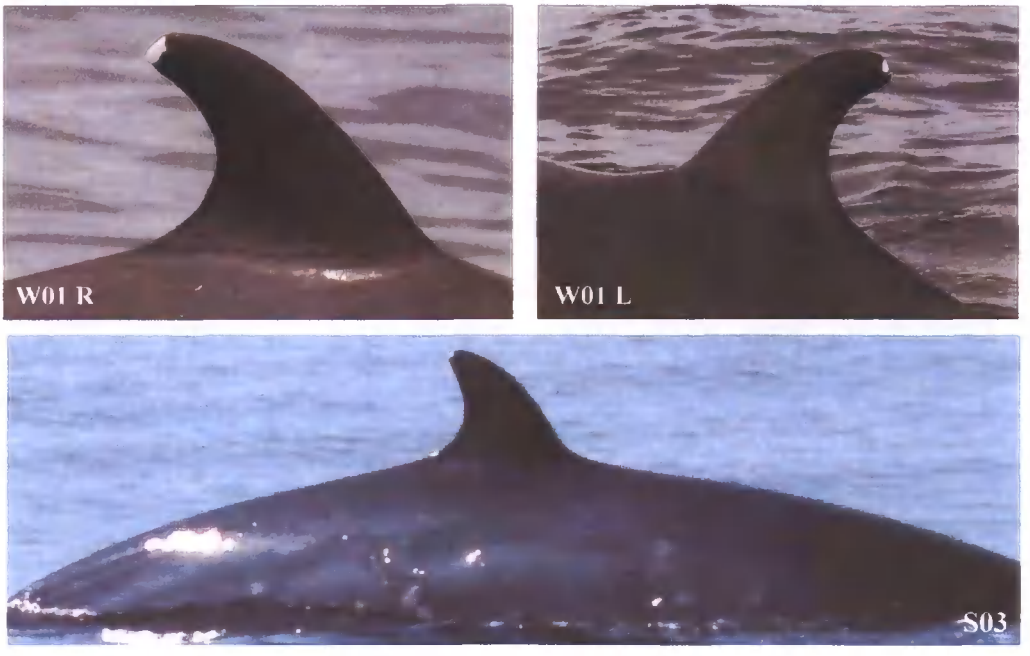
RESULTS

Site fidelity

Out of a total of 1723 photo-ID images analyzed, 1231 (71.4%) were considered useful for individual identification. Allowing for the possibility that animals which were identified only from the right side could have been identical to those which were photographed only from the left and vice versa, 54-60 individual minke whales could be identified around the Small Isles between 2003 and 2007: Forty-eight individuals were identifiable from both sides, six were identified only from the right, and six only from the left. The most important identifying feature were nicks in the trailing (n=23) or leading (n=2) edge of the dorsal fin, or at the base (n=2) or tip (n=2) of the fin, followed by distinctive fin shape (n=18). Both nicks and fin shape allowed individual identification from both sides (Figure 3.1a). Body scars (n=12) and dark or light pigmentation on body or fin (n=12) were also used for recognition, but in most cases only as additional features to fin shape, unless the scarring was extreme (Figure 3.1b). Both could only be applied for identification from one side and required high quality photographs in good lighting conditions. For 26 individuals, a combination of several of these identifying features was used for recognition, especially when no nicks in the dorsal fin were present (Figure 3.1c).

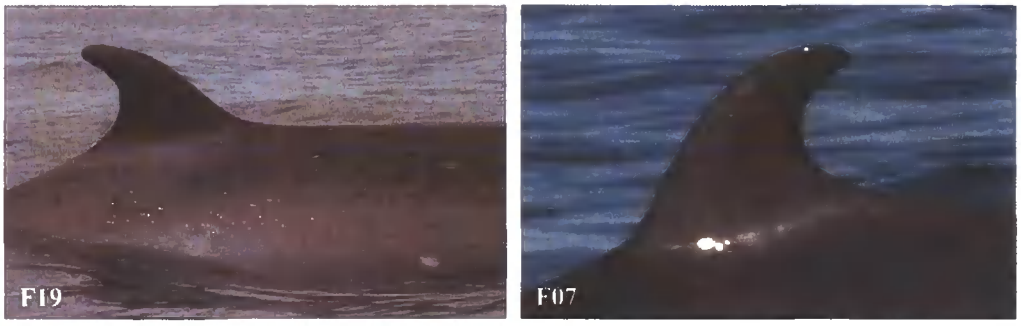


a) Nicks in trailing edge (N04, N25) and tip of fin (N25), and distinctive fin shapes (B03, F02) used for individual identification. B03 has a tall, upright fin leaning slightly to the right, F02 had part of its fin cut off, resulting in a characteristic triangular (porpoise-like) shape.



b) Permanent pigmentation on the tip of the fin (W01) and body scarring (S03) used to identify individuals from one side.

Figure 3.1. Examples of different features used for individual identification of minke whales: a) nicks in dorsal fin and fin shape, b) body scars and pigmentation, and c) combinations of several marks.



c) Combination of different features used for individual identification: F19 shows some irregularity in the trailing edge of the dorsal fin, as well as two distinctive white spots on the flank. F07 shows a rounded fin shape, combined with a black spot on the left-hand side of the fin.

Figure 3.1, continued. Examples of different features used for individual identification of minke whales: a) nicks in dorsal fin and fin shape, b) body scars and pigmentation, and c) combinations of several marks.

At least 21 individual minke whales were photographed in 2003, 25 in 2004, 6 in 2005, 3 in 2006, and 17 in 2007. The majority of individuals (n=32) were encountered only once, but 26 whales were re-sighted twice or more within (Table 3.2, Figure 3.2), and six individuals also between years (ID numbers N06, W01, F02, F03, F06 and N21 in Table 3.3; Figure 3.3a) within the area around the Small Isles during the five fieldwork seasons. Site fidelity within a season was lowest in 2005 (no re-sightings between days) and highest in 2004 and 2007 (10 and 14 individuals seen on more than one day, respectively). In 2003 and 2006, one individual could be positively re-identified between days (Table 3.2). The highest re-sighting rates within years coincided with two periods of calm weather combined with apparently high local prey abundance (5-8 Sept. 2004 and 20-24 July 2007; Table 3.2), when whales were feeding in groups of up to 10 individuals. No permanent associations between individuals could be detected, however, and animals appeared to move relatively independently of one another.

Two matches were found with animals photographed from the *Marguerite Explorer* between 1992 and 2001, and eight definite and one likely match with animals from the SLS/HWDT catalogue (Table 3.3, Figure 3.3b). The longest time span between re-sightings of the same individual was 13 years (for both N15 and N25; Table 3.3).

No common pattern could be detected between individuals with respect to spatial (Figures 3.2, 3.3) or seasonal (Table 3.3) distribution of re-sightings either within or between years. Some whales seemed very faithful to one particular location over a few days (e.g. S06 in 2006; Figure 3.2), or were photographed within the same small area

after more than two weeks (S03; Figure 3.2) or even between years (F03, Figure 3.3a). Others appeared to range more widely, both within the study area and beyond (e.g. N06; Figure 3.3b). The same applied to seasonal occurrence (Table 3.3): Individuals like N15 were photographed in every month between May and September, whereas at the other extreme, N16 only appeared to use the area in August.

Table 3.2. Dates for re-sightings of individuals within years. Individuals marked with an asterisk were also re-sighted between years. $_F$ = feeding behaviour (surface lunge) observed; $_b$ = associated with seabirds, and feeding behaviour suspected.

Individual ID	Dates	Interval between 1st and last sighting	No. days seen
S03	6_b / 24 Aug. 2003	18 days	2
B01	22_F / 31 Aug., 5_F / 7_F Sept. 2004	16 days	4
B05	5_F / 6_F / 7_F Sept. 2004	2 days	3
F07	5_F / 6_F / 7_F / 8_b Sept. 2004	3 days	4
F09	17_F Aug., 8_F Sept. 2004	22 days	2
F10	6_F / 7_F Sept. 2004	1 day	2
N02	24 Aug., 6_F / 7_F / 8_F Sept. 2004	15 days	4
N06*	5_F / 7_b / 8_F Sept. 2004	3 days	3
N19	6_F / 7_F / 8_F Sept. 2004	2 days	3
O02	17_F Aug., 6_b Sept. 2004	20 days	2
W15	5_F / 8_F Sept 2004	3 days	2
S06	11 / 12 / 15 Aug. 2006	4 days	3
F02*	21_b / 22_b / 23_b / 24_b July 2007	3 days	4
F06*	22_b / 24 July 2007	2 days	2
F19	20_b / 21_b / 22_b / 23_F / 29 July 2007	9 days	5
F20	22_F / 24_b July 2007	2 days	2
F21	21_b / 23_b July 2007	2 days	2
F22	20_b / 21_b / 22_F / 23_b / 24_F July 2007	4 days	5
F23	21_b / 22_F July 2007	1 day	2
N21*	21_b / 23_F July 2007	2 days	2
N24	20_b / 23_b / 24_F July 2007	4 days	3
N25	21_b / 22_F July 2007	1 day	2
O01	21_b / 22_F July 2007	1 day	2
S07	21_b / 22_b / 23_F July 2007	1 day	3
S08	21_b / 22_b July 2007	1 day	2
W01*	20_b / 21_b / 22_F / 23_b / 24_b July 2007	4 days	5

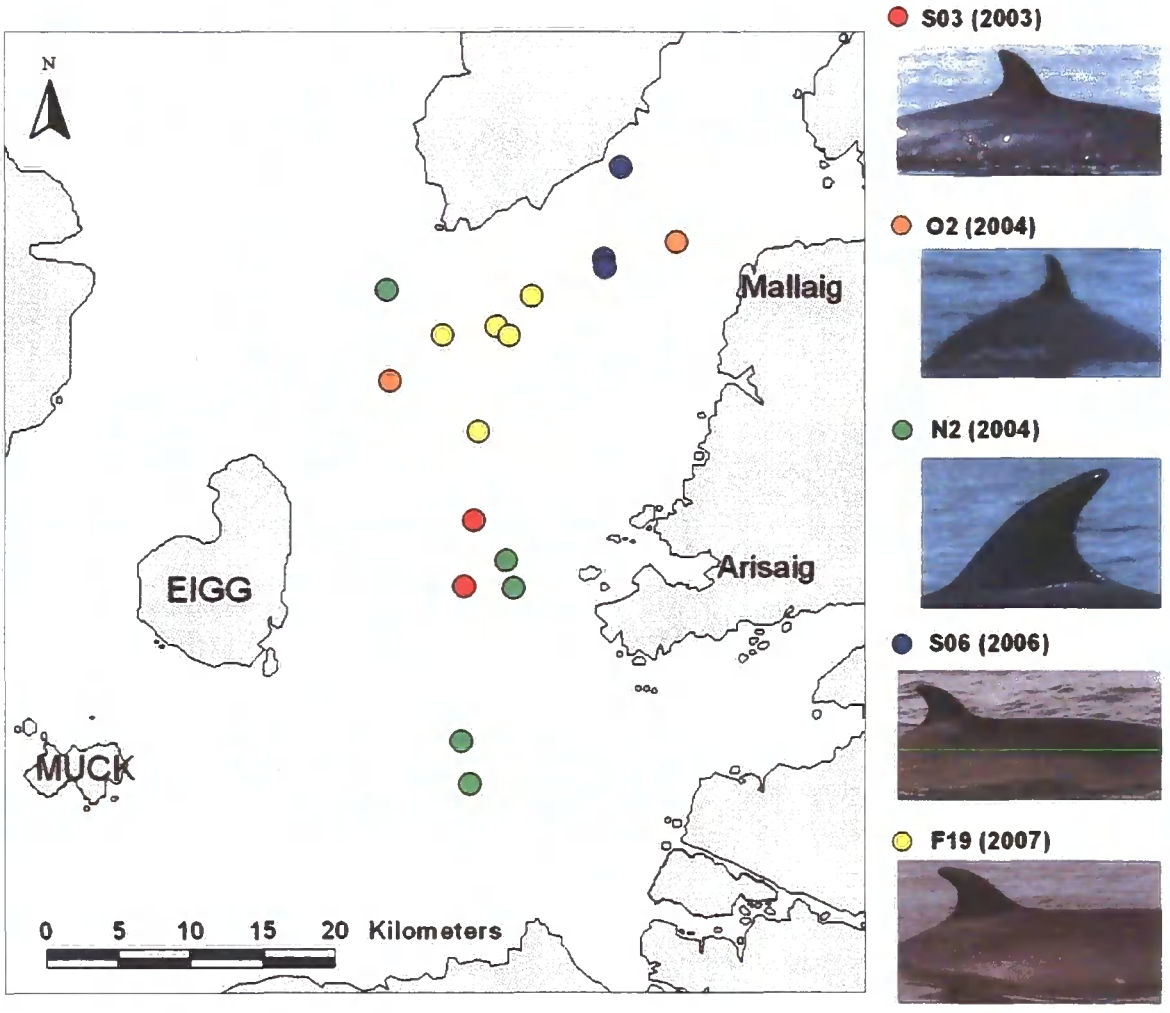


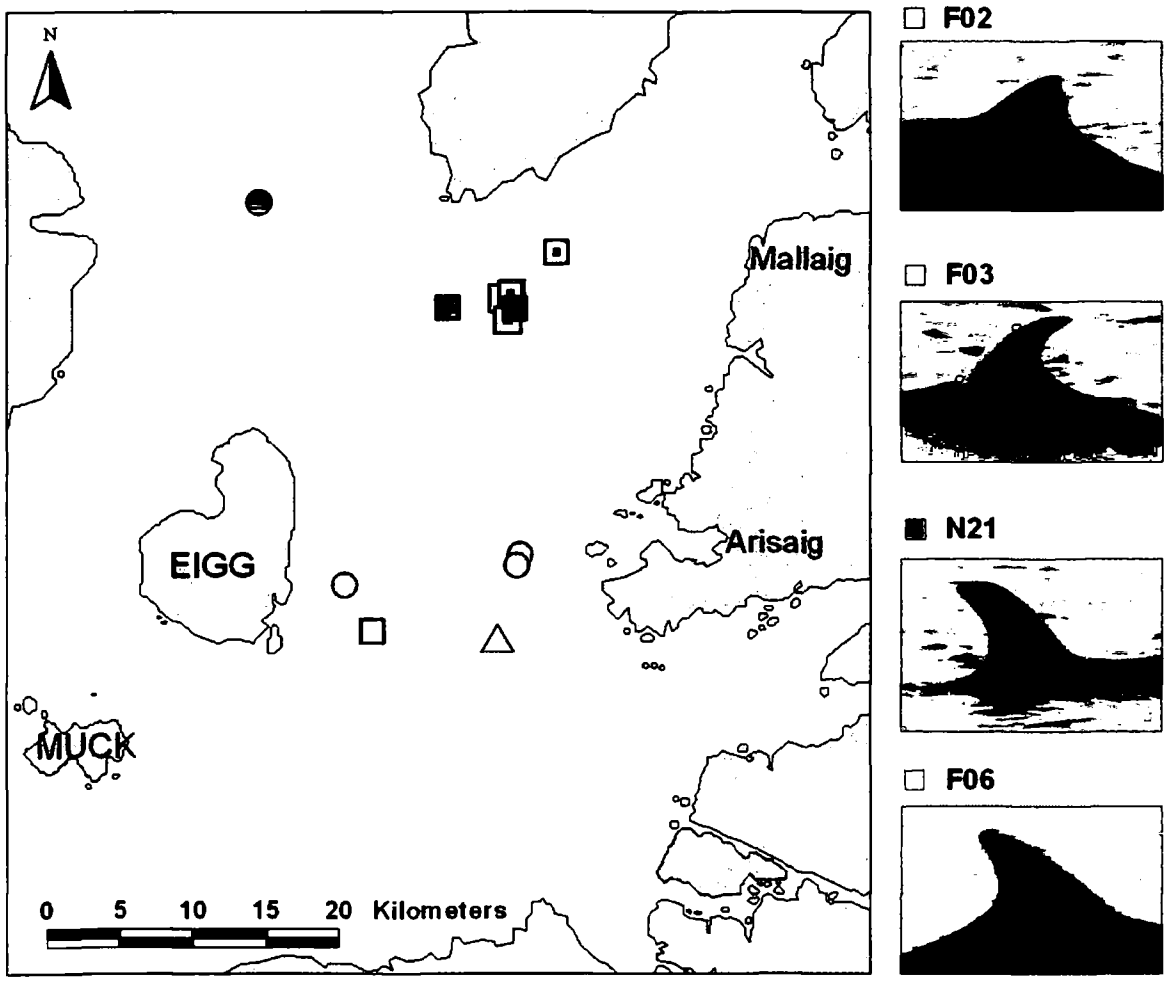
Figure 3.2. Five examples of re-sightings of individuals within years.

Table 3.3. Dates for re-sightings of individual minke whales between years. Numbers in columns for months represent dates within those months. Dates in italics indicate photos taken by Sea Life Surveys or the Hebridean Whale and Dolphin Trust; # = photos taken by Peter Evans from the *Marguerite Explorer*; and * = sightings / photos taken by Ronnie Dyer from *MV Sheerwater*. The identity of F02 for the sighting in 2004 was inferred from the description, but could not be confirmed by a photograph and is therefore written in brackets. For sightings during fieldwork seasons 2003-07 and from *MV Sheerwater*: $_F$ = feeding behaviour (surface lunge) observed; $_b$ = associated with seabirds, and feeding behaviour suspected.

Ind. ID	Year	Month					Years between 1st and last sighting	No. years seen
		May	June	July	Aug	Sept		
N15	*1990*				*14*		13	9
	1991	*24*		*4*	*27*			
	1992				*14*	*20*		
	1993			*13*		*17*		
	1995				*1, 2, 6*			
	1997		*10*	*20*				
	1999	*17*	*1*					
	2000			*18, 20*				
	2003				23_F			
N16 probable	*1993*				*30*		10	5
	1996				*13*			
	1997				*24*			
	2000				*31*			
	2003				16			
N06	*1994*			*5*		*11*	10	5
	1996				*23, 26*			
	2000			*25*		$3^{\#}$		
	2003				11_F			
	2004					5_F, 7_b, 8_F		
N25	*1994*			*3*			13	6
	1999					*14*		
	2001			*28*				
	2002					*22*		
	2005		*X*					
	2007			21_b, 22_F				
W01	*1995*		*22*				12	5
	2002				29*			
	2003				5			
	2004				14*			
	2007			20_b, 21_b, 22_F, 23_b, 24_b				
N24	*1999*			*6*			8	2
	2007			20_b, 23_b, 24_F				
N04	*2000*				*10, 11, 13, 14, 15*		8	6
	2001			*25, 26, 30*	*3*	*19*		
	2002					*23*		
	2003			*16*				
	2004					5_F		
	2008	11*						
S05	2000					$3^{\#}$	3	3
	2001	*31*						
	2003				12_F			
F13	*2002*	*6*					4	4
	2003	*26*						
	2004					8_F		
	2006		*27*					

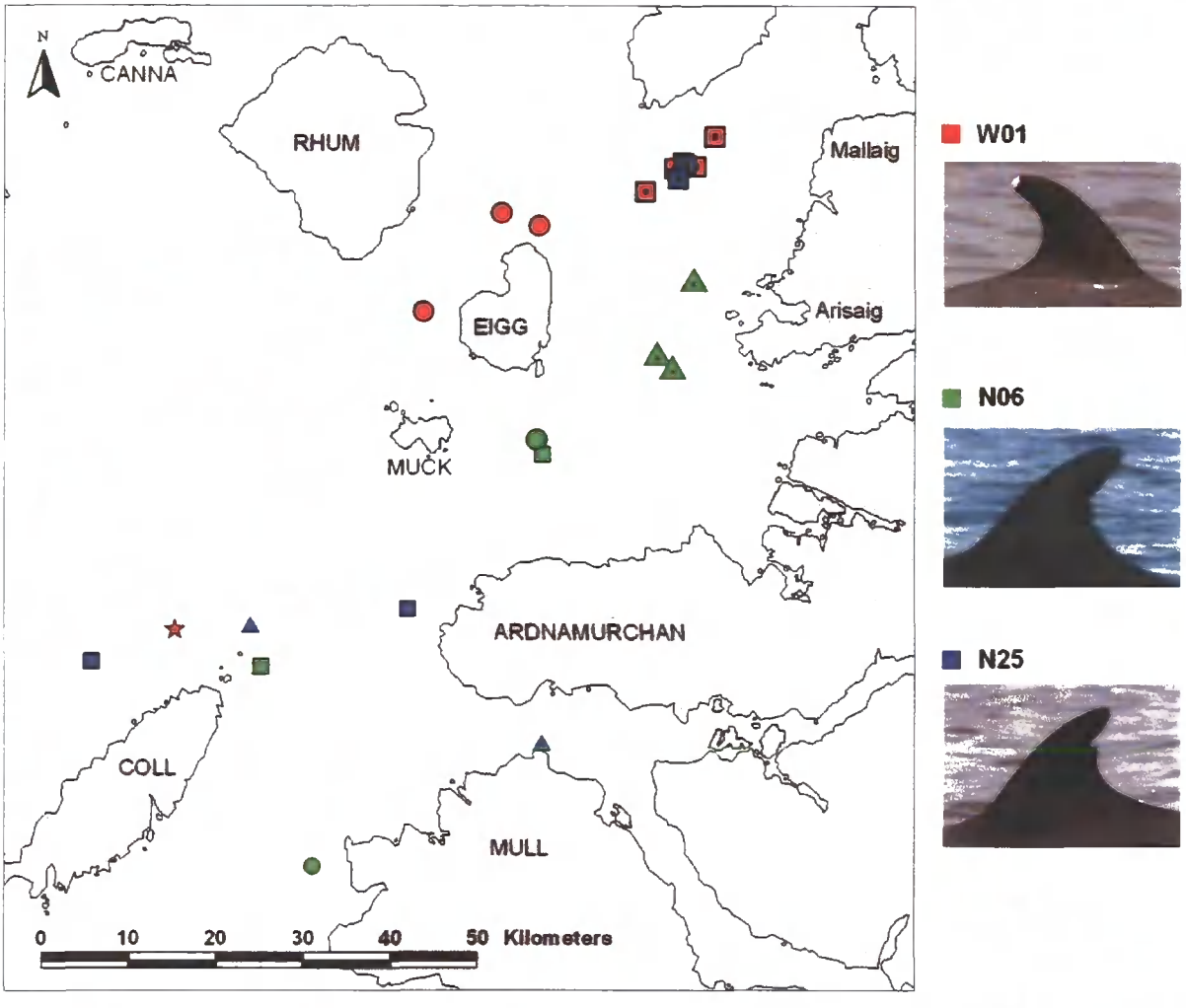
Table 3.3, continued.

F02	2003 (2004) 2007	21* 21_b, 22_b, 23_b, 24_b	10	4	3
F03	2003 2004		11 8_F	1	2
F06	2003 2007	22_b, 24	23_F	4	2
N21	2004 2007	21_b, 23_F	24_b	3	2



a) Four examples of re-sightings of individuals within the study area between years. Multiple sightings of an individual within the same year are represented by a dot in the middle of the symbol (in this case all re-sightings within a year for F02, N21 and F06 occurred in 2007). Squares = July, circles = August, and triangles = September.

Figure 3.3. Re-sightings of individual minke whales between years, a) within and b) beyond the study area.



b) Three examples of matches between years with SLS/HWDT catalogue. The smaller symbols represent sightings by SLS/HWDT, the larger symbols sightings from this study. Symbols containing a dot in the middle represent sightings of an individual within the same year. Stars = June, squares = July, circles = August, and triangles = September.

Figure 3.3, continued. Re-sightings of individual minke whales between years, a) within and b) beyond the study area.

Diving behaviour and use of the physical environment for foraging

The highest frequency of dive durations for all individuals combined occurred in the 10-20s interval (Figure 3.4). No sharp decline in overall frequency of dive duration was apparent after 40s, but the category 40-50s still showed a higher frequency than all subsequent categories. In order to allow for a safety margin, the cut-off value between dives forming part of a breathing sequence and potential foraging dives was therefore set at 50s (Figure 3.4). This resulted in a sample size of 30 individuals which fulfilled the criterion of having been followed for at least 30min or showing a minimum of 10 dives

>50s. Nineteen (63%) of these animals could be individually identified. Only one identified whale was followed on two consecutive days (S06 in 2006; Table 3.4); focal follows of all others were confined to a single day. Three individuals were followed twice within the same day (Table 3.4), but since the duration between the two focal follows was only short (<45min) and was caused in all cases by temporarily losing the animal, these were counted as the same sequence (but with a forced gap). This resulted in a total of 31 focal follow sequences (with the two days of coverage for the same individual counted separately). The duration of successful focal follow sequences ranged from 26min to 2h 54min, amounting to a total of 1775 recorded dives (37.5h), 693 (28.25h) of which lasted longer than 50s. The maximum dive time for which any possibility of a missed surfacing could be excluded was 10min 10s (Table 3.4). Based on their track-lines (i.e. the number of cells visited per unit time), the whales' behaviour during 21 (68%) focal follows was classed as foraging, and seven individuals (22.5%) were classed as travelling. Three sequences (9.5%) appeared to include a transition between foraging and travelling or vice versa, based on a relatively abrupt change in the direction of the animals' movement, combined with a switch from moving in a straight line to a more unpredictable course with finer coverage of cells (Figure 3.5). No consistent differences in dive patterns could be found between animals, interpreted by their tracks as foraging or travelling. However, a change in surfacing behaviour from irregularly spaced dives to a more regular pattern of several short breathing intervals followed by a long dive observed in one individual (No. 20, Figure 3.6) coincided exactly with the time it was interpreted to switch between foraging and travelling based on its track alone. The dive patterns between other foraging individuals varied widely, however, showing both regular sequences between long dives and short breathing intervals (as in animal No. 20 while travelling) and highly irregularly spaced dives (Figure 3.6).

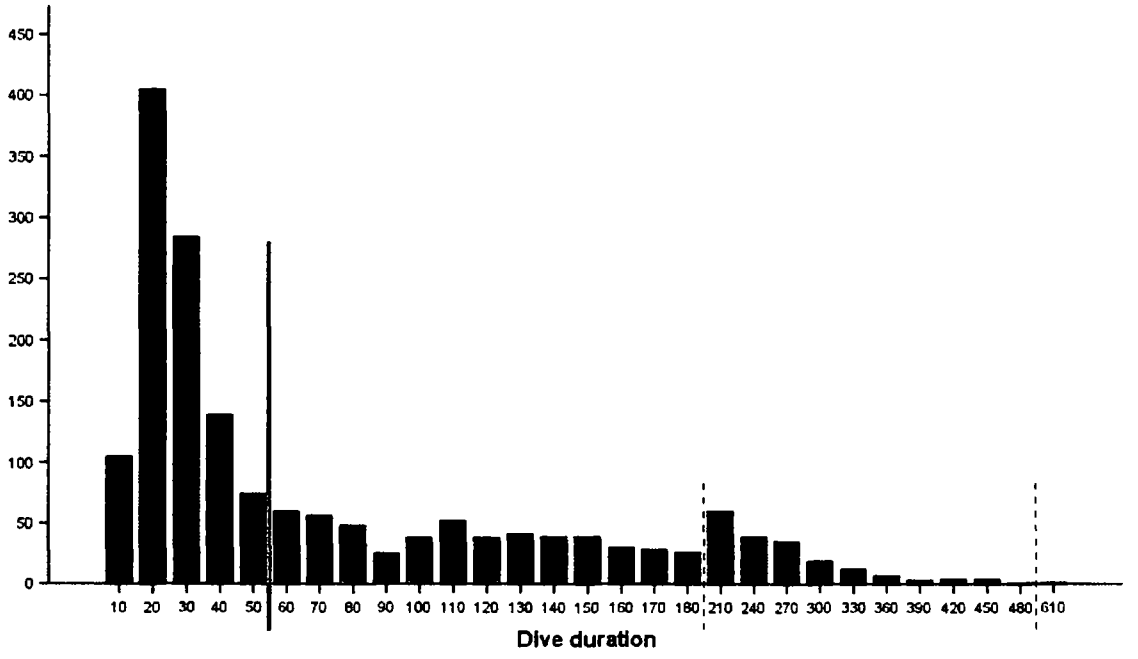


Figure 3.4. Frequencies of dive duration for all individuals combined. Figures along the x-axis represent the upper margins of intervals in seconds (e.g. x=80: frequency of dives between 70 and 80s). The cut-off value between dives considered as part of a breathing sequence and potential foraging dives for all individuals was set at x=50s, indicated by the grey line. The two dashed lines indicate changes between 10s and 30s, and above 30s intervals, respectively, in order to take account of the lower frequencies of long dives in the graph.

Table 3.4. Summaries of focal follows conducted around the Small Isles between 2003 and 2007.

Ind. No.	Ind. ID	Date	Time start	Time end	Duration (min)	Max dive time (s)	No. surfacings	No. dives >50s
1	unidentified	4.8.2003	16:47	17:13	26	242	21	10
2	unidentified	4.8.2003	19:27	20:15	48	250	47	19
3	unidentified	5.8.2003	19:28	20:03	35	335	26	10
4	unidentified	6.8.2003	10:49	11:29	40	167	35	10
5	unidentified	7.8.2003	10:44	11:48	64	320	49	24
6	F02	10.8.2003	11:49	12:59	70	422	39	17
7	N12	10.8.2003	15:10	17:44	154	360	109	48
8	F03	11.8.2003	11:44	14:32	168	420	106	50
9	F05	11.8.2003	15:53	16:42	49	343	47	17
10	N06	11.8.2003	17:38	18:26	48	280	35	14
11	S05	12.8.2003	10:44	11:11	27	124	31	14
12	W02	12.8.2003	12:38	13:16	38	202	40	12
13	N17	12.8.2003	13:16	13:31	104	279	72	42
			14:12	15:41				
14	F04	12.8.2003	16:25	18:26	120	228	95	38
15	S01	22.8.2004	11:41	11:51	91	360	103	33
			12:08	13:29				
16	unidentified	22.8.2004	18:26	19:11	45	150	30	22
17	N02	24.8.2004	14:14	14:48	34	179	36	13
18	B01	31.8.2004	12:09	13:41	92	335	47	21
19	unidentified	4.9.2004	11:44	12:11	27	189	18	11
20	unidentified	10.9.2004	14:58	16:23	85	435	41	19
21	unidentified	10.9.2004	17:25	18:26	61	441	29	13
22	F15	9.8.2005	08:58	09:42	44	277	27	9
23	unidentified	11.8.2005	08:57	11:05	128	463	107	37
24	F14	11.8.2005	16:28	17:07	39	255	32	12
25	unidentified	14.8.2005	18:43	19:34	51	333	43	12
26	N23	4.9.2005	17:56	20:06	130	430	127	28
27	S06	11.8.2006	15:51	16:53	62	251	43	22
		12.8.2006	11:48	13:59	174	389	168	52
		12.8.2006	14:24	15:07				
28	F19	20.7.2007	13:35	15:49	134	610	125	41
29	W01	21.7.2007	15:18	15:47	29	170	31	15
30	F26	23.7.2007	10:41	11:12	31	380	16	8
Total					**37.5h**		**1775**	**693 (28.25h)**

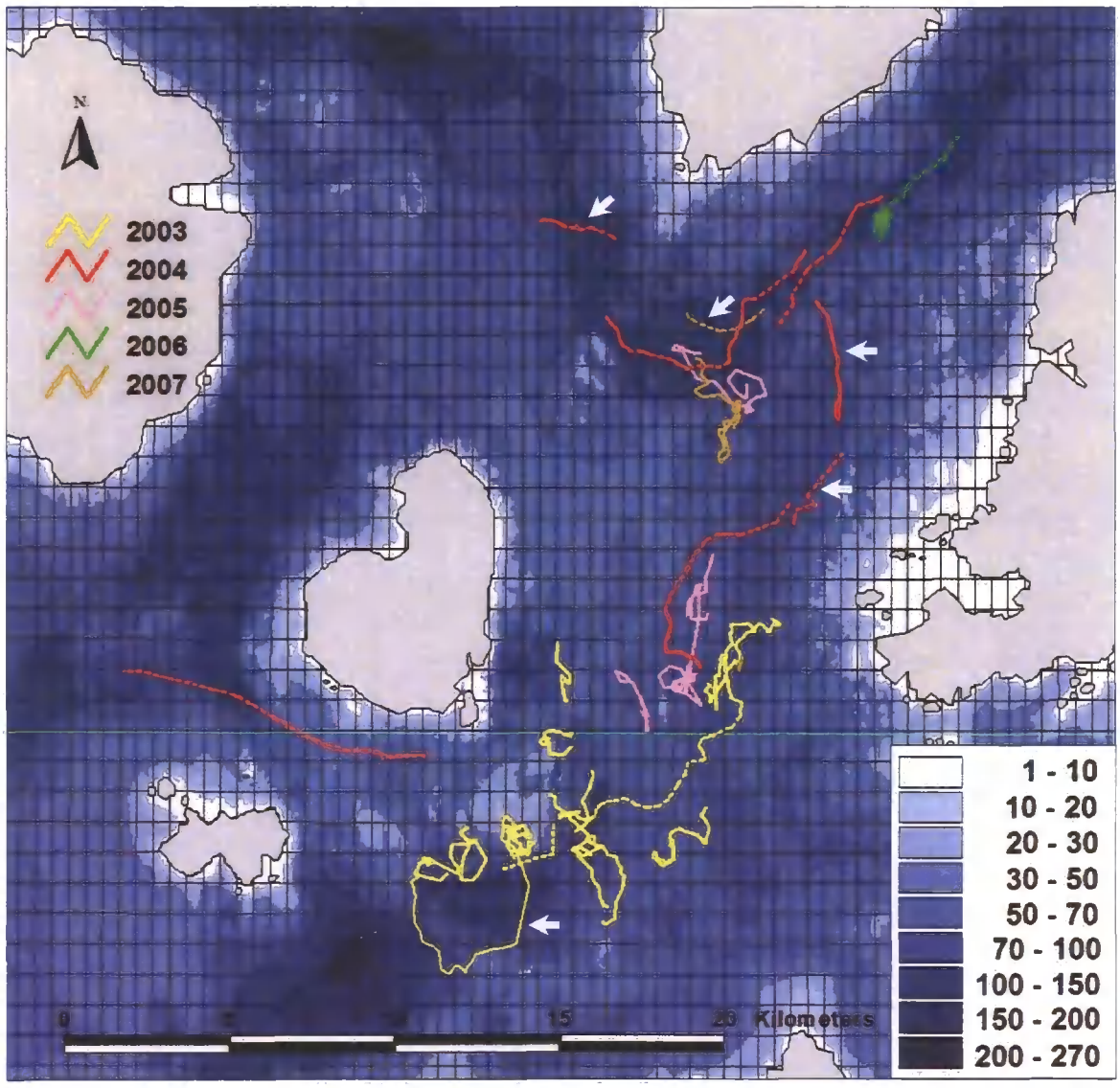
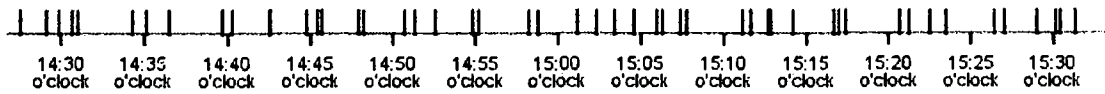


Figure 3.5. Tracks of the 30 focal follows included in the dive analysis. Solid lines represent individuals which were interpreted by their tracklines to be foraging (n=20), dotted lines represent animals which were thought to be travelling (n=7), based on their straighter routes. Tracks of three individuals were divided between foraging and travelling. The 0.5min cells, upon which the bathymetric and topographic summaries were based, are indicated. White arrows indicate tracks of individuals which were excluded from the behavioural analysis.

a) Ind. No. 7 (N12), 10.8.2003; foraging (over relatively wide area)

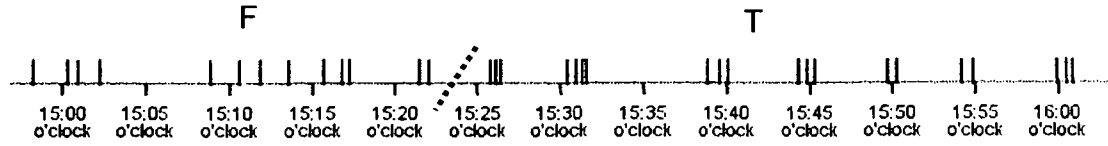
b) Ind. No.8 (F03), 11.8.2003; foraging



c) Ind. No.13 (N17), 12.8.2003; foraging

d) Ind. No. 14 (F04), 12.8.2003; foraging

e) Ind. No. 18 (B01), 31.8.2004; travelling



f) Ind. No. 20, 10.9.2004; foraging (F) and travelling (T)

Figure 3.6. Individual surfacing patterns of 10 focal animals over the course of an hour, representing samples for each year. Individual no.'s and names correspond to Table 3.4. The behaviour of each individual, interpreted from its trackline, is indicated. Note the change in surfacing behaviour between foraging and travelling for individual No. 20.

g) Ind. No. 23, 11.8.2005; foraging

h) Ind. No. 26 (N23), 4.9.2005; foraging

i) Ind. No.27 (S06), 12.8.2006; foraging

j) Ind. No. 28 (F19), 20.7.2007; foraging

Figure 3.6, continued. Individual surfacing patterns of 10 focal animals over the course of an hour, representing samples for each year. Individual no.'s and names correspond to Table 3.4. The behaviour of each individual, interpreted from its trackline, is indicated. Note the change in surfacing behaviour between foraging and travelling for individual No. 20.

A) DIVING BEHAVIOUR

As expected, most of the bathymetric and topographic variables showed strong co-linearity and were therefore excluded from any further analysis. Based on their lack of co-linearity and possible relationship with dive times, only mean depth, maximum slope, chlorophyll concentration and current strength were retained for inclusion in the models (Figure 3.7). Sea surface temperature was not correlated with dive time and was therefore excluded. Due to the large sample size (n=693), even weak correlations between the remaining variables were highly significant, but no co-linearity was detected ($r<0.5$; Figure 3.7). Mean depth, maximum slope, chlorophyll concentration and current strength could therefore all be included in the same model. All nominal explanatory variables showed significant relationships with dive times and were included in the further analysis

(see Figure 3.8 for results of Kruskal-Wallis and Mann-Whitney-U tests). In particular, dive times were longest during 2005, the poorest year with respect to minke whale sighting rates (Figure 3.8b; Chapter 2); dive lengths increased between July and September (Figure 3.8c), as well as through the day, with longest dives in low light conditions, i.e. during evening hours (Figure 3.8d); foraging whales showed longer dive times than travelling animals (Figure 3.8e); and minke whales dived longer around low and high tide than during flooding and ebbing (Figure 3.8f).

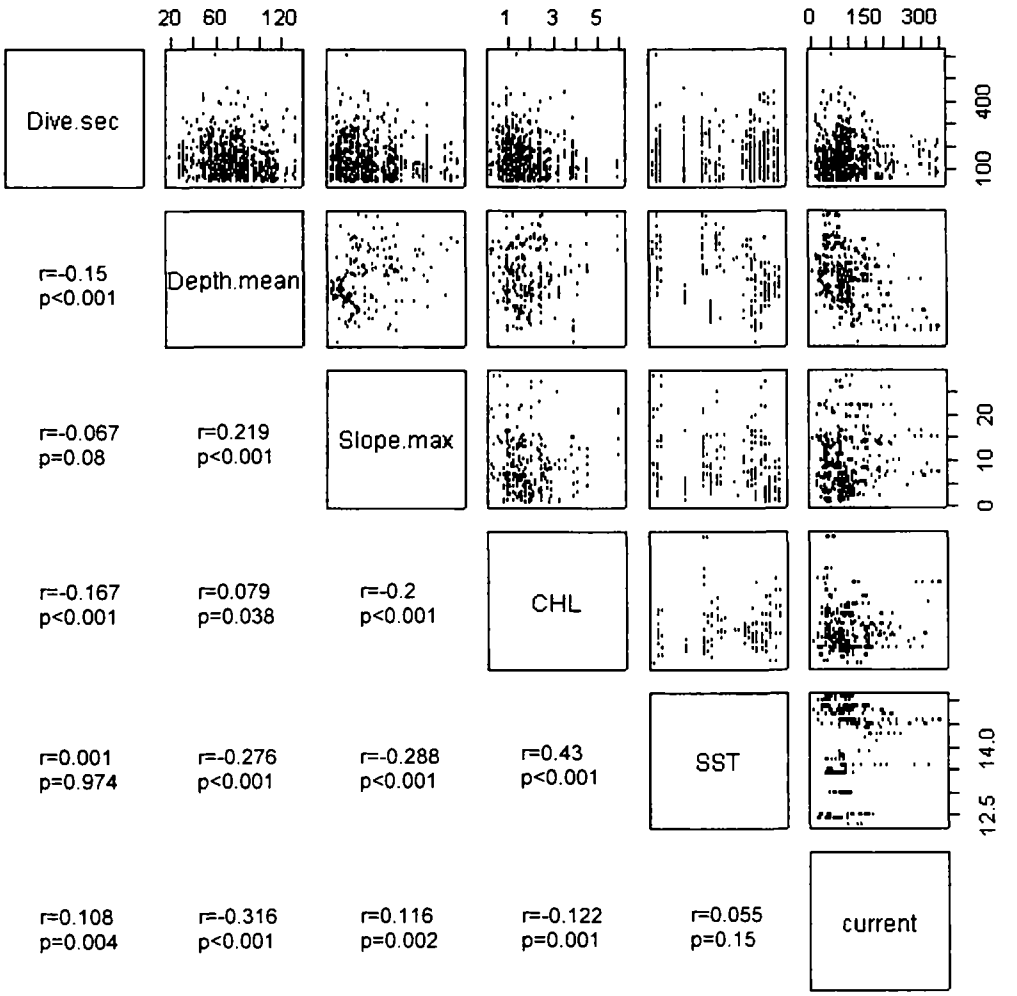
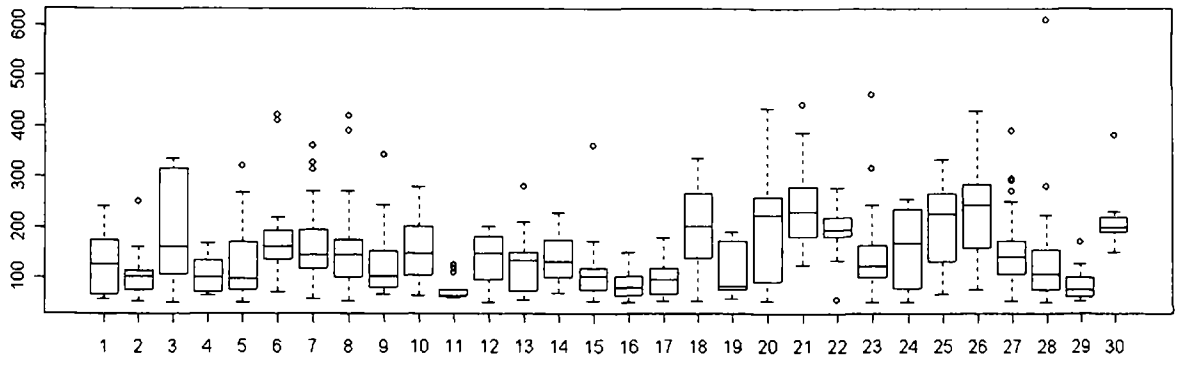
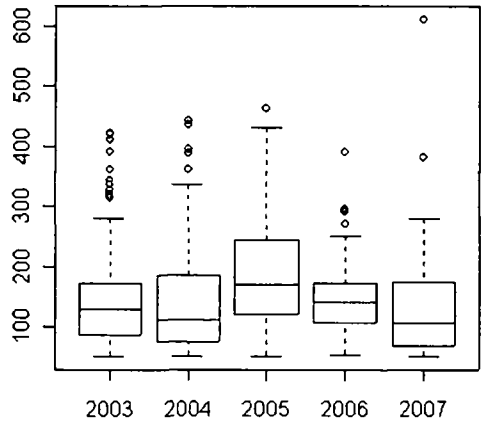


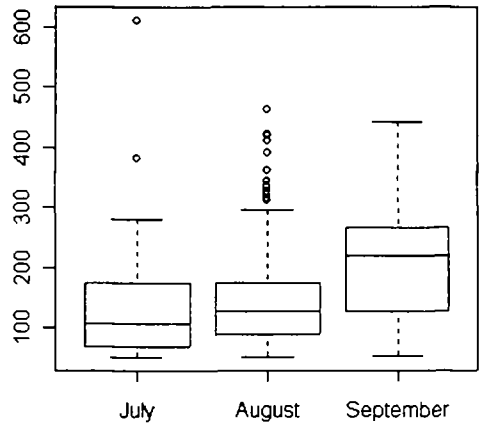
Figure 3.7. Pairplot of dive time and continuous explanatory variables considered for the GLM and regression tree. Spearman's r and significance levels for each variable pair are indicated in the lower left part of the graph.



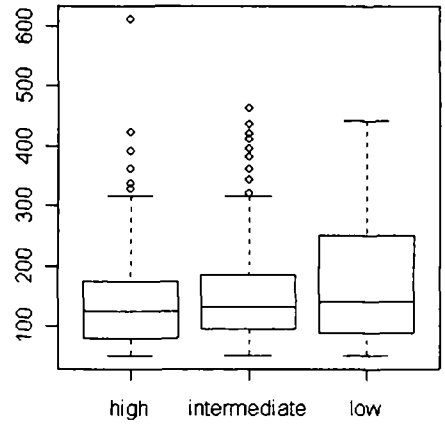
a) Individual: H=180.004, df=29, p<0.001



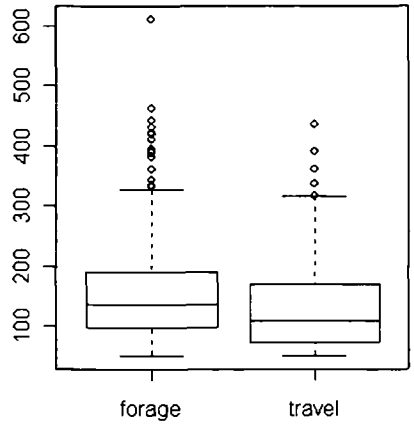
b) Year: H=31.961, df=4, p<0.001



c) Month: H=36.212, df=2, p<0.001

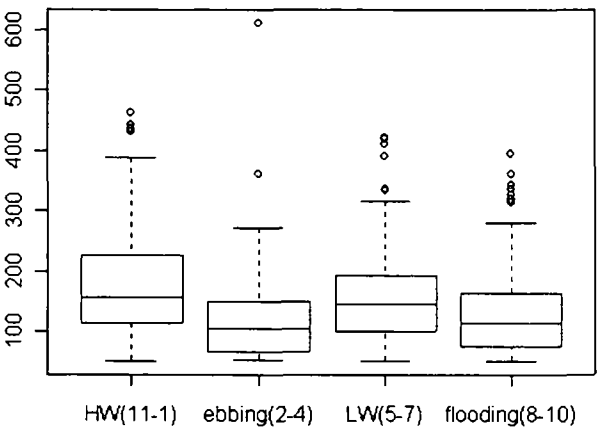


d) Light intensity: H=9.033, df=2, p=0.011



e) Behaviour: U=36212.5, p<0.001

Figure 3.8. Boxplots of dive times against all nominal explanatory variables selected for inclusion in the GLM and regression tree, with results from Kruskal-Wallis and Mann-Whitney-U tests, respectively.



f) Tidal state: H=62.392, df=3, p<0.001

Figure 3.8, continued. Boxplots of dive times against all nominal explanatory variables selected for inclusion in the GLM and regression tree, with results from Kruskal-Wallis and Mann-Whitney-U tests, respectively.

Based on the results of the regression tree, the factor "Individual" was the most important parameter in determining dive times. The optimal tree size determined by cross-validation was two (Figure 3.9), i.e. a tree with only the factor "Individual" included. The increase in goodness of fit of the tree with increasing number of splits is measured by the reduction in the error of the tree as a fraction of the root node error (which is the deviance divided by the number of observations; Zuur *et al.*, 2007). The tree of size two had an error of 84.8% of the root node error (=classification error with no splits), the second split only resulted in a further reduction to 79.5%, and the third split to 78.2%, with equally low decreases with each additional branch thereafter. The first and second splits were both based on the factor "Individual", and this tree of size three (Figure 3.10) was used to re-classify the 30 individuals into three categories for the GLM, i.e. individuals with overall short (n=8), intermediate (n=13), and long dives (n=9).

The result of the GLM was consistent with the regression tree: the only parameter left in the final model after stepwise backward selection was "Individual" ($F=7.987$, $p<0.001$), irrespective of whether the 30 individuals were re-classified into the three new categories or not. Even though significant differences in dive times were found between different years, months, tidal states, light intensities and behaviours when each parameter was

examined on its own (Figure 3.8), individual differences in fact appear to be the main factor in determining dive duration in minke whales around the Small Isles.

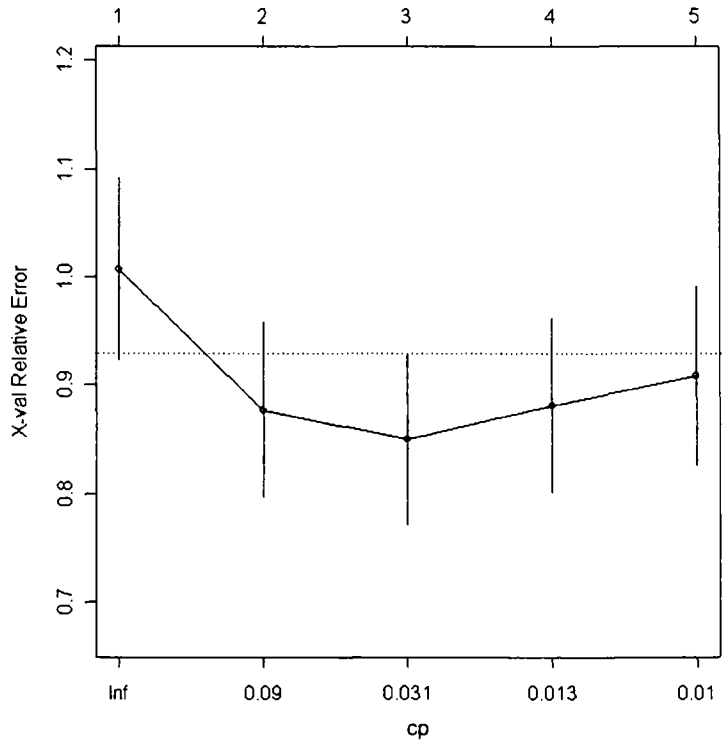


Figure 3.9. Determination of optimal tree size. The y-axis represents the relative error of the predictions calculated by cross-validation, cp stands for the complexity parameter of the tree. Corresponding tree sizes (i.e. the number of splits plus 1) are indicated along the top. The horizontal dotted line represents the mean error plus standard deviation of the cross-validations at convergence. According to the one standard deviation rule, the optimal tree size is at the cp for which the first mean error lies below the line, i.e. at cp=0.09 with a corresponding tree size of 2.

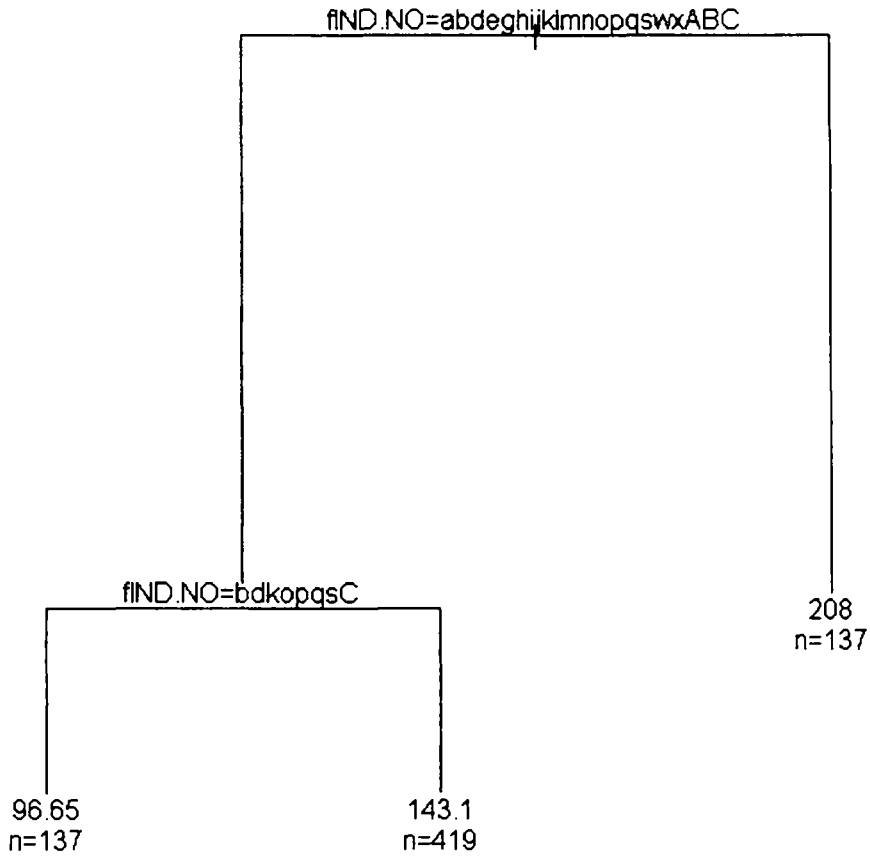
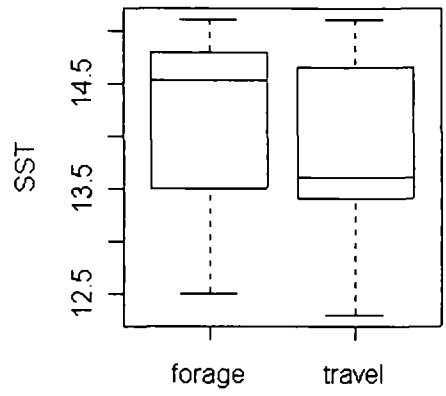


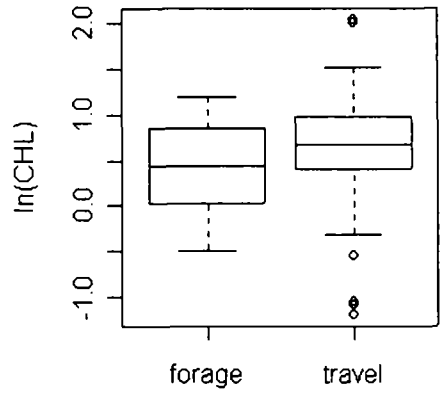
Figure 3.10. Regression tree of dive times, cut to size 3. The only important parameter for the groupings is "Individual" (named here fIND.NO). Mean dive times per group are indicated for each branch. Letters indicate individuals and are in the same order as individual numbers in Figure 3.8a. Letters at the top of the split apply to the left branch. Based on the three groups identified in this tree, the 30 individuals were re-classified for the GLM.

B) FORAGING AND TRAVELLING IN RELATION TO ENVIRONMENTAL PARAMETERS

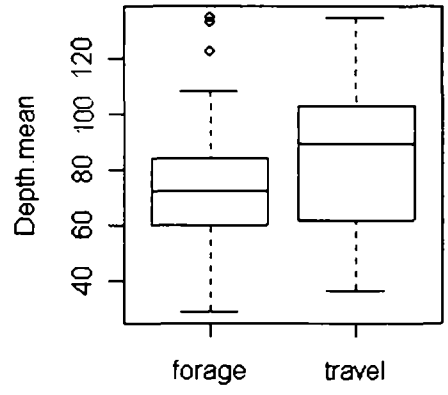
Based on the exploratory analysis, continuous explanatory variables selected for the behavioural analysis included sea surface temperature, chlorophyll-a, mean depth, maximum slope and current speed (Figure 3.11). The direction of the tidal current was included as a factor (Figure 3.12). Residuals of chlorophyll-a, maximum slope and tidal current showed deviations from a normal distribution in the univariate ANOVA's, but an ln-transformation resulted in normally distributed residuals in all three cases. Sea surface temperature and mean depth did not need to be transformed for inclusion in the logistic regression.



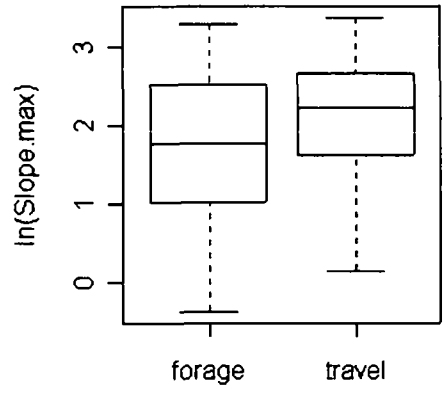
a) Sea Surface Temperature



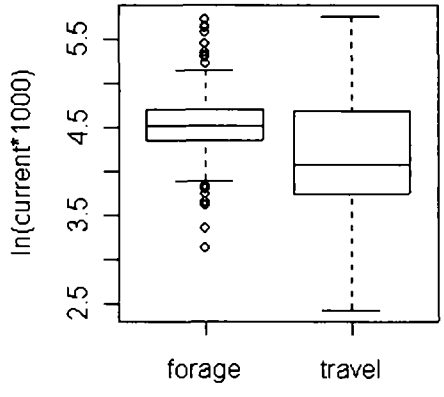
b) Chlorophyll-a



c) Mean Depth



d) Maximum Slope



e) Current Speed (m/s *1000)

Figure 3.11. Boxplots of continuous environmental variables included in the logistic regression for foraging vs. travelling.

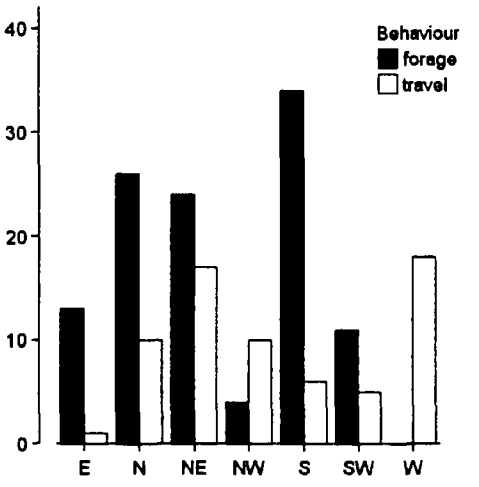


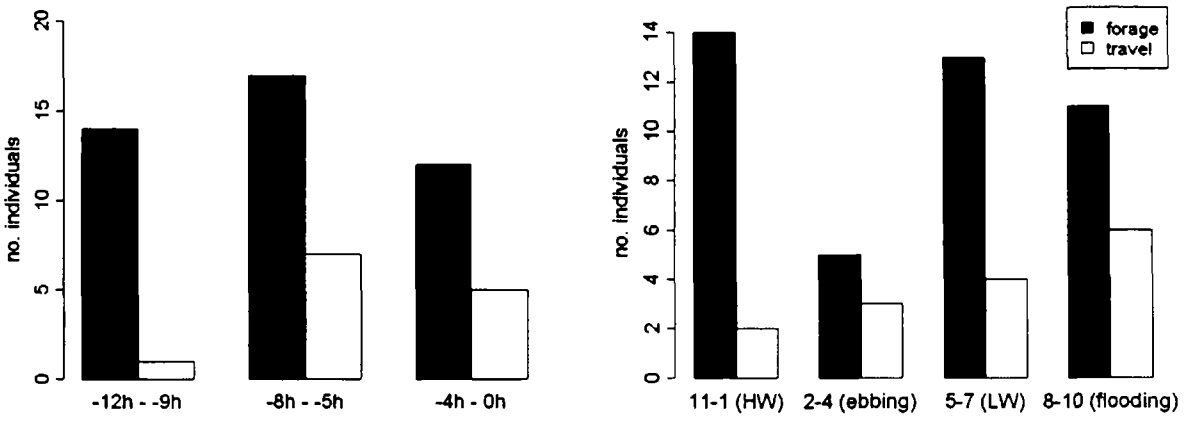
Figure 3.12. Histogram of the categorical variable 'Direction of tidal current' included in the logistic regression for foraging vs. travelling behaviour.

The only significant parameters included in the final logistic regression model were direction and strength of tidal current (Table 3.5): minke whales were more likely to forage in areas of strong tidal currents (regression coef. = 1.1713, std. error = 0.3722; Figure 3.11), and travelling was more likely in areas with a current flow in a north-westerly as opposed to easterly (the dummy variable) direction (regression coef. = -3.0781, std. error = 1.2268; Figure 3.12). The model including both tidal strength and direction explained almost half of the total variance in the data (Nagelkerke $R^2 = 0.458$).

Table 3.5. Final model of logistic regression on behaviour (foraging vs. travelling).

Parameters included	df	Deviance	AIC	Likelihood ratio	p-value
Current direction & strength		164.373	180.373		
- strength	1	175.689	189.689	11.316	<0.001
- direction	6	223.853	227.853	59.480	<0.001

By contrast, no difference could be found between foraging and travelling behaviour at different times of day (Chi-square = 3.464, df = 2, p = 0.177) or different tidal states (Chi-square = 2.996, df = 3, p = 0.392; Figure 3.13).



a) Hours before sunset b) Tidal state

Figure 3.13. Number of individuals represented for a) different times of day and b) tidal states. HW = high water, LW = low water.

Feeding strategies and interactions with seabirds

A total of 606 seabird aggregations were encountered between 2001 and 2007 (excluding 2002), of which 438 (72%) could be fully counted. In all, 17 species were found associated with these groups, including common guillemots (*Uria aalge*), razorbills (*Alca torda*), puffins (*Fratercula arctica*), herring gulls (*Larus argentatus*), greater (*Larus marinus*) and lesser (*Larus fuscus*) black-backed gulls, kittiwakes (*Rissa tridactyla*), Manx shearwaters (*Puffinus puffinus*), gannets (*Morus bassanus*), shags (*Phalacrocorax aristotelis*), great (*Stercorarius skua*) and arctic (*Stercorarius parasiticus*) skuas, common (*Sterna hirundo*) and arctic (*Sterna paradisaea*) terns, storm petrels (*Hydrobates pelagicus*), sooty shearwaters (*Puffinus griseus*) and fulmars (*Fulmarus glacialis*). However, the last nine species contributed less than 0.4% (and then dominated by shags and gannets) to the total number of individuals, and were excluded from the analysis.

Among the four guilds, Manx shearwaters dominated with respect to overall number of individuals, but auks were present in feeding aggregations most frequently (Table 3.6). A moderate negative correlation ($-0.7 < r < -0.5$) was detected between numbers of large gulls and Manx shearwaters, whilst correlations between numbers of individuals for all other pairs of guilds were weak ($r<0.5$). Due to the large sample sizes, all correlations were significant ($p<0.001$), but no strong co-linearity was detected (Figure 3.14), and group sizes of all guilds could therefore be included in the same model. The same applied when only presence / absence of guilds were taken into consideration (Table

3.7). Seabird aggregations were distributed all over the study area, but the largest groups were confined to the area around the entrance to the Sound of Sleat between the north end of the Isle of Eigg and Mallaig on the west mainland coast, and between Eigg and Arisaig (Figure 3.15).

Table 3.6. Descriptive statistics for seabird aggregations, divided into the four guilds. CGL = common guillemot, RAZ = razorbill, PUF = puffin, HG = herring gull, GBB = greater black-backed gull, LBB = lesser black-backed gull.

		No. groups	% groups	Total no. ind.	% ind.	Group size Max	Mean	st. dev
Auks	(68.5% CGL) (31.4% RAZ) (0.1% PUF)	492	81.2	25785	18.6	2000	59	153
Gulls	(95.2% HG) (4.6% GBB) (0.2% LBB)	281	46.4	22617	16.3	1100	52	95
Kittiwakes		248	40.9	14246	10.3	3000	33	177
Manx Shearwaters		304	50.2	76141	54.9	3500	174	447
TOTAL		606		138789		3700	317	512

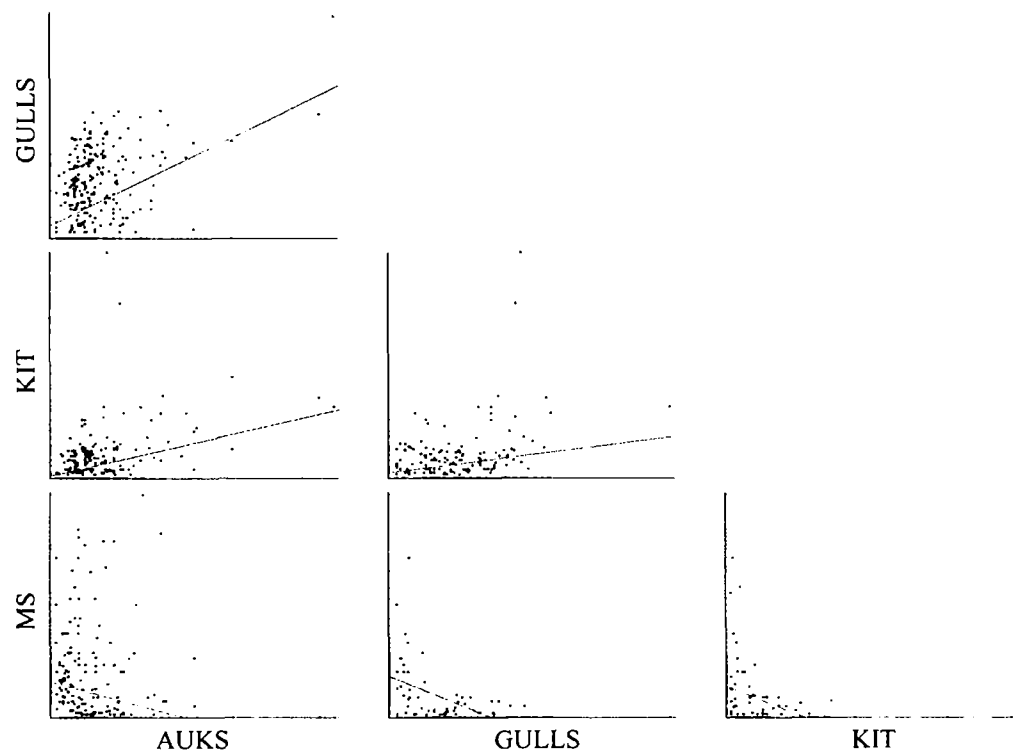


Figure 3.14. Correlations between numbers of individuals between the four guilds. The axis range for each group is from 0 to the maximum group size. All group sizes are root-transformed.

Table 3.7. Proximity matrix (Russell and Rao Measure) for presence / absence of seabird groups, indicating in what proportion of aggregations two guilds were seen together.

	Auks	Gulls	Kittiwakes
Gulls	0.442		
Kittiwakes	0.370	0.279	
Manx Shearwaters	0.348	0.117	0.134

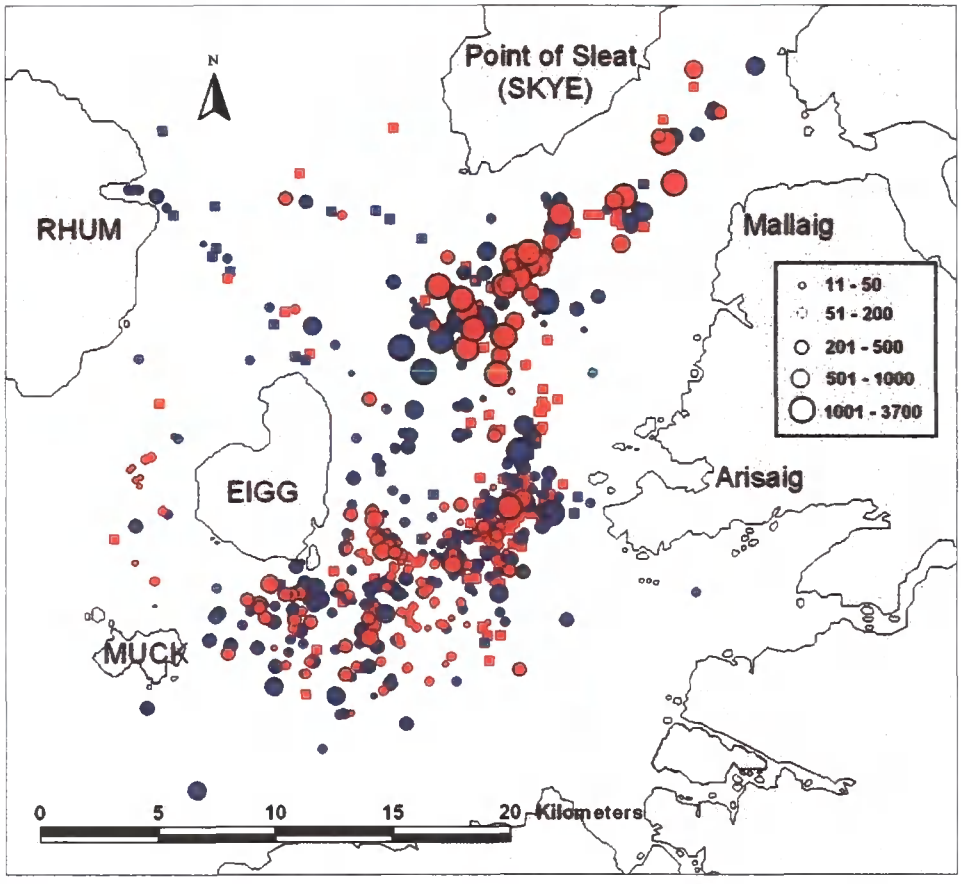


Figure 3.15. Locations of seabird aggregations with (red) and without (blue) minke whales associated. Sizes of symbols are proportional to overall group size of bird aggregations which were counted. Squares represent bird groups which were not counted.

Minke whales were associated with 48.3% of all recorded seabird aggregations (n = 606), or 39.5% of fully counted groups, respectively (n = 438). There was no obvious spatial segregation between bird groups with and without minke whales present (Figure 3.15). The presence and group size of auks in seabird aggregations were the most important variables in determining whether a minke whale was associated with birds: the likelihood of a minke whale being present with a seabird aggregation increased slightly but

significantly with the number of auks present (Figure 3.16; logistic regression: global $p < 0.001$, B = 0.094, odds ratio = 1.099, 95% CI: lower = 1.054, upper = 1.146), although this variable only explained a small percentage of the total variance (Nagelkerke R^2 = 0.069). All other variables initially included in the model were non-significant (Figures 3.16-18). This result remained the same when the model was reduced to presence / absence of functional bird groups and overall number of guilds present: only the presence of auks remained significant (Figure 3.19) and was included in the final model (global $p < 0.001$, B = 1.012, odds ratio = 2.751, 95% CI: lower = 1.768, upper = 4.279; Nagelkerke R^2 = 0.047), whereas the presence of all other guilds, as well as the number of groups present (Figure 3.17b) were insignificant. However, if individual guilds were not included in the model, but only the total number of individuals in the aggregation instead, overall group size, the Simpson's Index, and dominant guild were all necessary to explain the presence of minke whales (Figures 3.16-18; global p = 0.001, Nagelkerke R^2 = 0.08). A whale was more likely to be associated with larger seabird aggregations (B = 0.028, p = 0.011, odds ratio = 1.028, 95% CI: lower = 1.006, upper = 1.051) with high diversity (Simpson's Index: B = 0.546, p = 0.036, odds ratio = 1.726, 95% CI: lower = 1.035, upper = 2.878), and if the group was dominated by auks (dominant group: p = 0.003; B_{Auks} = 1.067, p = 0.031, odds ratio = 2.908, 95% CI: lower = 1.102, upper = 7.675).

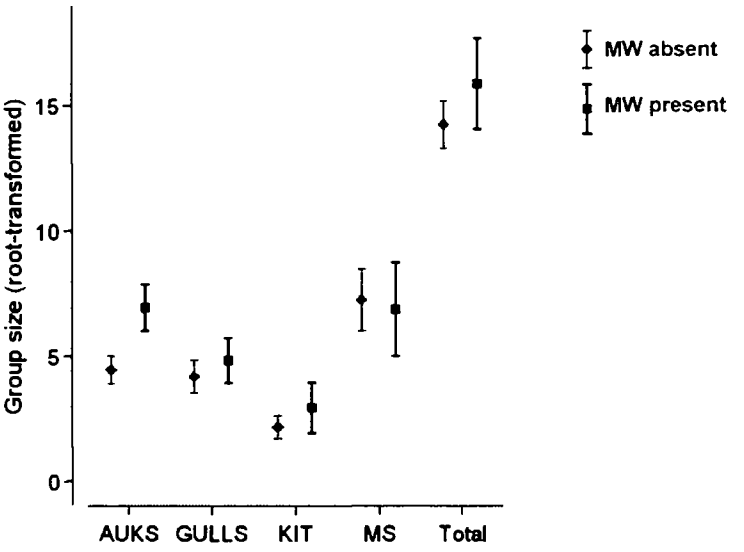


Figure 3.16. Mean group sizes (+/- 95% confidence interval) of the four guilds and total size of seabird aggregations for presence / absence of minke whales (MW). N=438. KIT = kittiwakes, MS = Manx shearwaters.

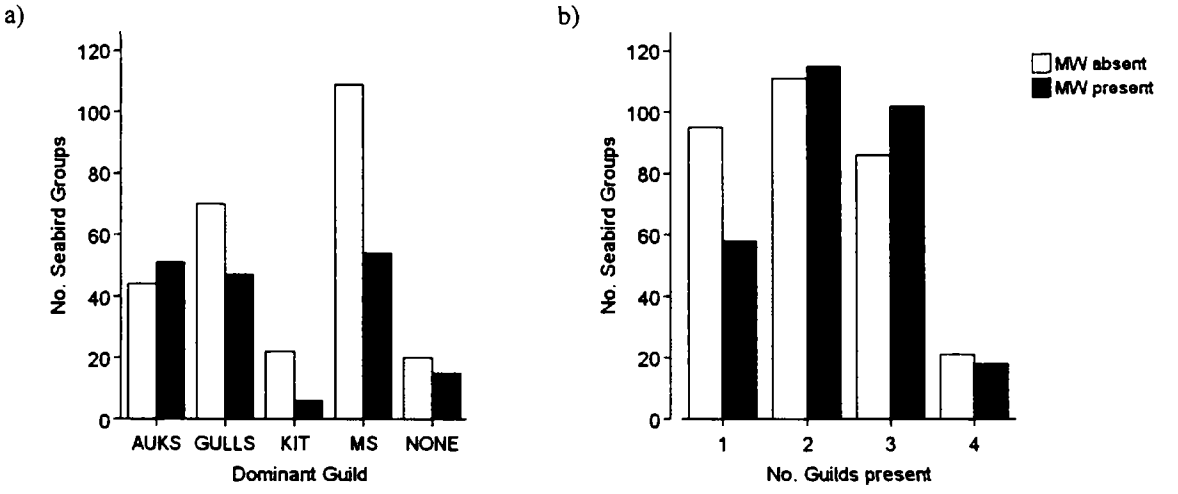


Figure 3.17. Presence / absence of minke whales with bird aggregations, a) dominated by different guilds (n=438; fully counted groups only), and b) with different numbers of guilds present (n=606; all groups). KIT = kittiwakes, MS = Manx shearwaters, MW = minke whale.

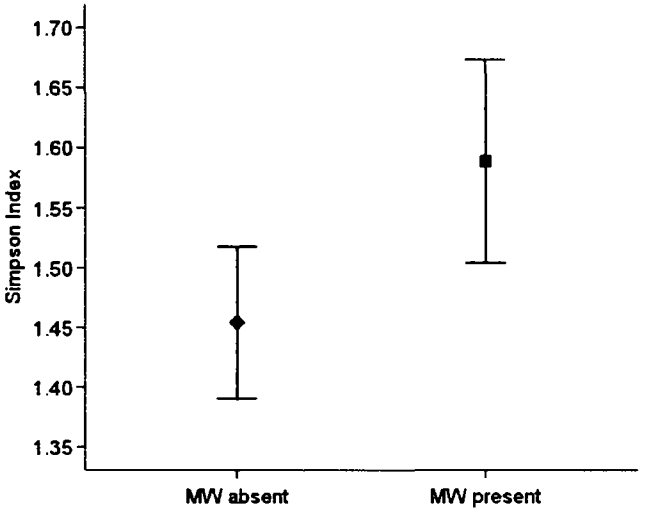


Figure 3.18. Minke whale presence in dependence of the Simpson's Index of a seabird aggregation with respect to the four guilds (n=438).

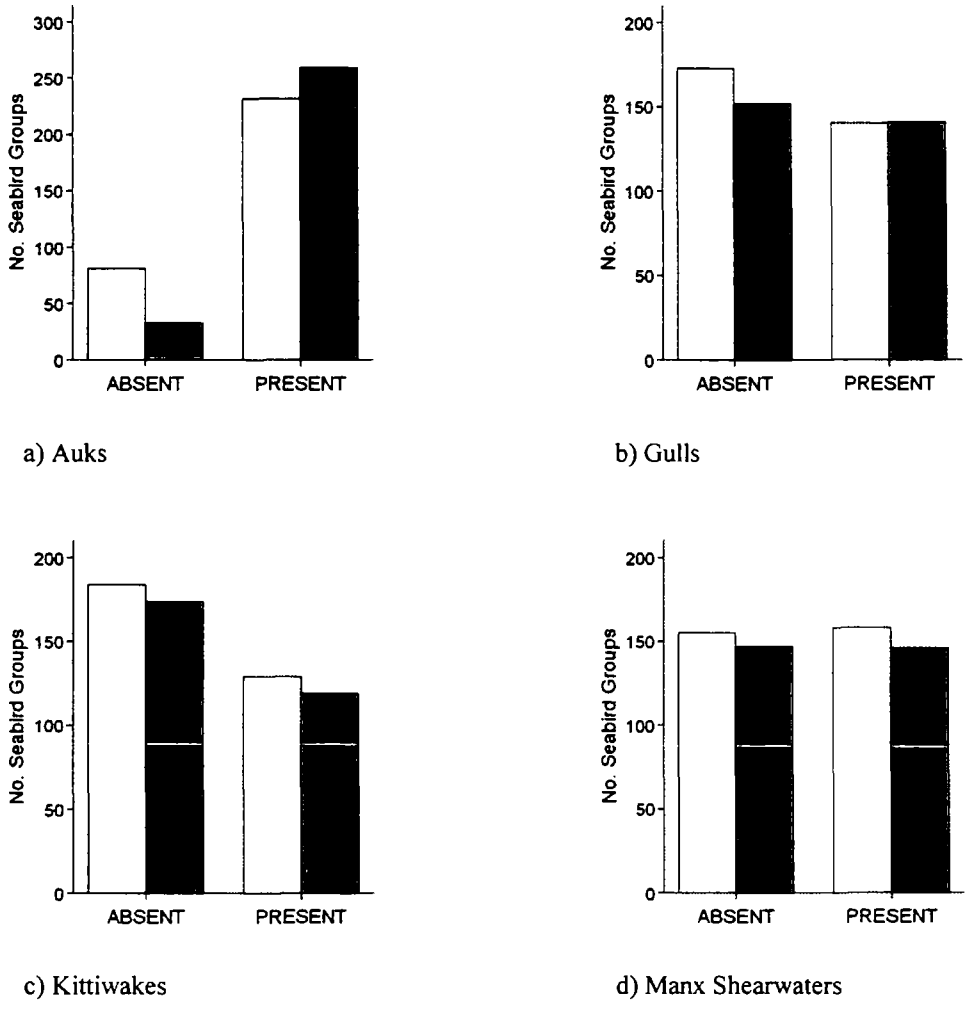


Figure 3.19. Presence / absence of minke whales with seabird aggregations in dependence of presence / absence of the four guilds. White bars = minke whale absent, black bars = minke whale present. N=606

As expected, the likelihood of observing a minke whale surface-feeding was significantly higher if kittiwakes and large gulls (for both: B = 0.729, p = 0.014, odds ratio = 2.072, 95% CI: lower = 1.162, upper = 3.696; global $p < 0.001$, Nagelkerke $R^2 = 0.104$) were present. On the other hand, surface-feeding activity by the whales was independent of the presence of auks and Manx shearwaters (the two guilds able to dive for fish), as well as of the number of guilds present (Figures 3.20, 3.21).

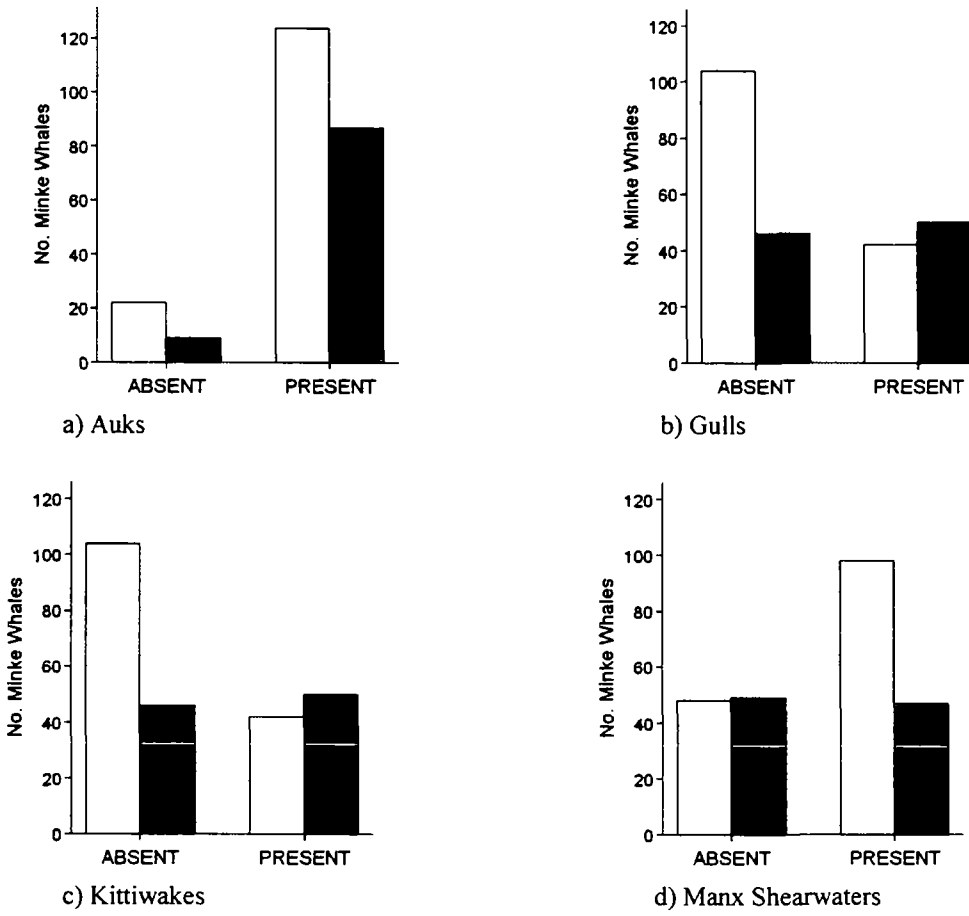


Figure 3.20. Surface feeding activity of minke whales in relation to presence / absence of the four seabird guilds. White bars = no surface feeding (n=146), black bars = surface feeding observed (n=96).

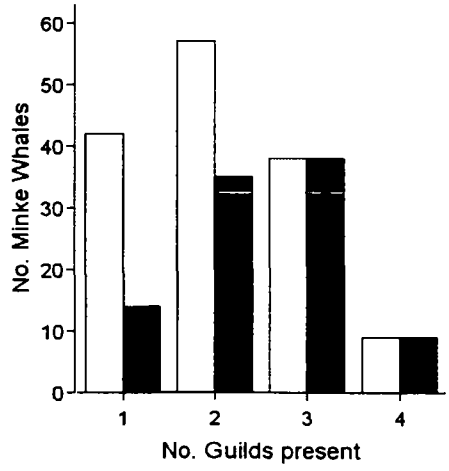


Figure 3.21. Observations of surface-feeding activity by minke whales in relation to the presence of different numbers of seabird guilds. White bars = no surface-feeding observed, black bars = surface-feeding observed.

DISCUSSION

Site fidelity

No consistent ranging patterns could be detected between individually identified minke whales, with some individuals being photographed within the same small area over the course of several days (e.g. in the Sound of Sleat in 2006 and 2007), but other whales having apparently large home ranges, indicated by their absence from the study area for days or weeks before returning, and a high number of single sightings. Minke whale distribution around the Small Isles was more or less continuous, and no evidence was found of exclusive adjoining ranges between individuals as described for animals off Washington State (Dorsey, 1983). As expected, the degree of site fidelity between days was positively correlated with the intensity of feeding activity: most re-sightings of the same individuals within years occurred during several days of calm weather in September 2004, as well as July 2007, when animals were feeding in groups of four up to ten whales. It might be argued that the favourable weather alone could have resulted in better photographic conditions and thus better quality of the photo-ID pictures, so that matching individuals between days became easier, or that resulting high encounter rates over the short term increased the likelihood of re-sighting the same individuals. However, similar weather conditions were encountered in 2003 without resulting in higher re-sighting rates between days. It is therefore more likely that these findings represent a real pattern in whale residency within the study area due to favourable feeding conditions. Surface stabilization through calm, sunny weather combined with neap tides following a period of mixing by wind and tides enables rapid growth of phytoplankton cells (Pingree *et al.*, 1968). This in turn results in the proliferation of zooplankton, which attracts small shoaling fish. It would therefore be expected that feeding conditions for minke whales should be stable over the course of several days when the water is stratified. Indeed, the two periods with high re-sighting rates between days both occurred during neap tides combined with calm and sunny conditions, following previously unsettled weather.

Re-sighting rates of individuals between years were also lower around the Small Isles by comparison with the San Juan Islands (Dorsey, 1983; Hoelzel *et al.*, 1989). In part, this may be explained by the more subtle markings of Hebridean whales: the conspicuous small oval scars (probably caused by cookie-cutter sharks), which were used as an important identifying feature of individual minkes on the west coast of North

America (Dorsey *et al.*, 1990; *personal observation*), are largely absent in North Atlantic animals (Gill *et al.*, 1994; *personal observation*). In addition, a larger proportion of - as yet unmarked - young whales appear to use the Hebrides as a feeding ground by comparison to the San Juans (*personal observation*) or the Gulf of St. Lawrence (U. Tscherter, *personal communication*). The degree of interannual site fidelity can therefore not be compared directly between regions.

Predictably, a total lack of re-sightings of animals from other seasons coincided with the lowest total number of individuals identified in the two poorest years (2005 and 2006) with lowest overall minke whale sighting rates (see Chapter 2). All years with sighting rates of ≥0.5 whales per hour also yielded matches with animals from other seasons. The observed patterns of site fidelity both within and between years confirm that minke whales adapt their summer home ranges to prey availability. If the spatial and temporal distribution of resources is predictable and feeding conditions are good, the animals remain within a small area; if prey patches are unpredictable, minke whales appear to increase their home ranges accordingly. This is also consistent with the threshold foraging behaviour reported for baleen whales off Newfoundland (Piatt & Methven, 1992): if prey density falls below a certain threshold, foraging becomes unprofitable, and the animals move away to look for food elsewhere. The overall short residence times in the study area and the apparently large home ranges of Hebridean minke whales together suggest that prey distribution in the region is patchy and relatively unpredictable. It should therefore be beneficial to the animals to adopt a generalist foraging strategy rather than specialize in one type of feeding within a small area as e.g. minkes around the San Juan Islands off Washington State seem to do.

Diving behaviour and use of the physical environment for foraging

Dive times during daylight hours were determined primarily by individual differences, although temporal effects (yearly, seasonal and tidal, as well as light intensity), as well as behaviour (foraging vs. travelling), were found to also influence dive duration when tested for each parameter separately. Gunnlaugsson (1989) measured the longest dives for a minke whale tracked in deep open water (1800m depth) off Iceland, compared to shorter dives in shallower regions (≤350m). Areas in which focal follows were conducted in the present study were no deeper than 250m. Bathymetry may therefore have an effect on dive time only at more extreme depths, beyond those occurring around the Small Isles

on the continental shelf. Furthermore, a depth effect would only have been expected if minke whales adjusted their foraging in the water column according to bathymetry. This would be expected in species feeding near the sea floor, but not necessarily for pelagic feeders. Blix & Folkow (1995) found that minkes (with time-depth recorders attached) off northern Norway and Svalbard foraged more in the upper depth layers (≤50m), and this seems to apply to Hebridean whales, too, judging by both the lack of a relationship between dive times and bathymetry, and the fact that there was frequent feeding activity at the surface.

Differences in dive times would also have been expected to be significant in the model for different behavioural categories such as foraging vs. travelling, and possibly with environmental parameters commonly associated with these behaviours, even when corrected for individual effects. However, the present results are also consistent with those from radio-tagged minkes examined by Blix & Folkow (1995) in that the only differences they found in dive times between behavioural categories involved sleeping animals at night, whereas dive duration was very similar between feeding and cruising individuals. They calculated that the energetic cost of swimming is remarkably low in the minke whale (e.g. by comparison to gray whales). This might explain the non-significance of differences in dive times between normal daily behaviours which would otherwise be expected to involve different energy requirements. Individual effects on dive duration, on the other hand, probably involve a number of factors such as age, size and sex, as well as nutritional status and overall body condition of the animal. These parameters are extremely difficult to determine in the field, and no attempt was therefore made to correct for them in the model. Although no obvious differences in individual surface-feeding strategies could be detected, as occurs for example for minkes in the San Juan Islands (Hoelzel *et al.*, 1989) and the Gulf of St. Lawrence (Tscherter & Morris, 2007), more subtle individual foraging specializations undetectable at the surface may exist in Hebridean whales, and could be a further factor accounting for the strong individual effects on dive times. Since all animals were followed within a relatively small study area and were probably feeding mainly on the same prey, no adjustment of dive times was necessary according to different prey types, so that variation in dive duration based only on individual factors makes sense.

The most important environmental variables associated with foraging behaviour as opposed to travelling were the strength and direction of tidal currents. Travelling

behaviour was observed only more frequently than foraging when the current was flowing in a westerly or north-westerly direction, i.e. away from the mainland. Whether this direction results in less suitable foraging conditions than during current flow from more open areas towards the mainland or down the Sound of Sleat is unknown, however. The three individuals which showed travelling behaviour while the current was flowing NW or W, respectively, involved a single animal moving out of the Sound of Sleat (SW then W), one travelling SW near Maxwell Bank, and one moving out of the study area between Eigg and Muck in a westerly direction. All three animals were thus travelling with the tidal current, at least two of them apparently on their way out of the study area. Moving with the current was not a general pattern for all travelling whales, however; travel directions against the current or at right angles to it were also observed. Assuming that the relationship between minke behaviour and current direction was not solely a sampling effect, the two animals which were probably leaving the study area might have been taking advantage of the flow direction for a longer journey, whereas other travelling individuals may only have been translocating to another foraging area nearby, irrespective of the current relative to their swimming direction.

The positive correlation between foraging activity and strength of tidal current was anticipated, since tidally active areas are not only important locations for nutrient renewal through mixing of water masses (Pingree *et al.*, 1968), but also have the potential of channelling and herding small prey such as bait fish (Simard *et al.*, 2001). These locations have previously been identified as important feeding areas for other cetaceans such as harbour porpoise (Evans & Borges, 1996; Pierpoint, 2008; Marubini *et al.*, 2009), which show dietary overlap with minkes (Santos & Pierce, 2003; Santos *et al.*, 2006). For minke whales, tidally active areas have been identified qualitatively as favourable feeding locations (e.g. Evans, 1982; Gaskin, 1982; Hoelzel *et al.*, 1989) and have been linked with their distribution through bathymetric slope (Ingram *et al.*, 2007). However, when corrected for other environmental variables, current strength played no role in determining minke distribution *per se* on the west coast of Scotland (see Chapter 2). On the other hand, the significant positive relationship between current strength and foraging behaviour indicates that this parameter is important for minke whales within a smaller area, particularly at a fine scale (both spatial and temporal). In other words, it appears to determine which locations, and at what times, are worth investigating for prey in greater detail, given that more broad-scale environmental parameters (such as bathymetry, temperature and phytoplankton concentration) indicate that the region is worth visiting at

all. Distributing themselves according to these latter parameters, but then fine-tuning their foraging behaviour within an area according to the predictable daily and local variation in the direction and strength of the tidal currents, would make sense for minke whales energetically, since broad-scale movements would be determined mainly by variables changing relatively slowly (over days or weeks in the case of phytoplankton concentration or water temperature) or not at all (bathymetry), whereas fine-scale movements can readily be adjusted according to a parameter changing over a matter of hours, but with a regular and predictable pattern.

Feeding strategies and interactions with seabirds

Interactions between two marine top predator groups, marine mammals and seabirds, may in some cases be used to make inferences about the feeding behaviour of marine mammals which in most cases cannot be observed directly underwater. Close associations between minke whales with several seabird taxa were used in this study to obtain an insight into the foraging strategies and feeding behaviours of the whales. Predictions were made on the most likely association patterns of the whales with specific seabird guilds with respect to 1) the most likely relationship between the two groups (who profits from whom?), 2) the mechanism of locating prey patches (visually vs. acoustically), and 3) the surface-feeding behaviour of minke whales.

1) Relationship between minke whales and seabirds: In most cases of cetacean – seabird interactions, seabirds appear to take advantage of cetaceans making prey available near the surface (Harrison, 1979; Evans, 1982; Pierotti, 1988; Camphuysen & Webb, 1999). The positive relationship between overall size of the seabird aggregation and its diversity with the presence of a minke whale found in the third logistic regression model is intuitive, since a larger fish-shoal near the surface is expected to attract both whales and a large number and variety of birds, but it does not allow any inferences about the relationship between whales and seabirds, other than that both are feeding on the same prey. In the present analysis, however, the closest association was detected between minke whales and auks, and this result was consistent between the three different logistic regressions: a minke whale was more likely to be associated with a bird aggregation when auks were present, their numbers were high, and when they represented the dominant guild within the aggregation. In the first two analyses, numbers and presence of auks,

respectively, were the only significant parameters left in the final model. These results can be interpreted as either simply a particularly close link between minke whales and auks with respect to diet (neutralism), or a real interaction.

Whereas it is probably true that the overlap in diet between minke whales and auks is particularly strong, this also applies to kittiwakes (Table 3.1). In order to determine whether the close relationship between whales and auks is based purely on neutralism or whether there might be a positive interaction between the two taxa, it is important to know who tends to arrive at fish-shoals first. Whereas the other three seabird guilds - large gulls, kittiwakes and Manx shearwaters - are very mobile and can follow each other or (potentially) minke whales in search of food, auks tend to be more stationary, often sitting on the water in rafts. Based on this behaviour, their foraging strategy may involve waiting in potentially productive locations until the foraging conditions become more favourable, whereas both minke whales and the other seabird taxa move around more. Since no feeding hot-spots could be identified in particular locations within the study area, these two different strategies may yield similar pay-offs. Minke whales appear to adjust their foraging activity according to the tidal currents (i.e. both spatially and temporally; see above). The implication from this result on foraging strategy is that the animals move around the study area to locations with comparatively strong currents at any state of the tidal cycle, i.e. covering a large area and thus increasing the chances of finding prey frequently. Given their low energetic cost of swimming (Blix & Folkow, 1995), this strategy is likely to be more rewarding than it would be for auks, which expend more energy during flight than other seabirds due to their short, narrow-winged, low-endurance wing design with heavy wing-loading in proportion to their body weight (Gaston, 2004: pp. 51-57). Waiting in prospective productive locations would therefore be energetically beneficial to auks, yielding fewer but potentially more reliable feeding opportunities than for whales and the other seabird taxa. Although small groups of auks did sometimes join in on already actively feeding seabird aggregations, they were never observed joining minke whales or potentially following them. Combined with the fact that auks are capable of driving fish towards the surface themselves, it is therefore more likely that minke whales joined auks on feeding locations rather than vice versa, and that it was mainly the case that whales were utilizing resources that the auks (and other seabirds which had arrived before the whale) were already feeding on. This conclusion was also reached independently from observations during focal follows: the surfacing location of a focal whale previously not associated with birds could often be predicted to

occur in the direction of an actively feeding seabird aggregation that had formed at some distance, before the animal would lunge in the centre of the group. Since every surfacing position of the focal animal was known and the boat was kept close to it, the focal whale could not have been involved in herding the fish-shoal towards the surface. This behaviour of exploiting fish-shoals already herded by auks may not be restricted to surface-feeding only, but could also occur at depth. Indeed, close associations between 50-300 auks, 2000-3000 Manx shearwaters and up to eight minke whales at a time were observed (particularly in July 2007), mostly without any obvious surface-feeding activity by the whales. The virtual absence of kittiwakes and large gulls (i.e. the two guilds dependent on prey close to the surface) was a further indication that prey - which was clearly present judging by the unusually high densities of both whales and seabirds - was distributed mainly at depth.

Although the strong association between minke whales and auks in feeding aggregations suggests that minke whales do exploit prey patches already herded by auks when they happen to become available in the whales' vicinity, auks and whales appeared to behave largely independently of each other most of the time, and there was no indication that minkes were concentrated in locations where auks were present. No evidence was found for foraging specializations by individual minke whales as described by Hoelzel *et al.* (1989) for the population in the Juan de Fuca Strait, WA. However, the nature of the behaviours and habitat observed there, together with the more frequent re-sightings of individual whales, made the detection of this more likely in that study. Furthermore, surface feeding behaviour without associated seabirds was rarely observed around the Small Isles.

Three focal whales switched between "bird-association" feeding and surface-feeding without seabirds present within the same general area, and during periods of high activity during 2004 and 2007 in the Sound of Sleat, group members of a feeding aggregation of three to six whales associated with seabirds would occasionally lunge at a distance of up to 500m away from the aggregation in an area where no birds were present. Surface-feeding also occurred when no auks were present, but, instead, only gulls, kittiwakes or Manx shearwaters. The whales do therefore corral fish independently in this area when needed, although taking advantage of fish already herded by auks is likely to be a more energy-efficient and thus preferable feeding strategy for the animals when these opportunities are available.

Where resources are patchy and unpredictable, it should be advantageous to an animal to be opportunistic. In the same way that minke whales sometimes may profit from the feeding activities of auks, but otherwise herd fish on their own, the larger gulls, kittiwakes and especially single-species flocks of Manx shearwaters likely joined both auks but also minke whales, if the latter were driving fish towards the surface. The fact that these three seabird guilds were not good predictors of the presence of a whale is further indication that joining foraging minkes represents only one of probably many strategies for these groups for finding food. Kittiwakes and particularly large gulls were also frequently observed accompanying fishing vessels. Other "natural" feeding opportunities for all seabirds, including auks, may have involved harbour porpoises, seals or predatory fish such as mackerel driving fish-shoals close to the surface. Harbour porpoises were observed in association with 93 (15.3%) seabird aggregations, and harbour seals with at least four (0.7%). Mackerel could never be observed directly, but the presence of one or more gannets with 62 (10.2%) bird groups may have been an indication that mackerel were present, since they are a well-known prey of this species (Nelson, 2002). It is unlikely that mackerel were involved in bringing to the surface a very high proportion of the fish-shoals on which the birds were feeding, however, since a particular spatial pattern would be expected in this case. The best mackerel fishing grounds in the area are on and around Maxwell Bank (Figure 2.1b; Chapter 2), (C. & R. Dyer, *personal communication*), and yet no spatial clustering of feeding aggregations in those locations was recorded.

2) Mechanism of locating prey patches: Only auks played a significant role in the prediction of whether a minke whale was present in the vicinity of a seabird group or not. If minke whales relied on visual cues to locate prey patches, as suggested for humpback whales in the Northwest Atlantic (Pierotti, 1988), a close association between feeding minke whales and flocks of kittiwakes - the most conspicuous seabird group - would have been expected. In the same way as kittiwakes serve other seabirds as indicators for a prey patch, they might lead minke whales to a fish-shoal. However, no significant positive relationship was detected between either presence or number of kittiwakes in a feeding aggregation with the presence of a whale. This suggests that minke whales are unlikely to use conspicuous seabirds as visual cues to locate feeding locations in the way that humpbacks may do.

A whale might conceivably use the noise generated by a seabird feeding aggregation (although this is heard predominantly above water or close to the surface) or by a tight fish-ball itself that is being chased by auks to pin-point its exact position, at least at short to intermediate ranges. At long range, i.e. a kilometre or more away, physical characteristics of the environment such as current strength and direction (see above) are probably more important in predicting where favourable feeding conditions are likely to occur.

3) Surface-feeding behaviour: Minke whales were often seen in association with seabird groups without showing any obvious feeding activity at the surface. Under those circumstances, it was impossible to tell whether the animal was foraging or feeding at greater depth. As expected, the visible surface-feeding activity of minke whales associated with seabird aggregations showed a positive relationship with the presence of the two surface-feeding seabird guilds - kittiwakes and larger gulls - whereas it was independent of the presence of auks and Manx shearwaters, which are both able to dive for fish. The presence of kittiwakes and large gulls can thus be regarded as a relatively reliable indicator of fish close to the surface. On the other hand, a close association between minke whales and auks or Manx shearwaters without obvious surface lunges and in the absence of large gulls or kittiwakes, would be a likely indication for feeding activity at depth.

In conclusion, the association patterns with seabirds are consistent with the apparently opportunistic nature of minke whale foraging to optimize energy gain per unit time during the relatively short, but intensive, summer feeding season. The whales appear to combine an ability to exploit fish-shoals herded by auks when available, probably as a means of saving prey handling time, with an adjustment in foraging vs. traveling behaviour according to predictable fine-scale variations in the environment (i.e. tidal currents). Additionally, changes in both seasonal and interannual site fidelity according to prey availability indicate that minke whales show high degrees of plasticity with respect to their behavioural patterns as an adaptation to the patchiness and spatial and temporal unpredictability of resources on their summer feeding grounds.

GENERAL DISCUSSION & CONCLUSIONS

As a species, the minke whale is recognized as a generalist, being widely distributed over the world's oceans and, by comparison to other balaenopterids, showing relatively large population sizes and feeding on a wide variety of prey (both fish and krill; Stewart & Leatherwood, 1985; Perrin *et al.*, 2002). Concentrating upon the North Atlantic form, *Balaenoptera acutorostrata acutorostrata*, and on one particular feeding area - the west coast of Scotland - the aim of this thesis was to shed light on how behavioural and ecological factors influence patterns of habitat use of the species during the non-breeding season, and the extent to which these reflect population structure.

Three main hypotheses were examined. The first, that habitat use within a feeding area should be determined by biotic and abiotic factors associated with the optimisation of foraging efficiency, was supported. The spatial distribution of minke whales both over the entire Hebrides and within a smaller core study area was related to the abiotic variables bathymetry, topography and water temperature, as well as the biotic variables phytoplankton concentration and sandeel presence (the former in autumn, the latter in spring). Moreover, temporal changes in the use of the study area were paralleled by 1) interannual differences in phytoplankton concentration (which likely affects the distribution of zooplankton and fish); 2) sprat landings (the main prey species of minke whales in the core study area during late summer and autumn); and 3) changes in seabird numbers and their breeding success (those taxa that feed on the same prey as minkes).

The second hypothesis, that site fidelity (already demonstrated by other authors, and confirmed within the small core study area here) should be adaptive since local environmental conditions require learning for efficient prey exploitation, was also supported, by a) the fact that foraging behaviour was linked to the strength and direction of tidal currents, the exploitation of which requires intimate knowledge of the physical characteristics of an area, and b) the fact that a dietary switch from sandeels to sprat, which was evident through the season, was linked with a change in the relative importance of relevant environmental parameters in determining minke whale distribution. Temperature influences the availability of sandeels in the water column (Winslade, 1974), and was relevant in determining minke whale distribution in spring, whereas phytoplankton concentration is likely to influence the distribution of the pelagic

sprat, and was thus relevant for minke distribution in August and September. Knowledge of the relationships between which environmental parameters determine the availability of different prey species within an area suggests experience through learning.

The final hypothesis, that site fidelity to feeding grounds would be reflected by genetic differentiation between these areas, was rejected. No spatial differentiation was found between any of the feeding grounds examined. Instead, the presence of two cryptic breeding populations was detected, which formed mixed assemblages in all feeding areas with adequate sample sizes.

Foraging efficiency through learning and flexibility: In the Hebrides, minke whales appear to combine detailed knowledge of the local biotic and abiotic conditions relevant for foraging with a high degree of behavioural flexibility. No obvious individual feeding specialisations could be identified comparable to observations around the San Juan Islands off Washington State (Hoelzel *et al.*, 1989) or in the St. Lawrence Estuary (Tscherter & Morris, 2007), although individual differences in dive times might have been an indication for behavioural specialisations undetectable from surface observations. Individual minkes around the Small Isles also did not specialise in the use of particular localised areas as has been observed both in the San Juans and the St. Lawrence. Instead, the feeding and foraging behaviour of animals in the Hebrides showed various elements of opportunism and high adaptability to temporally variable local conditions in every respect that was investigated. At a fine spatial scale, the whales demonstrated a capability for opportunistically exploiting fish-shoals concentrated towards the surface in tight bait-balls by auks when they became available in their vicinity, thus probably saving energy on herding fish themselves. On the other hand, the animals were highly mobile during foraging, as suggested by the dependence of foraging (as opposed to travelling) behaviour on the tidal currents. An important prerequisite for this mobility during foraging is likely to be the low energetic cost of swimming in this species (Blix & Folkow, 1995).

The dependence of foraging activity upon tidal conditions gives the selection of suitable prey patches within a local area both a spatial and temporal component. Being able to predict the strength and direction of tidal currents at particular times and locations requires intimate knowledge of the local conditions, which can only be acquired through learning. The same applies to the switch in diet between spring and late summer and the corresponding changes in association with physical environmental parameters. In spring, when the distribution of minke whales on the west coast of Scotland matches that of

predicted sandeel presence, suggesting that sandeel are the target prey, it makes sense for the animals to orient not only towards likely sandeel habitat (determined mainly by bottom sediment type), but to concentrate upon areas where the fish are active in the water column, as determined by temperature (which can change over time). This relationship does not apply to all prey species that minke whales take (for example sprat). Consequently, water temperature appears to play a less important role in the distribution of the animals later on in the season, when their main diet is thought to change from sandeels to sprat, and chlorophyll concentration instead becomes more important in determining their distribution. The relationships between the particular times and locations at which different prey species are likely to be available in large enough quantities to sustain a whale, and what temporally variable parameters have to be taken into account to predict their availability, probably all need to be learned through experience, and are likely to be specific to a particular feeding ground. Considering that minke calves are usually independent by the time they arrive in their feeding areas, and mother-calf pairs are uncommon during summer, a young whale may have to acquire an understanding of these complex relationships mostly on its own. However, an ability to learn from conspecifics is also possible. If a novel feeding strategy used by one individual can be copied by others over time, as suggested for minke whales in the St. Lawrence (Tscherter & Morris, 2007), learning from other whales the relevant foraging skills suitable for a particular area seems feasible for a calf.

Site fidelity and environmental variables: The necessity to become familiar with local environmental conditions and to learn how to use them for efficient exploitation of the particular prey species that an area has to offer, assumes a certain degree of site fidelity to a feeding ground. Indeed, site fidelity previously reported for animals from both Scotland and other parts of the North Atlantic was also found for the small core study area around the Small Isles. However, re-sighting rates were considerably lower by comparison to the San Juan Islands (Hoelzel *et al.*, 1989) or the St. Lawrence (Tscherter & Morris, 2007), and were not in agreement with individuals showing strong specializations to a particular local area. This might be due to differences in prey distribution between the different geographic regions. Where food is locally abundant, animals would be expected to show smaller home ranges, whereas they should range over larger distances if the distribution of resources is more patchy. Bottlenose dolphins, for example, also show differences in the size of their home ranges in different habitats, which is most likely related to the

distribution of their prey in each area (see Würsig & Würsig (1979), and Wells *et al.* (1980)). If the spatial and temporal distribution of minke whale prey is more variable on the west coast of Scotland by comparison to the San Juans and St. Lawrence, the animals should show larger home ranges, possibly combined with higher behavioural flexibility, in this habitat. Around the Small Isles, this relationship also seemed to have a temporal component. When feeding conditions were evidently good, based on high feeding activity of both whales and seabirds, re-sighting rates of the same individual minkes between days were high (this applied particularly to 5-8 September 2004 and 20-24 July 2007; Table 3.2). At other times, however, individuals were rarely seen in the study area on more than a single day within a field season. The conclusion that the animals are highly mobile during foraging, based on the dependence of foraging and travelling behaviour upon the tidal currents, is therefore consistent with the findings from photo-ID: the whales appear to range over wide distances, not only within the core study area over the course of the tidal cycle, but also over a much greater spatial scale during their entire summer feeding season in the Hebrides, only staying within a local area as long as feeding conditions are particularly good.

At both spatial scales investigated, minke whale distribution showed a dependence not only on fixed environmental parameters (depth and topography), but also on temporally variable predictors (temperature and chlorophyll concentration). In combination with a knowledge of the fixed physical features of an area and its prey species, these latter variable parameters may help the whales assess where feeding conditions will be favourable, and could be an explanation for their highly flexible patterns of habitat use. Water temperature (and temperature differences indicating fronts) can be sensed by a whale over the skin, and phytoplankton concentrations themselves might be assessed visually by the relative turbidity of the water. This would enable an animal to orient towards likely concentrations of its pelagic prey according to these parameters at intermediate to long distances (perhaps exceeding tens of kilometres). Given that the combination of depth, topography, temperature and phytoplankton concentration make an area worth visiting, foraging behaviour at the local scale can then be fine-tuned according to parameters which change over a matter of hours, but in a predictable manner, such as tidal currents. Exploiting dynamic environmental conditions at both small and large spatial scales to locate worthwhile prey patches seems energetically profitable for minke whales. Their prey is mostly pelagic and its spatial and temporal distribution therefore more unpredictable than that of benthic prey. Relying

solely on fixed environmental parameters or a limited feeding area for finding prey would carry the risk of having to wait until feeding conditions improve and would waste valuable time within a comparatively short window of feeding opportunity during the summer months. An orientation according to temporally variable parameters such as water temperature and phytoplankton concentration during foraging would also be consistent with large between-year shifts in the distribution of minke whales within the Barents Sea, depending on the fluctuating location of the Polar Front (Bjørge, 2001).

Movements on feeding grounds: In agreement with their mobility during foraging and flexibility in local habitat use, minke whale sighting rates in the Hebrides were highly variable between years, not only around the Small Isles, but also over the entire west coast of Scotland. In the same years that sighting rates were very low in the Hebrides, unusually large numbers of minkes were reported off the north coast of Scotland (during early summer 2005 and 2006), whilst comparatively high sighting rates also occurred off the Isle of Man in the Irish Sea (Sea Watch Foundation, *unpublished data*). Although it is unknown whether individuals from the Hebrides were amongst them, this is quite possible, given the interannual distributional shifts observed in the Barents Sea, which occurred over a much larger area (Bjørge, 2001). By contrast to some other North Atlantic feeding grounds of the species (e.g. Jan Mayen or Iceland, which are more clearly separated from each other), the Hebrides by no means represent an isolated summer feeding area for minkes. Around the British Isles, the continental shelf is particularly broad, and suitable feeding areas used by the animals during summer occur in the Irish Sea (especially the St. George's Channel and to a lesser extent around the Isle of Man), off the south and west coasts of Ireland, in the Hebrides, off the north coast of Scotland (including the Northern Isles) and throughout the central and northern North Sea (Evans *et al.*, 2003). These areas are directly adjacent to each other, so that the Hebrides represent only one location in an almost continuous potential feeding ground encompassing the northern half of the British Isles, and probably beyond. Due to the proximity of these feeding areas to one another, available prey species (e.g. sandeels and clupeids around the British Isles) and physical environmental parameters are both likely to be similar, so that particular foraging strategies suited to one local area may be applied to another adjacent to it without too much loss in foraging efficiency. Individual minke whales normally spending the summer months feeding in the Hebrides may therefore find it relatively easy to switch to an alternative feeding area off northern Scotland or in the

Irish Sea, if prey densities within their usual summer range fall below a certain threshold. However, in order to test this hypothesis, animals would need to be satellite-tagged over a sufficiently long period of time.

Movements and population structure: From minke whale feeding grounds over the entire North Atlantic, only two breeding populations could be identified, and these were relatively closely related. The existence of two populations implies that North Atlantic minke whales segregate on at least two separate breeding grounds, although their locations are unknown. They are likely to be located in offshore areas, based upon observations of a general offshore movement of animals during autumn, combined with a paucity of sightings near the coast in winter (Anderwald & Evans, 2007). Despite their mobility, a certain degree of site fidelity or traditional use of a particular winter range (as is the case for gray and humpback whales: Rice & Wolman, 1971; Clapham, 2009), may therefore exist, but the question of minke whale movements during winter remains completely open until a reasonable number of individuals can be satellite-tracked for extended periods of time.

Mixing of breeding stocks in feeding areas, as suggested previously for another balaenopterid in the North Atlantic, the fin whale (Daníelsdóttir *et al.*, 1991; Bérubé *et al.*, 1998), was also detected for minke whales in the present study. Mixed assemblages of the two populations were found on every summer feeding ground with sufficient sample sizes for genetic analysis, which is consistent with findings for this species from the western North Pacific (Wada, 1991; Pastene *et al.*, 1992; Goto & Pastene, 1997), although on a much wider geographic scale. Wherever the breeding grounds in the North Atlantic may be, the presence of representatives from both populations in feeding areas as far apart as the St. Lawrence Estuary and Svalbard implies migration distances of at least, and probably well in excess of, half the breadth of the North Atlantic (i.e. over 2000km one way). This is also in agreement with the large distance covered by a sub-adult minke whale satellite-tagged in Denmark, which travelled to the Azores, Madeira and into the Mediterranean within only three months (Teilmann *et al.*, 2005). Although this particular individual might have been traumatized by being caught in a net, therefore behaving atypically (it travelled south during the summer, when animals are normally concentrated in northern areas, and then entered the Mediterranean, where minke whales are only vagrant visitors), the distance of its journey may not be atypical for the species during migration. The high mobility of the animals is thus reflected not only on a local (the

Small Isles), or intermediate (the Hebrides with adjacent feeding areas), but also the wider geographic scale (the North Atlantic).

The presence of mixed assemblages of the two breeding populations on summer feeding grounds appears to be largely consistent with the flexible patterns of habitat use found within the Hebrides. Minke whale distribution within the study area was determined by physical (both fixed and temporally variable) and biotic factors of the environment, and differences in the use of this feeding area in response to temporal changes in some of the biotic variables were detected between years even within the relatively short time period of this study. The temporal use of habitat is therefore likely to be associated with changes in physical and biotic environmental variables over time, and the consequent movement of individuals between feeding areas according to these long-term changes would likely then generate mixed assemblages of breeding populations on feeding grounds.

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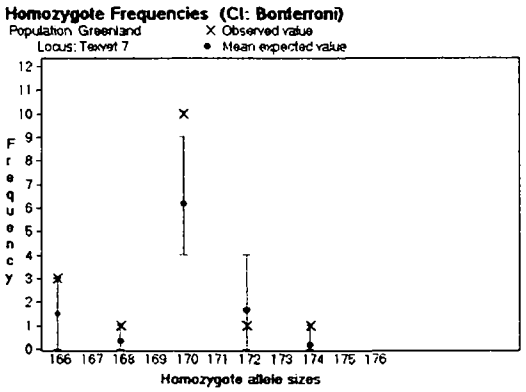
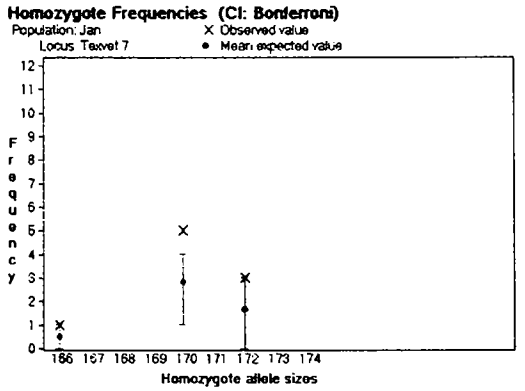
APPENDIX

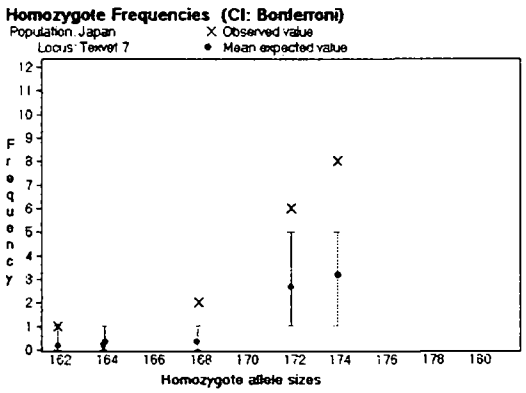
Appendix 1.1. Expected and observed homozygote frequencies for the locus – population combinations for which the presence of possible null alleles was suggested in MICROCHECKER 2.2.3



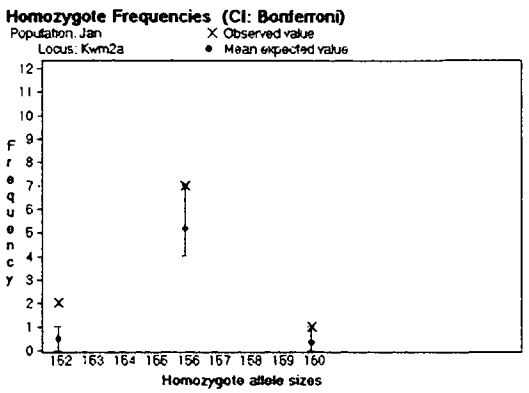
a) Texvet 7 for Greenland



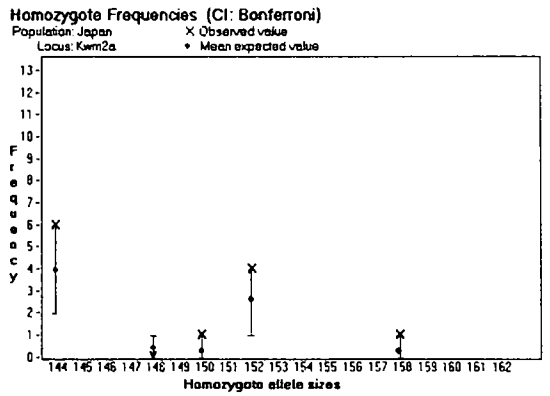
b) Texvet 7 for Jan Mayen



c) Texvet 7 for Japan



d) Kwm2a for Jan Mayen



e) Kwm2a for Japan

Appendix 1.2a. Pairwise Fst values for all populations with Texvet 7 included. Abbreviations for populations are the same as in Table 1. F_{st} values are listed above, significance values below the diagonal.

	UK	GR	IC	CN	NS	SV	JM	JP
UK	-	0	-0.002	0.00736	0.00642	-0.00287	0.00634	0.18354
GR	0.45	-	-0.00088	0.00773	0.00719	0.00068	0.01049	0.20413
IC	0.80	0.59	-	0.00599	0.00109	-0.0026	0.00349	0.194
CN	0.08	0.08	0.11	-	0.01093	0.00049	0.00691	0.18543
NS	0.03	0.03	0.31	0.04	-	-0.00045	0.00317	0.20421
SV	0.89	0.36	0.90	0.42	0.53	-	0.00018	0.18435
JM	0.10	0.03	0.20	0.17	0.24	0.45	-	0.19795
JP	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	-

* p-values which were still significant after Bonferroni correction ($p<0.0028$).

Appendix 1.2b. Pairwise Fst values for all populations with Kwm2a excluded. Abbreviations for populations are the same as in Table 1. F_{st} values are listed above, significance values below the diagonal.

	UK	GR	IC	CN	NS	SV	JM	JP
UK	-	0.00035	-0.00223	0.01167	0.00115	-0.00263	0.00936	0.18918
GR	0.41	-	0.00091	0.01186	0.00828	0.00169	0.01583	0.20093
IC	0.81	0.33	-	0.0105	0.00042	-0.00152	0.00684	0.18951
CN	0.03	0.04	0.04	-	0.01347	0.00535	0.01369	0.18963
NS	0.32	0.02	0.39	0.03	-	-0.00286	0.00254	0.18912
SV	0.84	0.26	0.72	0.15	0.83	-	0.00323	0.18358
JM	0.06	0.01	0.08	0.07	0.30	0.25	-	0.2017
JP	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	0.0001*	-

* p-values which were still significant after Bonferroni correction ($p<0.0028$).

Appendix 1.3. Linkage disequilibrium for regional comparisons: P-value for each locus pair across all regions (Fisher's method).

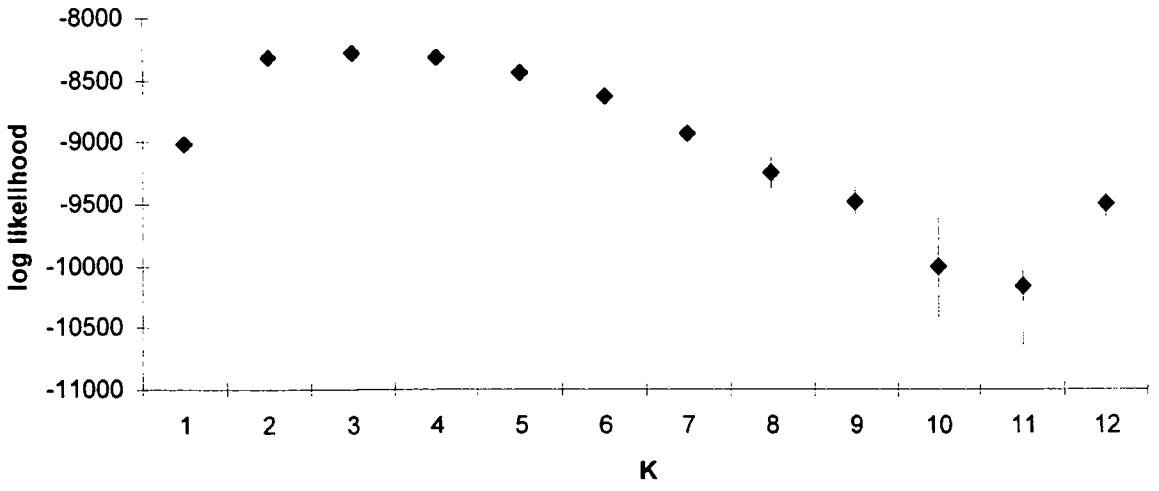
Locus pair			Chi2	df	P-value
EV1	&	Kwm2a	26.161	16	0.05181
EV1	&	GATA28	27.706	16	0.03427
Kwm2a	&	GATA28	14.627	16	0.55213
EV1	&	GT509	19.815	16	0.22867
Kwm2a	&	GT509	19.994	16	0.22049
GATA028	&	GT509	30.340	16	0.01632
EV1	&	Igf-1	16.582	14	0.27914
Kwm2a	&	Igf-1	20.759	14	0.10797
GATA028	&	Igf-1	16.452	14	0.28653
GT509	&	Igf-1	22.851	14	0.06274
EV1	&	GATA417	16.114	16	0.44503
Kwm2a	&	GATA417	28.339	16	0.02879
GATA028	&	GATA417	13.864	16	0.60886
GT509	&	GATA417	32.143	16	0.00958
Igf-1	&	GATA417	28.279	14	0.01306
EV1	&	EV37	Infinity	16	Highly sign.
Kwm2a	&	EV37	29.040	16	0.02367
GATA028	&	EV37	31.435	16	0.01184
GT509	&	EV37	16.771	16	0.40054
Igf-1	&	EV37	16.063	14	0.30952
GATA417	&	EV37	16.710	16	0.40462
EV1	&	GATA098	17.140	16	0.37661
Kwm2a	&	GATA098	23.501	16	0.10098
GATA028	&	GATA098	23.004	16	0.11362
GT509	&	GATA098	22.824	16	0.11853
Igf-1	&	GATA098	25.317	14	0.03156
GATA417	&	GATA098	8.305	16	0.93925
EV37	&	GATA098	28.829	16	0.02512
EV1	&	ACCC392	15.941	16	0.45711
Kwm2a	&	ACCC392	18.781	16	0.28016
GATA028	&	ACCC392	37.963	16	0.00153
GT509	&	ACCC392	19.151	16	0.26089
Igf-1	&	ACCC392	17.083	14	0.25177
GATA417	&	ACCC392	Infinity	16	Highly sign.
EV37	&	ACCC392	18.793	16	0.27956
GATA098	&	ACCC392	16.570	16	0.41395

Appendix 1.4. Pairwise Rho_{st} values for all populations with IGF-1 excluded. Abbreviations for populations are the same as in Table 1. Rho_{st} values are listed above, significance values below the diagonal.

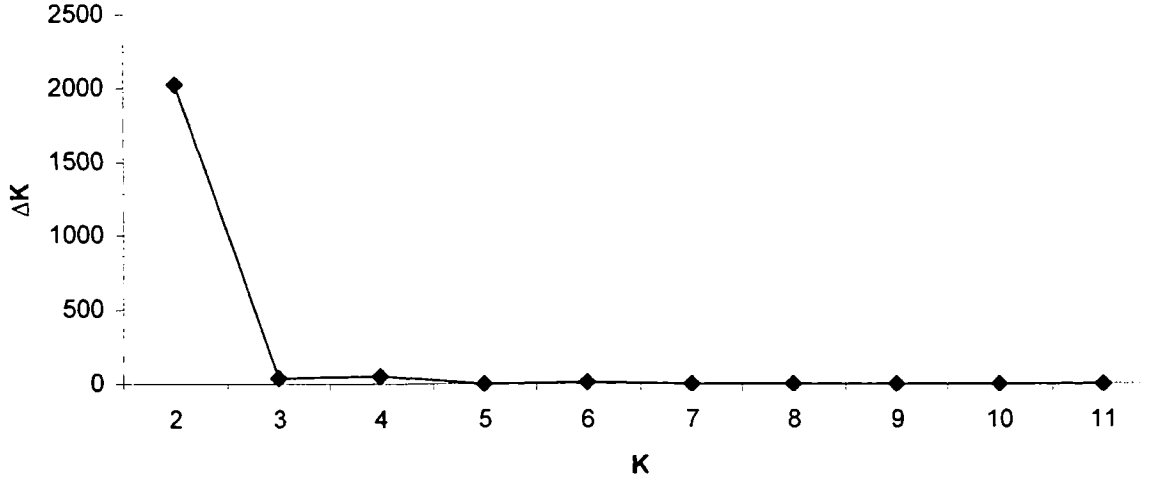
	UK	GR	IC	CN	NS	SV	JM	JP
UK	-	0.0029	0.0054	0.0036	0.0087	0.0035	0.0351	0.3956
GR	0.30	-	-0.0050	-0.0045	0.0058	-0.0045	-0.0031	0.4180
IC	0.17	0.81	-	-0.0047	0.0026	-0.0016	0.0114	0.4136
CN	0.34	0.64	0.63	-	0.0131	0.0017	0.0081	0.4346
NS	0.14	0.27	0.32	0.16	-	-0.0022	0.0133	0.4154
SV	0.26	0.77	0.59	0.41	0.60	-	0.0041	0.4069
JM	0.02	0.61	0.17	0.35	0.19	0.38	-	0.4459
JP	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	-

* p-values which were still significant after Bonferroni correction ($p<0.0028$).

Appendix 1.5. a) Average log likelihood values and b) second order rate of change of the likelihood function with respect to K (ΔK) for the STRUCTURE model including all North Atlantic samples and the out-group Japan.



a) Mean log likelihood values ± standard deviation between the four runs of equal K at different K's for the model with all populations included. The sharp increase in log likelihood values between K=1 and K=2 followed by the plateau for 2>K<5 indicate that 2 populations (North Atlantic vs. Sea of Japan) are represented by this model.



b) ΔK at different K's for the model with all populations included. The peak at K=2 confirms that only 2 populations (North Atlantic vs. Sea of Japan) are present.

Appendix 1.6. Linkage disequilibrium for comparison of STR2 vs. STR3: P-value for each locus pair across both populations (Fisher's method).

Locus pair			Chi2	df	P-value
EV1	&	Kwm2a	3.915	4	0.41767
EV1	&	GATA028	4.766	4	0.31217
Kwm2a	&	GATA028	4.708	4	0.31856
EV1	&	GT509	3.157	4	0.53192
Kwm2a	&	GT509	8.137	4	0.08669
GATA028	&	GT509	1.008	4	0.90863
EV1	&	IGF1	3.507	4	0.47676
Kwm2a	&	IGF1	11.965	4	0.01761
GATA028	&	IGF1	4.252	4	0.37301
GT509	&	IGF1	7.336	4	0.11915
EV1	&	GATA417	5.951	4	0.20284
Kwm2a	&	GATA417	2.232	4	0.69312
GATA028	&	GATA417	3.695	4	0.44885
GT509	&	GATA417	6.560	4	0.16102
IGF1	&	GATA417	7.351	4	0.11846
EV1	&	EV37	11.017	4	0.02638
Kwm2a	&	EV37	12.047	4	0.01700
GATA028	&	EV37	17.748	4	0.00138
GT509	&	EV37	2.802	4	0.59154
IGF1	&	EV37	4.050	4	0.39933
GATA417	&	EV37	8.377	4	0.07869
EV1	&	GATA098	1.624	4	0.80439
Kwm2a	&	GATA098	0.696	4	0.95184
GATA028	&	GATA098	3.286	4	0.51113
GT509	&	GATA098	4.252	4	0.37297
IGF1	&	GATA098	8.036	4	0.09028
GATA417	&	GATA098	5.342	4	0.25399
EV37	&	GATA098	8.033	4	0.09036
EV1	&	ACCC392	4.640	4	0.32628
Kwm2a	&	ACCC392	2.322	4	0.67680
GATA028	&	ACCC392	3.172	4	0.52945
GT509	&	ACCC392	4.638	4	0.32648
IGF1	&	ACCC392	1.800	4	0.77257
GATA417	&	ACCC392	1.978	4	0.73985
EV37	&	ACCC392	1.671	4	0.79590
GATA098	&	ACCC392	1.373	4	0.84888

Appendix 1.7. Numbers of individuals from STR2 and STR3 assigned correctly and incorrectly by GeneClass2.

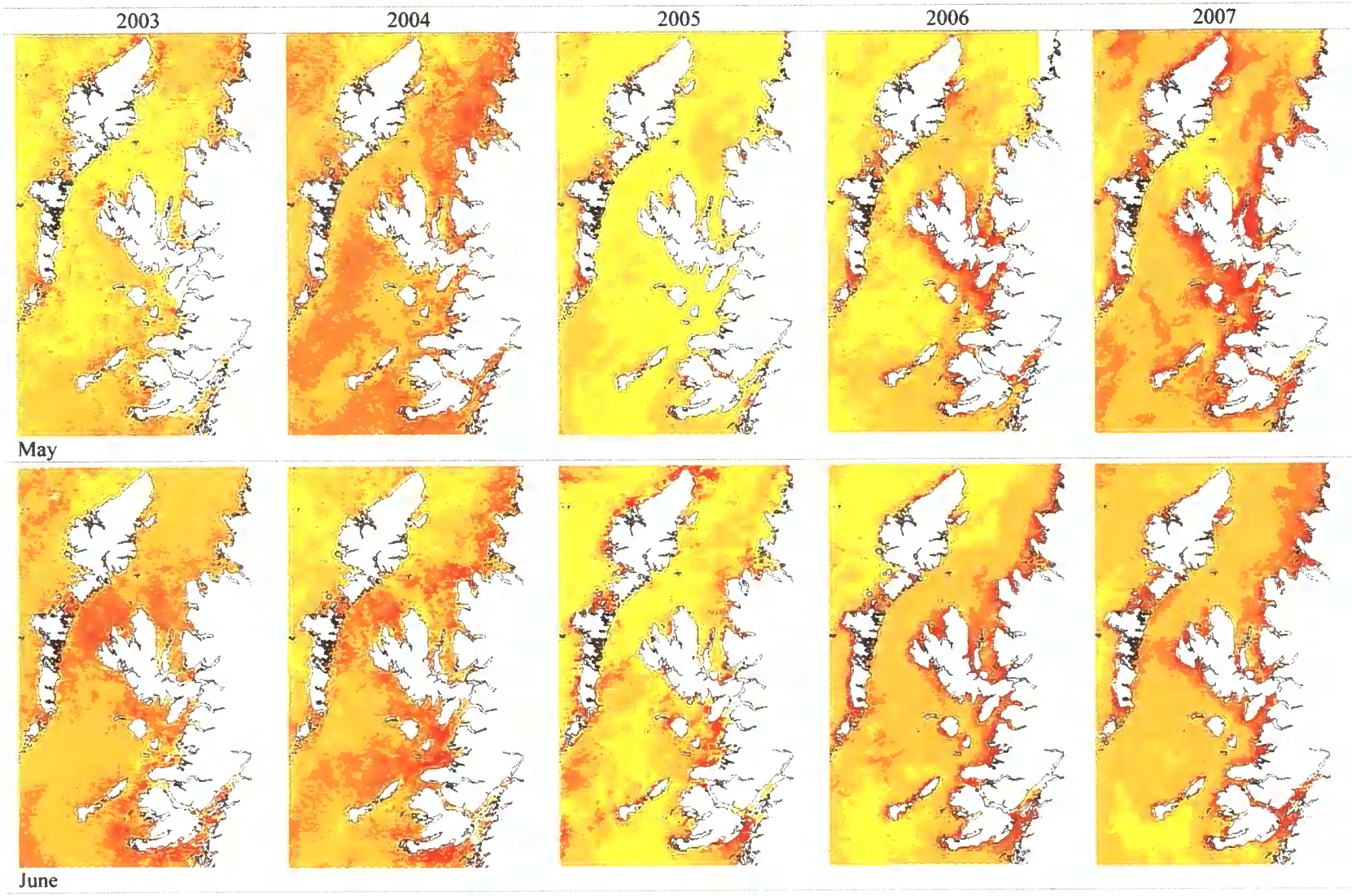
a) overall

	Assigned to:	
Origin:	STR2	STR3
STR2	125	8
STR3	6	123

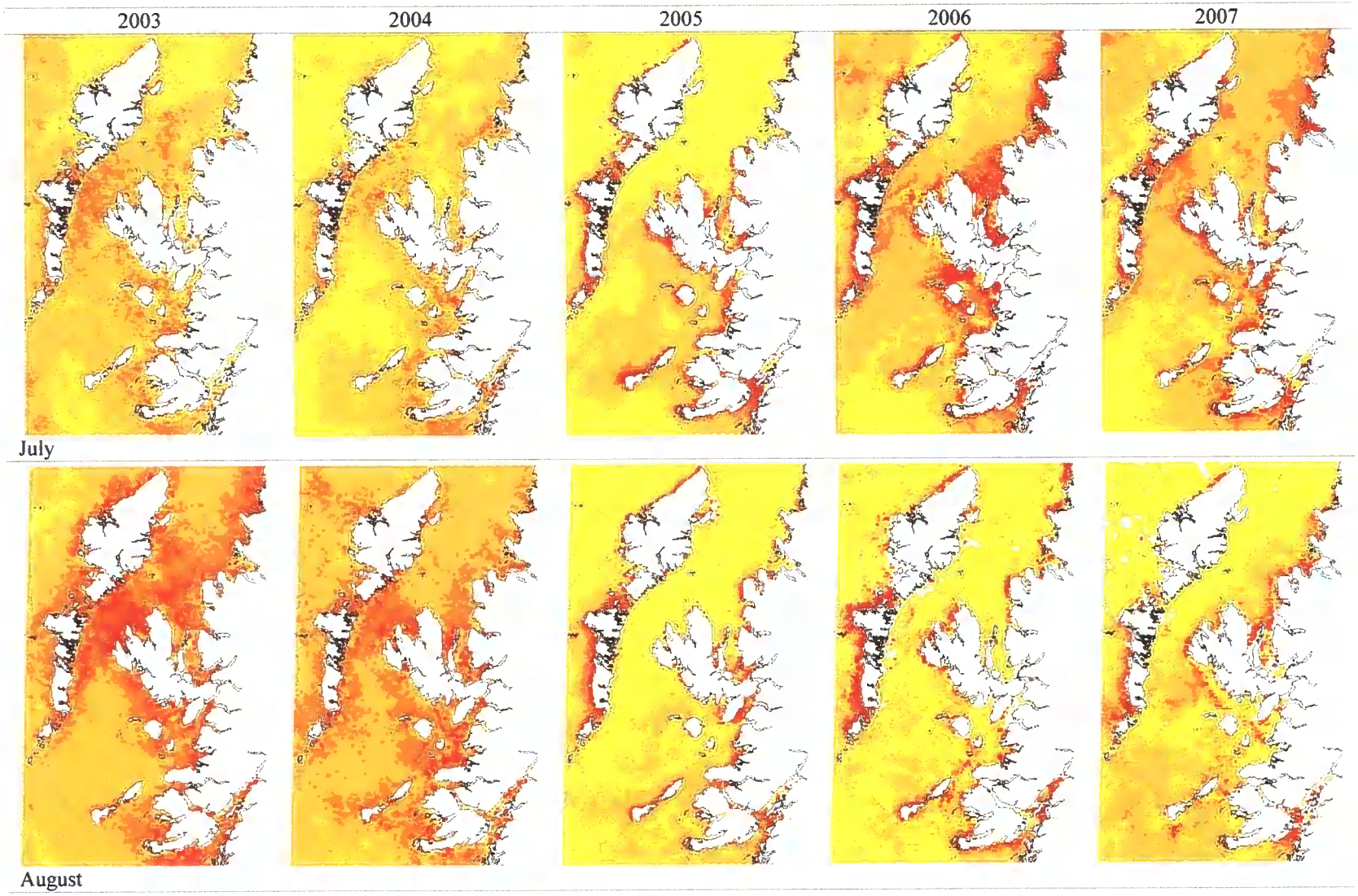
b) per geographic region (see Table 1.1 for abbreviations)

	Correct assignment:		Incorrect assignment:	
	STR2	STR3	STR2 to STR3	STR3 to STR2
UK	17	23	1	2
GR	11	24	1	-
IC	30	28	1	1
CN	6	8	-	1
NS	23	11	2	-
SV	18	25	3	2
JM	13	4	-	-
IR	4	-	-	-
SP	3	-	-	-

Appendix 2.1. Chlorophyll concentration May – September for entire Hebrides during the years with most survey coverage around the Small Isles.



Appendix 2.1, continued.



Appendix 2.1, continued.