

**Structure and dynamics of the
Gulf of Maine humpback
whale population**

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of the requirements for the degree of
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Abstract

Population structure and vital rates of Gulf of Maine (GOM) humpback whales, *Megaptera novaeangliae*, were studied by a combination of longitudinal data, region-wide surveys and modern mark-recapture statistical methods. Demography and rates of exchange were examined among six GOM areas. Juveniles and females were preferentially encountered in southern GOM habitats, including at the Studds Stellwagen Bank National Marine Sanctuary (SBNMS). Multi-state modelling also revealed unequal probabilities of movement between areas that was not explained by inter-area distance, adjacency, whale density or dominant prey type. Aerial surveys and photo-identification data indicated that the population was likely closed to migration between June and September. Otherwise, seasonal trends in population composition were consistent the demographically staggered migration reported in other oceans. Over-wintering occurred, but there was little evidence that a significant number of humpback whales failed to undertake or complete migration each year.

Vital rates varied with sex, age and time. Juveniles exhibited lower and more variable survival than adults and so were a potential source of downward bias in “non-calf” survival estimates. Males exhibited higher survival than females and achieved maximal survival at age five, the estimated age at male puberty. By contrast, females did not reach peak survival until the current average age at first birth (8.78 years, $s = 2.33$). The latter was significantly higher than previous estimates and females that recruited by age seven had a lower likelihood of subsequent survival than those that recruited late. Costs of reproduction persisted into adulthood, with breeders exhibiting lower survival than non-breeders. Calves born during years of low fecundity exhibited lower survival than those born when fecundity was high, possibly due to lower maternal investment. Costs of reproduction have not previously been described in cetaceans, but are consistent with the risks potentially associated with capital breeding.

Chapter 1:

Introduction

1.1 North Atlantic population

Humpback whales (*Megaptera novaeangliae*, Borowski 1781) have a world-wide oceanic distribution that is characterised by summer occupancy of mid- to high-latitude feeding areas and winter occupancy of low-latitude breeding areas (Clapham and Mead, 1999). In the North Atlantic, summer feeding aggregations occur in the Gulf of Maine, eastern Canada, west Greenland, Iceland and Norway (Katona and Beard, 1990; Smith *et al.*, 1999), although patterns of movement and exchange suggest that they likely comprise only four discrete populations (Stevick *et al.*, 2006). Fidelity to a specific feeding area is strong and maternally directed, such that calves born in low latitudes are recruited to their mother's feeding range during the period of maternal care (Martin *et al.*, 1984; Baker *et al.*, 1986; Clapham and Mayo, 1987b; Clapham and Mayo, 1990).

In winter, most individuals migrate from their separate feeding grounds to shared low latitude waters where mating and calving takes place. The principal North Atlantic breeding range lies along the Atlantic margins of the Antilles, from Cuba to northern Venezuela (Winn *et al.*, 1975; Balcomb and Nichols, 1982; Whitehead and Moore, 1982). The largest modern breeding aggregations occur at the Greater Antilles where photo-identification research has confirmed the presence of individuals from all primary feeding areas (Katona and Beard, 1990; Clapham *et al.*, 1993b; Mattila *et al.*, 1994; Palsbøll *et al.*, 1997; Smith *et al.*, 1999; Stevick *et al.*, 2003a). The eastern Caribbean was an important site of historic humpback whale fisheries in the North Atlantic (Mitchell and Reeves, 1983; Reeves *et al.*, 2001; Smith and Reeves, 2003). Although sightings persist in those areas, modern humpback whale abundance appears to be low (Winn *et al.*, 1975; Levenson and Leapley, 1978; Swartz *et al.*, 2003). Winter aggregations also occur at the Cape Verde Islands in the Eastern North Atlantic (Reiner *et al.*, 1996; Reeves *et al.*, 2002; Moore *et al.*, 2003). This was also an important site of historic commercial whaling (Smith and Reeves, 2003), but its modern importance remains unclear.

Humpback whales do not undertake a coastal migration in the Northern Hemisphere and this has limited insight into specific routes and timing (CeTAP, 1982; Mate *et al.*,

1998; Reeves *et al.*, 2004). In the Southern Hemisphere, migration occurs over several months in each direction and is demographically staggered (Chittleborough, 1965; Dawbin, 1966, 1997). Migration distances vary substantially among North Atlantic feeding populations migrating to the same breeding site (Stevick *et al.*, 2003a) and humpback whales are sporadically encountered in mid- to high-latitude waters while other whales are still on the breeding ground (Ingebrigtsen, 1929; Matthews, 1937; Mackintosh and Brown, 1956; Williamson, 1961; CeTAP, 1982; Sigurjónsson and Gunnlaugsson, 1990; Straley, 1990; Christensen *et al.*, 1992; Clapham *et al.*, 1993a; Weller *et al.*, 1996; Clapham *et al.*, 1997; Gregr *et al.*, 2000; Charif *et al.*, 2001; Barco *et al.*, 2002; Frantzis *et al.*, 2004; Thiele *et al.*, 2004; Kemper, 2005). It is unclear how many individuals are found outside the breeding ground in winter and whether they are over-wintering, late to depart or early to return.

Despite their wide ranging movements, humpback whales also exhibit high rates of annual return, within-season occurrence and occupancy to specific sites. It has been reported that 76% of the calves observed at one well-studied GOM area returned there as juveniles, and 89% of animals seen throughout their juvenile years returned when mature (Clapham and Mayo, 1987b). When observations are limited to one portion of a feeding ground, it is difficult to preclude equally high rates of return elsewhere. However, studies based on two or more feeding habitats have confirmed individuals to return to certain areas more often than expected by chance (Weinrich, 1998; Straley *et al.*, 2002; Larsen and Hammond, 2004; Stevick *et al.*, 2006). The factors that shape habitat preferences are not well-understood, but appear to include maternal distribution during the calf year (Clapham *et al.*, 1993a; Weinrich, 1998). There is presently no evidence that feeding ground distribution is influenced by social bonds after weaning (Weinrich and Kuhlberg, 1991; Clapham, 1993).

1.2 Gulf of Maine population

1.2.1 Stock identity

The Gulf of Maine (GOM), located at the eastern U.S./Canadian border, is the site of the southern-most summer feeding population in the North Atlantic. The species is observed regularly between April and October (CeTAP, 1982; Baraff and Weinrich, 1993; Clapham *et al.*, 1993a) and feeding aggregations can occur as late as December (Geraci *et*

al., 1989). Sightings are also made sporadically between January and March, the peak mating and calving season in the West Indies (CeTAP, 1982; Clapham *et al.*, 1993a).

Studies of exchange with other high latitude feeding grounds suggest that the GOM is a relatively discrete population (Stevick *et al.*, 2006). Nevertheless, approximately one-quarter of individuals identified in the coastal waters east of Nova Scotia (the Scotian Shelf) have also been catalogued in the GOM (Clapham *et al.*, 2003). Individuals have also been re-sighted in several more distant locations in eastern Canada and, exceptionally, off west Greenland (Katona and Beard, 1990; Stevick *et al.*, 2006). Given that exact migration routes between feeding and breeding grounds are not known, some of these individuals could have been seen while passing through the GOM in either direction (Katona and Beard, 1990; Stevick *et al.*, 2006). However, periodically high rates of exchange with eastern Canada has also occurred during periods of low GOM prey availability (Stevick *et al.*, 2006).

Since the 1990s, GOM humpback whales have also been encountered off the U.S. mid-Atlantic states (Swingle *et al.*, 1993; Wiley *et al.*, 1995). Sightings occur primarily in winter but extend into the peak of the summer feeding season in some cases. Nearly half of live whales and approximately one-third of stranded animals had a GOM sighting history (Barco *et al.*, 2002). The recent increased use of this region may represent a shift from another unidentified supplemental feeding area (Wiley *et al.*, 1995) or geographic expansion due to population growth (Barco *et al.*, 2002). However, 27% of the whales identified were from eastern Canada, making it unlikely that this reflects a simple southern expansion of the GOM feeding range (Barco *et al.*, 2002).

1.2.2 Distribution and prey

Within the GOM, humpback whales are broadly distributed from Cape Cod to south-west Nova Scotia (CeTAP, 1982; Hamazaki, 2002). Aggregations typically occur in areas of bathymetric relief such as shallow banks, ledges and slopes (CeTAP, 1982; Payne *et al.*, 1986; Hamazaki, 2002). However the density of humpback whales at each site varies within and between years, presumably in relation to local fluctuation in prey (Payne *et al.*, 1986; Payne *et al.*, 1990; Weinrich *et al.*, 1997). Humpback whales are generalists, feeding on a variety of schooling fish species and euphausiids across their range. Dietary preferences in the GOM have been inferred primarily based on observations of surface feeding and the spatial distribution of prey species. Sand lance, *Ammodytes* spp., is

generally thought to be the preferred prey species in the southern GOM (Overholtz and Nicolas, 1979; Hain *et al.*, 1982; Hays *et al.*, 1985; Payne *et al.*, 1986; Payne *et al.*, 1990; Weinrich *et al.*, 1992; Hain *et al.*, 1995; Weinrich *et al.*, 1997). Sand lance prefer relatively shallow, sandy substrates (Meyer *et al.*, 1979; Robards *et al.*, 1999) which are found predominantly in the southern portion of the region. Atlantic herring, *Clupea harengus*, can be found throughout the GOM, but is thought to be the main piscine prey from Jeffreys Ledge north (Hain *et al.*, 1982; Paquet *et al.*, 1997; Weinrich *et al.*, 1997). Large temporal fluctuations have been documented in the abundance of both Atlantic herring and sand lance stocks in the GOM over the past 30 years (Meyer *et al.*, 1979; Overholtz and Friedland, 2002). Large-scale shifts in humpback whale distribution are thought to reflect the differential availability of these prey types (Payne *et al.*, 1990; Clapham *et al.*, 1993a; Weinrich *et al.*, 1997).

Euphausiids are also a documented prey species in the GOM (Paquet *et al.*, 1997), but there are no data with which to determine their importance in the diet. Whereas these are the primary prey of humpback whales in the Southern Hemisphere, Kenney *et al.* (1997) theorised that they comprise no more than 5% of the diet of GOM whales. An unusual mortality event in the 1980s revealed mackerel as a prey species in the GOM (Geraci *et al.*, 1989). Barlow and Clapham (1997) characterised mackerel as an “uncustomary” prey in the region; however, it was also one of three items identified (in addition to krill and fish bones) in the stomach contents of five humpbacks caught at the northern mouth of the GOM in the late 1960s (Mitchell, 1973).

Larem *et al.* (1997) reported the stomach contents of one southern GOM carcass to contain a very different suite of prey, including: Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*) and weakfish (*Cynoscion regalis*). These coastal fish species were also detected in humpback whales stranded south of the GOM during the same period. Larem *et al.* (1997) interpreted their results as evidence that humpbacks consume these species as far north as Massachusetts, while noting that these fishes are not common north of New Jersey. However, these stomach contents may be indicative of a southerly distribution just prior to death, rather than exploitation of unusual prey types within the GOM.

1.2.3 Population structure and dynamics

GOM females born in the 1980s produced their first viable calf at an average age of six years (Clapham and Mayo, 1987a; Clapham, 1992; Barlow and Clapham, 1997). Consecutive year calving occurs infrequently in this population and others (Clapham and Mayo, 1987b; Clapham and Mayo, 1990; Glockner-Ferrari and Ferrari, 1990; Weinrich *et al.*, 1993; Barlow and Clapham, 1997). Instead, the average mature GOM female gives birth to a single calf every 2 to 3 years (Clapham and Mayo, 1987b; Clapham and Mayo, 1990; Barlow and Clapham, 1997). Calves are born between January and March and remain dependent until the autumn of the first year (Baraff and Weinrich, 1993). Wiley and Clapham (1993) reported that humpback whales were more likely to produce male offspring after longer than average inter-birth intervals. The authors hypothesised that such females were in superior maternal condition and interpreted their results as consistent with sex ratio manipulation theory (Trivers and Willard, 1973). However, they had no direct information on maternal condition and acknowledged that females reproducing more frequently might have been in equal, if not better condition.

Large mammal species generally exhibit high adult survival rates and this has proven to be the case for humpback whales as well as other large whales and sirenians (Buckland, 1990; Olesiuk *et al.*, 1990; Barlow and Clapham, 1997; Langtimm *et al.*, 1998; Caswell *et al.*, 1999; Chaloupka *et al.*, 1999; Best *et al.*, 2001; Rosenbaum *et al.*, 2002; Zeh *et al.*, 2002; Clapham *et al.*, 2003; Larsen and Hammond, 2004; Mizroch *et al.*, 2004; Bradford *et al.*, 2006; Ramp *et al.*, 2006). Estimates of juvenile and calf survival are less common in light of the need to observe individuals from birth. In the North Pacific, mortality in the first few months of life was estimated to be 0.182 (95% CI 0.023-0.518) based on a small sample of mothers identified on both their breeding and feeding grounds in the same year (Gabriele *et al.*, 2001). However, even that estimate does not account for deaths that occurred on the calving ground before a calf was detected. Barlow and Clapham (1997) approximated GOM 6+ month old calf survival at 0.875 (S.E.~0.047) for the period 1979-1991 based on a combination of return rates (0.828, 1979-1991) and the square of the adult female survival rate (maximum survival, 0.922), following Barlow and Boveng (1991). Rosenbaum *et al.* (2002) estimated mean juvenile survival by maximum likelihood techniques (0.7022, 1979-1995), but pooled calves with independent juveniles.

While it is often convenient to assume that vital rates are constant over time, this is unlikely to be the case in wild populations. Robust statistical techniques have yet to be applied to studies of reproduction in humpback whales. Rosenbaum *et al.* (2002) reported differential trends in fecundity between two clades of GOM matriline which they predicted could lead to significant changes in population genetic structure within 75 years. There is also an indication of lower fecundity following an “unusual mortality event” in the 1980s (Barlow and Clapham, 1997). Whereas modern mark-recapture statistical techniques were used to estimate other parameters in those studies, support for those findings came from a proportional fecundity analysis. With the availability of large, commercial whaling data sets fin whale fecundity rates have been shown to vary with maternal condition and prey abundance (Lockyer, 1986).

Caswell *et al.* (1999) found a significant decline in North Atlantic right whale survival from 0.99 (1980) to 0.94 (1994) that could not be explained by sampling bias. Mature females, in particular, appeared to at higher risk of mortality in the later period (Fujiwara and Caswell, 2001). Among GOM humpback whales, non-calf female survival in the 1990s was lower, but not significantly different than the 1980s estimate (0.950, SE 0.011, Clapham *et al.*, 2003). However, the apparent calf survival rate in the later period (0.51) was substantially lower than in the previous data set. This may have been due to a decrease in survival or emigration from the study area during the period examined.

The vast majority of GOM data were collected in a subset of the feeding range and so it is not known if these are representative of the overall population, or readily applicable to others. Population structure is typically difficult to estimate in free-ranging cetaceans. The overall sex ratio of humpback whale calves has been reported to be parity *in utero* (Chittleborough, 1965), on the West Indies calving grounds (Palsbøll *et al.*, 1997; Smith *et al.*, 1999) and after the initial migration to high latitudes (Clapham *et al.*, 1995). Biopsy-based sampling primarily in the south-west GOM indicated equal sex ratios among juvenile and sexually mature age classes (Clapham *et al.*, 1995).

Most previous studies of humpback whale age structure have been based on harvested animals, because data of interest can be measured directly (Nishiwaki, 1959, 1962; Chittleborough, 1965). Indeed, whaling literature has provided invaluable information on the relationship between characteristics such as age, size and sexual maturity. Age structure estimates from harvest data must nevertheless account for bias due to gunner selectivity and imposed harvest restrictions. Useful information can also be

obtained from samples of naturally stranded animals (e.g. Stevick, 1999); however, fewer animals are generally available for study and the results may be biased if animals of certain lengths or ages are more likely to die or be recovered after death. Live baleen whales can be aged with certainty when they have been photo-identified in the calf year. However, female sexual maturity is only positively known when viable offspring have been documented. Hamilton *et al.* (1998) used sighting history data to estimate that 69-74% of catalogued North Atlantic right whales were sexually mature. Aerial photogrammetry studies of the Bering Sea stock of bowhead whales suggested a mature fraction of 42% (Withrow and Angliss, 1992; Zeh *et al.*, 1993). More recently, underwater videogrammetry techniques have been applied to humpback whales on their Hawaiian breeding ground (Spitz, 1999). Although 61% of non-calf animals in that study were sexually mature based on their length, it is not clear that the animals sampled were representative of the breeding population, or any particular feeding population. Differences between feeding populations may be obscured when they mix on in single breeding area. Furthermore, some classes may be under-represented on breeding grounds due to age-related migratory behaviour.

1.3 Management context

Humpback whales are considered “vulnerable” to extinction by the World Conservation Union (Cetacean Specialist Group, 1996) and are an Appendix I (endangered) species under the Convention on International Trade in Endangered Species (CITES). In the North Atlantic, they were commercially exploited between the 17th and 20th centuries (Mitchell and Reeves, 1983; Smith and Reeves, 2002). The International Whaling Commission (IWC) granted North Atlantic humpback whales protection from commercial exploitation in 1955, and aboriginal whaling is now limited to St. Vincent and the Grenadines where catch limits have recently been increased to no more than 20 animals between 2003 and 2007 (IWC, 2004). The North Atlantic oceanic population was estimated to have numbered 11,570 (95% CI 10,290 - 13,390) animals in 1992-1993, and increasing at a rate of 3.1% (Stevick *et al.*, 2003b). However, there is no reliable estimate of population size prior to exploitation (Klinowska, 1991). The Scientific Committee of the IWC recently performed a Comprehensive Assessment to determine the status of the North Atlantic population, but was unable to adequately model population recovery with the available data (IWC, 2003).

The GOM population ranges between U.S. and Canadian territorial waters during the summer feeding season. In U.S. waters, this species is protected under the U.S. Endangered Species Act and Marine Mammal Protection Acts. Under the government of Canada's "Species at Risk Act", the North Atlantic humpback whale is not considered to be of management concern. The current size of the GOM population is not known with certainty, but is believed to lie in the high hundreds (Clapham *et al.* 2003). Vital rates indicate that the GOM population was increasing at a rate of 6.5% between 1979-1991 (Barlow and Clapham, 1997), but this growth may have declined in subsequent years (Clapham *et al.*, 2003).

More than half of GOM humpback whales have experienced non-lethal entanglements in fishing gear (Robbins and Mattila, 2001). An average of 9.7 carcasses are recovered along the U.S. east coast each year (Laerm *et al.*, 1997). Most of the carcasses recovered are juveniles (mean=902 cm, U.S. Northeast Region Stranding Network, unpublished data). Cause of death is rarely determined, at least three humpback whales are killed or seriously injured annually by human-related activities, generally entanglement in fishing gear or vessel strike (Waring *et al.*, 2003). Although the true entanglement mortality rate is more difficult to determine, Volgenau *et al.* (1995) estimated that observed mortalities would contribute to a net loss to the population when the least optimistic estimates of abundance, birth and natural mortality rates were assumed.

1.4 Thesis overview

Humpback whales can be identified from their natural markings, particularly the shape of the flukes and their unique ventral pigmentation pattern (Katona and Whitehead, 1981) and the shape and size of the dorsal fin (Katona and Whitehead, 1981; Clapham and Mayo, 1990; Gill and Burton, 1995; Blackmer *et al.*, 2000). Photo-identification research has been carried out in the GOM since the 1970s and catalogued sightings and life history data have been the basis of numerous studies of humpback whale biology and population dynamics. However, previous research was largely based on one geographic area and a single decade. To date, there has been no effort to determine whether those data can be assumed to be representative of the overall population.

Since 1989, photo-identification has also been conducted across the geographic range of the population. Furthermore, mark-recapture statistical methods have improved

and expanded the type of inference that can be made when individuals are not seen on every occasion (Lebreton *et al.*, 1992). In this thesis, I combine longitudinal data with broad scale sampling and mark-recapture statistical techniques to quantify GOM population structure and dynamics. In Chapter 2, I compare population composition and individual exchange among six GOM sites, including a U.S. National Marine Sanctuary. I quantify inter-area exchange by multi-state modelling techniques and evaluate the importance of the Sanctuary site relative to other areas occupied by humpback whales. Chapter 3 investigates the pattern of migration between the GOM and the West Indies breeding ground. I identify the period of migratory closure and evaluate two conflicting hypotheses about the timing of migration among demographic classes. I also attempt to determine whether there is significant evidence of over-wintering, especially among mature females.

Of all demographic parameters, apparent survival is the most commonly estimated by robust statistical techniques in this and other humpback whale populations. However, previous studies have focused on “non-calf” survival because only calves can be reliably differentiated by age in this species. In Chapter 4, I investigate age structure and age-specific survival in the GOM. I evaluate the effectiveness of “non-calf” estimates for monitoring within and between populations. I also report the first estimates of male humpback whale survival and a comparative analysis of age-specific survival between the sexes. The GOM has previously been an important source of data on reproduction in free-ranging humpback whales. However, most previous work used methods that did not account for probability of detection or survival. In Chapter 5, I investigate patterns of recruitment and adult fecundity, including costs of reproduction using multi-state mark-recapture techniques. Chapter 6 reports the first stock assignment of a humpback whale taken in the only legal hunt in the North Atlantic. I discuss the implications of that finding for the GOM and for the management of that fishery. Finally, in Chapter 7, I integrate thesis findings and discuss the challenges encountered and those likely faced in future studies.

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Chapter 2:

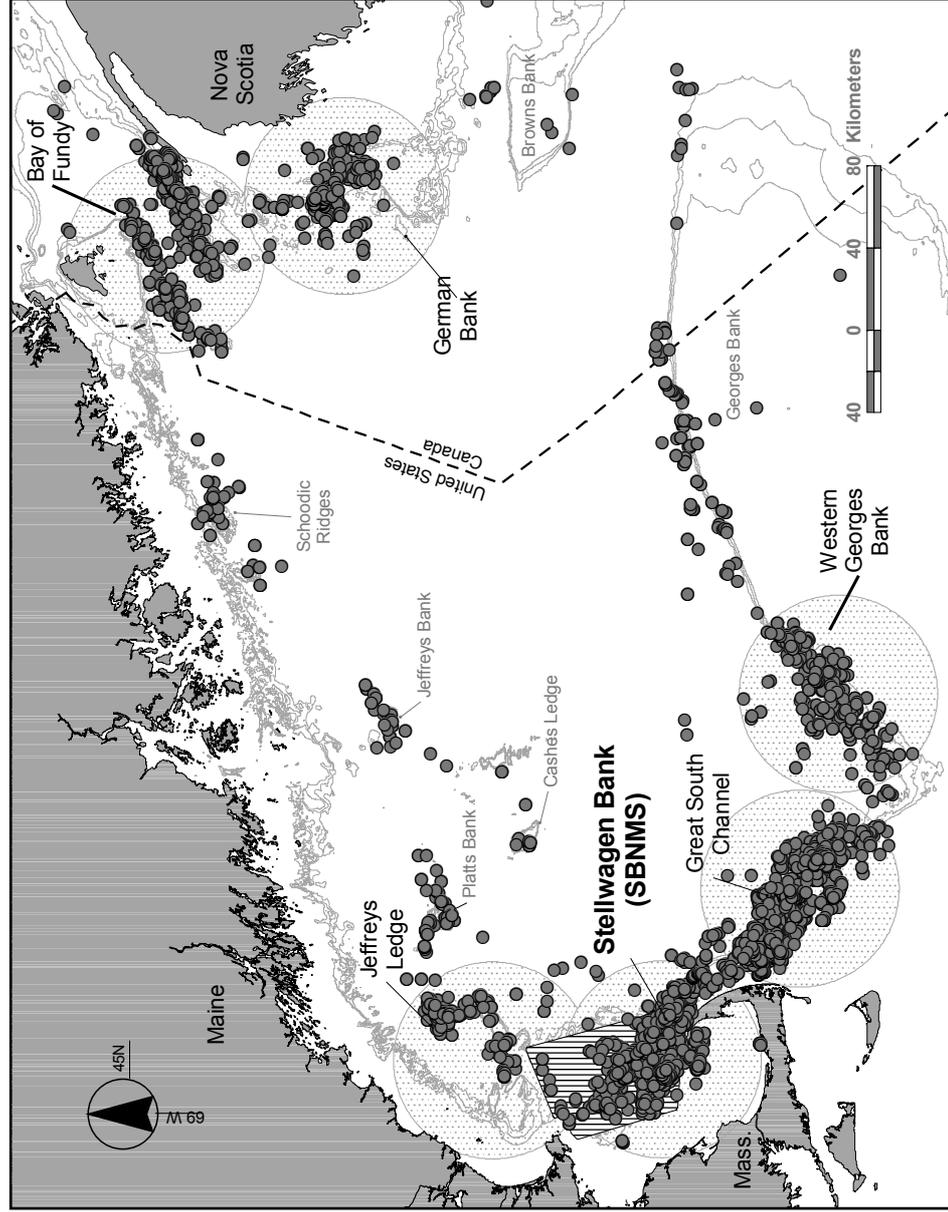
Humpback whale habitat use in the Gulf of Maine and implications for a marine protected area

2.1 Introduction

Marine protected areas (MPAs) are increasingly common in the conservation and management of ocean resources. Hoyt (2005) described over 500 existing and proposed MPAs world-wide that were either intended to protect cetaceans or had the potential to provide indirect benefit. However, scientific criteria for MPA site selection, design and evaluation are not yet well-established (Halpern, 2003; Roberts *et al.*, 2003). Conservation efforts that focus on geographic areas may not provide reliable protection for wide ranging animals if population structure and critical habitats are not well-understood. Synoptic studies are therefore particularly important for placing an MPA into a wider context, both at the design stage (e.g., Hooker *et al.*, 1999) and when evaluating management effectiveness.

Humpback whales migrate annually between discrete high latitude feeding grounds and shared low latitude breeding grounds. Recruitment to a feeding ground is maternally directed (Martin *et al.*, 1984; Baker *et al.*, 1986; Clapham and Mayo, 1987; Clapham and Mayo, 1990) and individuals exhibit high rates of annual return, within-season occurrence and occupancy to specific feeding sites (Clapham and Mayo, 1987; Clapham *et al.*, 1993; Weinrich, 1998; Calambokidis *et al.*, 2001; Larsen and Hammond, 2004). The Gulf of Maine (GOM) is the southern-most humpback whale feeding population in the North Atlantic. Individuals aggregate at a variety of shallow bathymetric features such as banks, ledges and slopes from coastal New England to south-western Nova Scotia (CeTAP, 1982; Payne *et al.*, 1986; Hamazaki, 2002). Stellwagen Bank is one such GOM area that has been under continuous study since the late 1970s (Figure 2.1). It was nominated as a U.S. National Marine Sanctuary in 1982 based on the fact that it was a consistent aggregation site for humpback whales and other marine life. However, at the time of its nomination there were relatively few data with which to determine the importance of Stellwagen Bank relative to other GOM areas used by humpback whales.

Figure 2.1: Sightings of humpback whales during GOM-wide surveys, 1989-2005. Labelled bathymetric features were areas surveyed annually and sampled approximately proportional to observed whale densities. Shaded areas indicate primary humpback whale aggregation sites, while the striped area represents the Stellwagen Bank National Marine Sanctuary (SBNMS). Independent, near-daily sampling was also conducted at SBNMS (data not shown).



The Gerry E. Studds Stellwagen Bank National Marine Sanctuary (SBNMS), as it is now known, became effective in 1994. The SBNMS encompasses Stellwagen Bank and extends northward to the southern edge of Jeffreys Ledge (Figure 2.1). At only 2,189 square kilometres (km), it encompasses less than 4% of GOM waters and the number of humpback whales found there varies widely from one year to the next (Payne *et al.*, 1990; Weinrich *et al.*, 1997). The SBNMS is also a managed resource area, equivalent to World Conservation Union MPA Category VI, (IUCN, 1994; Hoyt, 2005). Its establishment has facilitated scientific research and public outreach, but few restrictions have been imposed on human activities within its boundaries. Humpback whales are exposed to fisheries interactions, vessel traffic and vessel harassment (Laist *et al.*, 2001; Wiley *et al.*, 2003) and the potential for impact may actually be greater within the SBNMS due to its high simultaneous human use. The SBNMS is evaluating measures that could be taken to protect cetaceans, including placing restrictions on high risk human activities and expanding the sanctuary boundaries. However, it is not clear what the effect such actions could potentially have at the population level. This study uses photo-identification data collected within the SBNMS and GOM-wide to examine humpback whale habitat use and individual distribution patterns relative to this MPA.

2.2 Methods

2.2.1 Data collection

Individual humpback whales were identified from their natural markings, especially the ventral pigmentation of the flukes and the shape and size of the dorsal fin (Katona and Whitehead, 1981). Photographs of identifying features were obtained by research vessels engaged in photo-identification (photo-ID) surveys throughout the GOM. Surveys targeted known humpback whale aggregation sites at least once annually between June-September, 1989-2005 (Figure 2.1). The only exceptions were between 1994 and 1996, when surveys were logistically limited to western GOM areas. From 1989 through 1996, surveys were conducted from a 14-m sailing vessel. Since 1997, surveys have been performed from a 14-m twin-screw motorboat. The latter increased the efficiency of the surveys by minimising travel time to and from aggregation sites. Sampling was least intensive on eastern Georges Bank and Browns Bank because of the greater difficulty of reaching those offshore locations.

When more than one individual or group was encountered, the vessel moved systematically through the aggregation before continuing to search. If the area was not adequately covered in the time available, the vessel generally remained in the area overnight or returned to complete the sampling. Thus, unless an area was not surveyed, the number of animals sampled was more directly related to the number present than to the amount of effort employed. Multiple sightings of individuals within an area in a given year were pooled to indicate annual presence or absence at that location.

Demographic data for sighted individuals were obtained from the PCCS Gulf of Maine Humpback Whale Catalogue (Massachusetts, USA). Exact age was known only for whales that were dependent calves at first encounter. Calves were classified in the field based on their physical size, stereotypical behaviours and close, consistent association with a mature female. They were assumed to range from 3 to 9 months old when first observed and typically remained dependent until at least October of their first year (Clapham and Mayo, 1987; Baraff and Weinrich, 1993). Individuals that were independent when first catalogued prior to October were assumed to be at least one year old, but could have been older. Animals known to be less than five years old were assumed to be juvenile, while those aged five years or more were potentially sexually mature (Clapham, 1992). Sexes were assigned based on the external morphology of the genital slit (Glockner, 1983) or molecular genetic analysis of a skin sample obtained by biopsy sampling techniques (Palsbøll *et al.*, 1991; Palsbøll *et al.*, 1992; Bérubé and Palsbøll, 1996a, b).

2.2.2 Data analysis

2.2.2.1 Regional demography

The demographic characteristics of sightings at the SBNMS were compared to five other primary aggregation sites where at least 100 sightings were made over the course of the study (Figure 2.1). Encounter rates were calculated for each area based on the number of unique individuals identified, divided by the total number of sampling occasions in that area. That analysis was limited to the period 1997-2005 when sampling effort was highest and most consistent between years. The following metrics were also used for inter-area comparisons: 1) the proportion of independent juveniles out of all individuals of known maturational class, 2) the proportion of females out of all mature, sexed individuals, and 3) the proportion of mothers out of all mature females. Calves provided information about

the reproductive state of the mother, but were not otherwise included in analyses. Females known only from their calving histories were considered unsexed in this study, in order to prevent a bias toward females or calving events. The significance of categorical differences between areas was determined by G-test where $\alpha=0.05$ (Sokal and Rohlf, 1981).

2.2.2.2 Multi-state modelling

Multi-state mark-recapture models were used to estimate inter-area exchange while accounting for area-specific survival and detection probabilities (Arnason, 1972, 1973; Hestbeck *et al.*, 1991; Brownie *et al.*, 1993; Schwarz *et al.*, 1993; Lebreton and Pradel, 2002). The method is a generalisation of the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) and can be implemented in modern statistical software, such as program MARK (version 4.3, Cooch and White, 2006). In this study, aggregation sites were states that animals could move to and from between years, provided that they survived. In the Arnason-Schwartz (AS) multi-state model (Arnason, 1972, 1973; Schwarz *et al.*, 1993), the probability of movement to another site depended only on the present, with no memory of past movements (Brownie *et al.*, 1993).

The complexity of multi-state models greatly increases with the number of states and so analysis was limited to the six GOM areas with the largest sample sizes. It also focussed on adults of known sex to reduce survival heterogeneity in the model. Individuals were considered “marked” in the first year that they were photo-identified within a period of interest and annual sighting events were placed into an encounter history format coded by geographic area. When an individual was seen in two areas during the same year, it was assigned to the first area in which it was observed. We then selected a mark-recapture model containing all parameters of biological interest, evaluated the goodness of fit (GOF) of this “global” model to the data and examined support for reduced models and explanatory factors.

Mark-recapture models produce valid estimates only when the underlying data meet model assumptions. In the case of multi-state models, individuals within groups or states are expected to have an equal but independent probability of detection on the study site as well as an equal probability of survival to the next sampling period. Emigration is permitted, but it must be random and temporary. The sampling period should be brief relative to mortality processes, and individuals must be successfully recognised if re-

encountered. Survival heterogeneity was not expected because analysis was limited to adults and stratified by sex (see Chapter 4). Furthermore, a four-month sampling period (June-September) was expected to result in minimal within-period survival heterogeneity for this long-lived species (Hargrove and Borland, 1994). The broad scale of GOM-wide sampling was expected to reduce the potential for bias in re-sighting probabilities, such as those due to trap dependence and Markovian temporary emigration. The first refers to the case in which individuals that are present are more or less likely to be seen if seen previously (i.e., trap-happy or trap-shy, Sandland and Kirkwood, 1981; Pradel, 1993). The second situation occurs when individuals are more or less likely to remain in the study area if seen previously (Schaub *et al.*, 2004). Nevertheless, we used program U-CARE (version 2.2.5, Choquet *et al.*, 2005) to detect and diagnose unexpected heterogeneity in apparent survival (Test 3G.Sr and Test 3G.Sm) and re-sighting probabilities (Test M.ITEC and Test M.LTEC, Pradel *et al.*, 2003). We also used the median \hat{c} technique in program MARK (version 4.3, Cooch and White, 2006) to estimate a variance inflation factor (\hat{c}) to address residual over-dispersion, which could otherwise cause estimates to be artificially precise (Burnham *et al.*, 1987).

Model selection was performed in Program MARK based on Akaike's Information Criterion (Burnham and Anderson, 2002). Akaike's Information Criterion (AIC) evaluates the relative fit of each candidate model in light of the number of parameters necessary to achieve that fit. Selection was based on QAICc, a form that accounted both for small sample sizes and the inclusion of a variance inflation factor. The model with the lowest QAICc value was considered to have the most support from the data, and all other models were evaluated based on their distance from that preferred model (Δ QAICc). Those within 2 units were considered equally likely, whereas a model that differed by 10 units or more was inferred to have no support (Burnham and Anderson, 2002). The ratio of normalised QAICc weights of two models provided an indication of relative strength of support.

Available data were too sparse to examine patterns of movement annually by multi-state techniques. In the global model, parameters were estimated only with respect to sex and area. Model selection attempted to find the most parsimonious fit for re-sighting, survival and transition (movement) parameters, in that order. When unequal patterns of movement were indicated, covariate data were fitted in an effort to explain those results. Inter-area exchange was expected to depend on one or more of the

following: 1) the number of sightings at the destination area; 2) inter-area distance, as calculated by a great circle route between the geographic centre of each area (Bowditch, 1977); 3) whether or not the areas bordered directly upon each other; and 4) dominant local prey species. As discussed in Chapter 1, the latter was not known with certainty. Primary preferred prey species in the GOM are thought to be sand lance (*Ammodytes* spp., Overholtz and Nicolas, 1979; Hain *et al.*, 1982; Payne *et al.*, 1986; Payne *et al.*, 1990) and Atlantic herring (*Clupea harengus*, Hain *et al.*, 1982; Paquet *et al.*, 1997; Weinrich *et al.*, 1997), although other species have also been identified. Atlantic herring are widely distributed across the GOM (Overholtz, 2002), whereas sand lance prefer relatively shallow, sandy substrates (Meyer *et al.*, 1979; Robards *et al.*, 1999). The latter are found primarily in southern GOM areas where humpback whale distribution has been correlated with fluctuations in sand lance abundance (Payne *et al.*, 1986; Payne *et al.*, 1990). This study assumed that sand lance was the primary prey south of Jeffreys Ledge (Figure 2.1), although Atlantic herring might also be taken. Atlantic herring was the likely primary piscine prey from Jeffreys Ledge northward. We hypothesised that individuals would be more likely to move between areas favouring the same prey type. Georges Bank was problematic, as it was both sand lance habitat (Payne *et al.*, 1986) and an important spawning area for herring from late September through early October (Tupper *et al.*, 1998, cited in Overholtz 2002). Modelling was conducted assuming that either or both prey types were available.

2.2.2.3 Net inter-annual displacement

Multi-state modelling focussed on movement between areas, which was appropriate in light of the area-specific focus of the sampling. However, we were also interested in the magnitude of movements made by individuals, irrespective of their destination. When an individual was seen in two consecutive years during GOM-wide sampling, its net inter-annual displacement was calculated as the shortest distance between those sighting positions. Within-season re-sightings were not used because the sampling was not expected to provide equal re-sighting probabilities at all distance intervals. When an individual was seen on more than one occasion in a given year, the earliest sighting was selected, regardless of its location. The distance between two sightings was then calculated using an extension to program ArcView GIS 3.2 (Jenness, 2002). Groups of individuals with similar demographic characteristics were compared categorically based

on the frequency displacements exceeding 100 km. The latter was the approximate average distance between adjacent areas. The significance of categorical differences was determined by G-test where $\alpha=0.05$ (Sokal and Rohlf, 1981). Mean displacement distances were also reported with their standard deviations (*s*).

2.3 Results

2.3.1 Regional demography

Excluding calves, 837 unique individuals were seen on 2,600 annual occasions during GOM-wide surveys between 1989-2005. The vast majority of those sightings (83.2%) occurred in six broad GOM areas (Figure 2.1). Encounter rates at all areas varied considerably between years, but the main aggregation site in a given year tended to be either the Great South Channel or the Bay of Fundy (Table 2.1). Age class composition differed significantly between GOM areas ($G=155.33$, $df=12$, $p<0.001$), with juveniles being most prevalent in south-west habitats (Figure 2.2). Mature females were also favoured in southern areas (Figure 2.2, $G=56.01$, $df=6$, $p<0.001$). However, they were equally likely to be mothers regardless of where they were found ($G=9.28$, $df=5$, $p=0.098$). These patterns were also annually consistent, although annual sample sizes precluded formal statistical comparison.

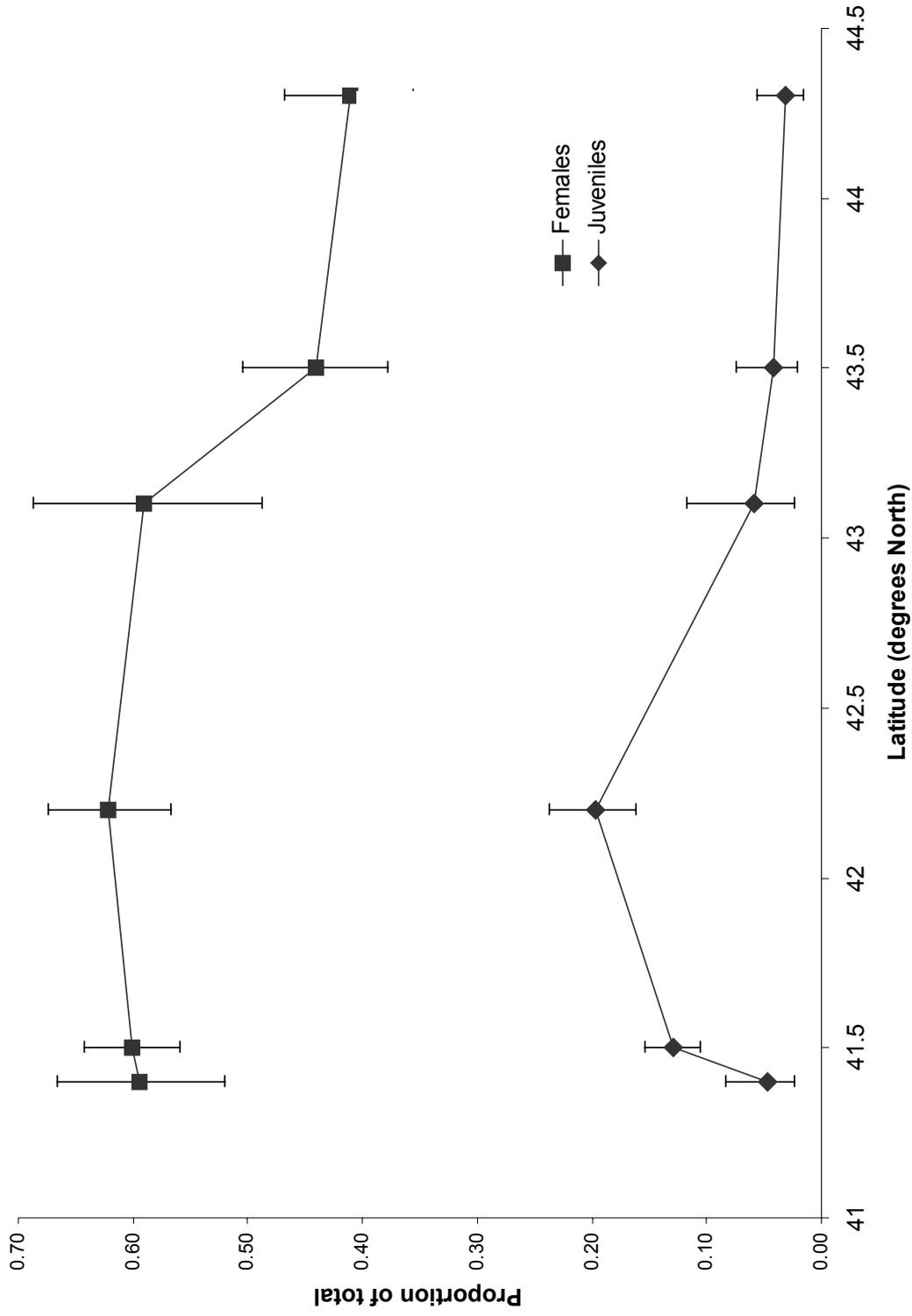
2.3.2 Multi-state modelling

A total of 513 adults (235 male, 276 female) were seen at one or more of the six primary aggregation sites between 1989 and 2005. Goodness of fit testing in Program U-CARE indicated no significant heterogeneity (overall test: $X^2=301.09$, $d.f.=291$, $p=0.330$, sexes pooled), and the variance inflation factor estimated by the median *c-hat* procedure indicated minor over dispersion (*c-hat*=1.023). We proceeded with model selection incorporating that value into the model. Unconstrained models with the lowest QAICc values were ones in which re-sighting probability varied by area (Table 2.1). Re-sighting probabilities were highest at the Bay of Fundy and at Stellwagen Bank and lowest at western Georges Bank and German Bank (Table 2.2). Adult survival did not differ

Table 2.1: Average number of individuals identified per area per sampling occasion, 1997-2005. The mean across years is shown with its standard deviation (s). The aggregation area with the highest encounter rate in a given year is highlighted. This was most frequently the Great South Channel or the Bay of Fundy. A dash indicates that an area was not sampled.

Year	Western Georges Bank	Great South Channel	Stellwagen Bank	Jeffreys Ledge	German Bank	Bay of Fundy
1997	6.0	74.5	25.0	1.0	-	2.0
1998	27.0	9.0	35.1	4.0	25.0	3.0
1999	0.0	16.0	57.6	2.0	107.0	11.5
2000	0.0	53.0	21.4	0.0	9.0	23.0
2001	0.0	0.0	36.8	0.0	61.0	50.0
2002	11.0	25.0	3.8	2.0	15.5	46.5
2003	6.7	73.0	24.4	4.5	19.3	53.5
2004	6.3	20.2	4.6	0.0	28.7	68.5
2005	17.7	37.0	13.6	4.3	2.0	66.5
Mean	8.3	34.2	24.7	2.0	33.4	36.1
s	9.1	27.2	17.0	1.9	34.6	26.5

Figure 2.2: The proportion of mature females (top) and independent juveniles (bottom) identified within each GOM area. The error bars indicate the 95% confidence interval. Juveniles made up a greater proportion of sightings at Stellwagen Bank (SBNMS) than at any other area. Mature females were preferentially distributed in the southern GOM.



between areas. There was indication of a lower survival among females (see also Chapters 4 and 5), but equal survival for both sexes was also plausible given the data. Both hypotheses were retained when modelling movement probabilities.

The model assuming equal probability of movement among areas received a high QAICc value indicating no support from the data (Model 8, Table 2.2). Movement occurred between all areas and was not estimated to differ between the sexes. However, individuals were more likely to remain in a given area than to move to one of the five others examined (Table 2.3). With the exception of Jeffreys Ledge, each area appeared to exhibit the most exchange with an adjacent area. However, none of the covariates that were fitted adequately explained inter-area movement, either singly or in combination. All fitted models had QAICc values greater than 10.

Individuals that moved from Stellwagen Bank were re-sighted primarily at the Great South Channel and secondarily at western Georges Bank (Table 2.3, Figure 2.3). Individuals encountered at the Great South Channel were also more likely to move to Stellwagen than to other areas. Although Jeffreys Ledge is also adjacent to Stellwagen, maximal exchange was with a more remote area (western Georges Bank).

2.3.3 Net inter-annual displacement

Although multi-state modelling did not consider annual timing of movement, exchange also occurred among all areas from one year to the next (Figure 2.4). Net inter-annual displacement ranged from 1 to 422 km, with a median distance of 55.6 km (Figure 2.5). Adults moved a mean distance of 90.3 km ($s=30.13$) between years, as compared to 62.6 km ($s=48.74$) for independent juveniles. They were also nearly twice (30.1%, $n=109$) as likely as juveniles (17.3%, $n=9$) to be re-sighted more than 100 km from their previous position ($G=3.93$, $df=1$, $p=0.047$). By contrast, males and females were equally likely to be seen at those distances ($G=0.02$, $df=1$, $p=0.880$). Displacement to and from the SBNMS involved all primary aggregation sites except for Jeffreys Ledge (Figures 2.6 and 2.7).

Table 2.2: Model selection for inter-area survival, re-sighting and movement probabilities. Modelling was limited to adults of known sex encountered in six GOM areas and incorporated a variance inflation factor of 1.023. Based on Akaike's Information Criterion ranking (QAICc), highlighted models were equally plausible given the data. Fitting covariate data to the movement parameter (not shown) did not improve the fit of Models 1 or 2.

Model	Survival probability	Re-sighting probability	Movement probability	Δ QAICc	QAICc Weights	# Parameters
1	.	area	area	0.000	0.545	37
2	sex	area	area	0.363	0.455	38
3	sex	area	sex*area	15.624	0.000	68
4	.	area	sex*area	17.003	0.000	67
5	area	area	sex*area	18.776	0.000	72
6	sex*area	area	sex*area	27.377	0.000	78
7	sex*area	sex*area	sex*area	34.325	0.000	84
8	sex*area	.	sex*area	365.927	0.000	67
9	sex	area	.	868.232	0.000	9

Abbreviations = constant (.), interaction effect (*).

Table 2.3: Adult re-sighting and movement probabilities among six primary GOM aggregation areas, 1989-2005. Sample sizes (N) reflect the number of annual sightings of unique individuals per area. Point estimates and their standard errors are from Model 1 in Table 2.1. Shaded areas represent the probability of remaining in the same area, conditional on survival and availability for sampling.

Departure area	N	Re-sighting probability	Movement probability, by arrival area					
			WG	GC	SBNMS	JL	GB	BF
Western Georges Bank (WG)	311	0.104 (±0.013)	0.707 (±0.025)	0.133 (±0.019)	0.086 (±0.016)	0.010 (±0.007)	0.062 (±0.013)	0.003 (±0.003)
Great South Channel (GC)	973	0.652 (±0.068)	0.151 (±0.034)	0.453 (±0.042)	0.318 (±0.027)	0.031 (±0.012)	0.032 (±0.013)	0.014 (±0.006)
Stellwagen Bank (SBNMS)	536	0.837 (±0.034)	0.130 (±0.020)	0.165 (±0.022)	0.619 (±0.025)	0.059 (±0.012)	0.007 (±0.005)	0.021 (±0.005)
Jeffreys Ledge (JL)	130	0.455 (±0.070)	0.221 (±0.055)	0.078 (±0.029)	0.116 (±0.030)	0.428 (±0.056)	0.076 (±0.032)	0.116 (±0.024)
German Bank (GB)	284	0.182 (±0.020)	0.019 (±0.009)	0.005 (±0.004)	0.010 (±0.005)	0.029 (±0.010)	0.710 (±0.025)	0.227 (±0.022)
Bay of Fundy (BF)	387	0.895 (±0.106)	0.030 (±0.014)	0.008 (±0.006)	0.034 (±0.011)	0.075 (±0.021)	0.333 (±0.068)	0.521 (±0.073)

Figure 2.3: Probability of movement between the SBNMS and other primary GOM areas, conditional on survival. Parameter estimates were based on Model 1, Table 2.2 and are depicted with their 95% confidence intervals. SBNMS exhibited the greatest exchange with the Great South Channel, but individuals were twice as likely to go toward the Great South Channel than to arrive from there.

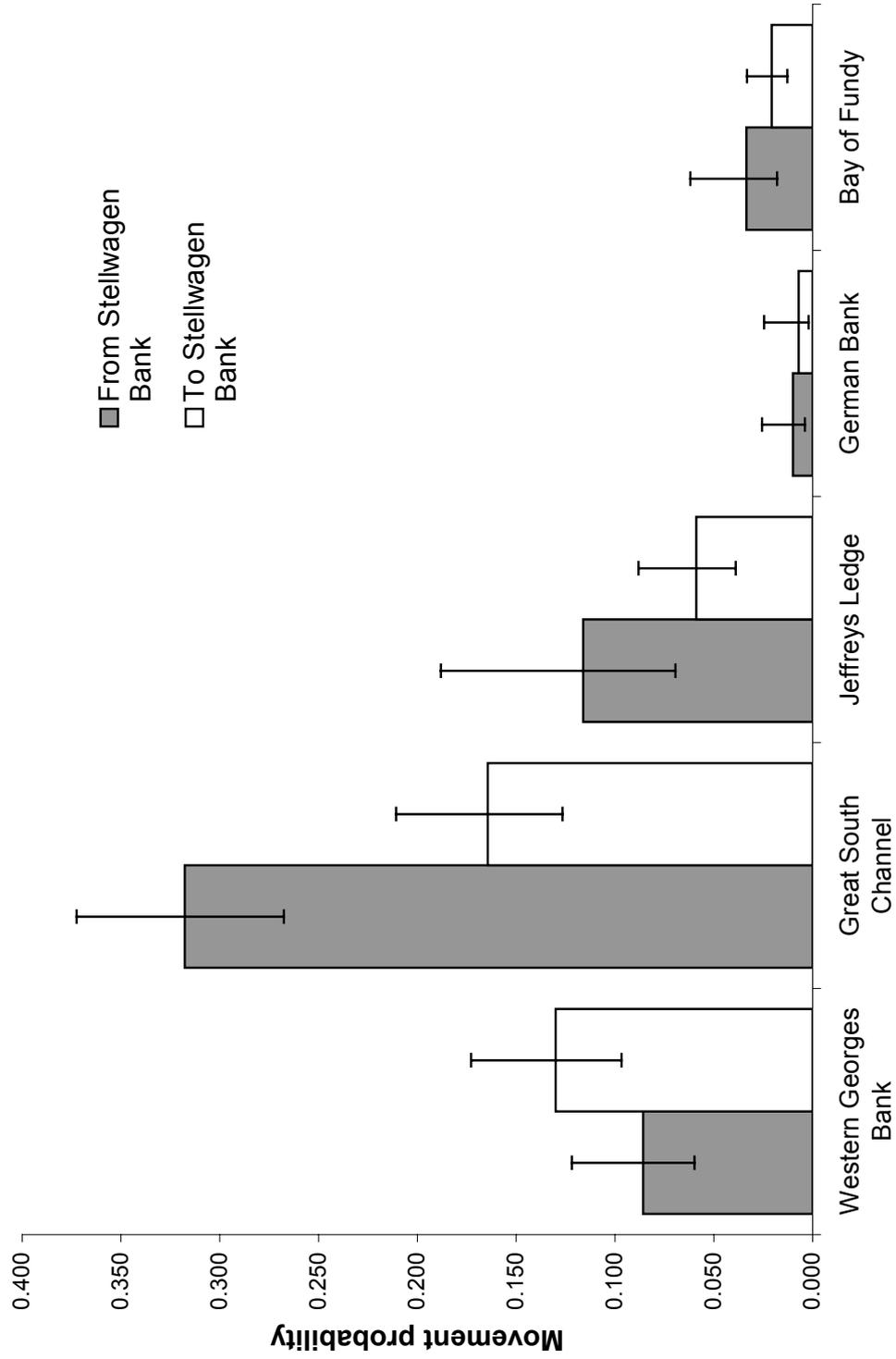


Figure 2.4: Inter-annual displacements of individual humpback whales observed during GOM-wide surveys, 1989-2005. Lines indicate direction of exchange and not a route taken between areas. Shaded areas indicate primary aggregation sites shown in Figure 2.1. The striped area represents the Stellwagen Bank National Marine Sanctuary (SBNMS). Exchange occurred between all areas, but was most common between SBNMS and the Great South Channel.

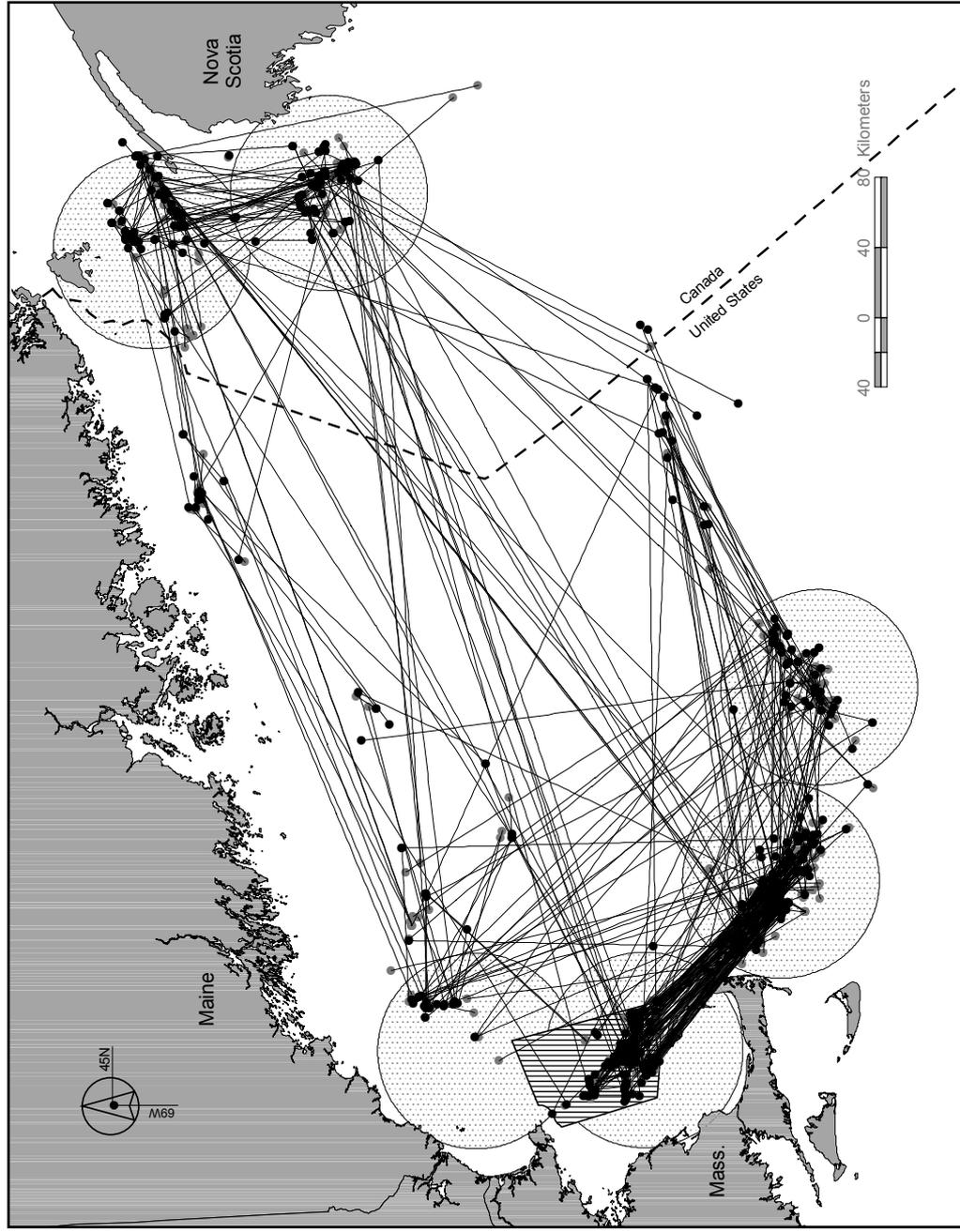


Figure 2.5: Inter-annual displacement distances for all individuals re-sighted between years, 1989-2005. Areas visited are shown in Figure 2.4.

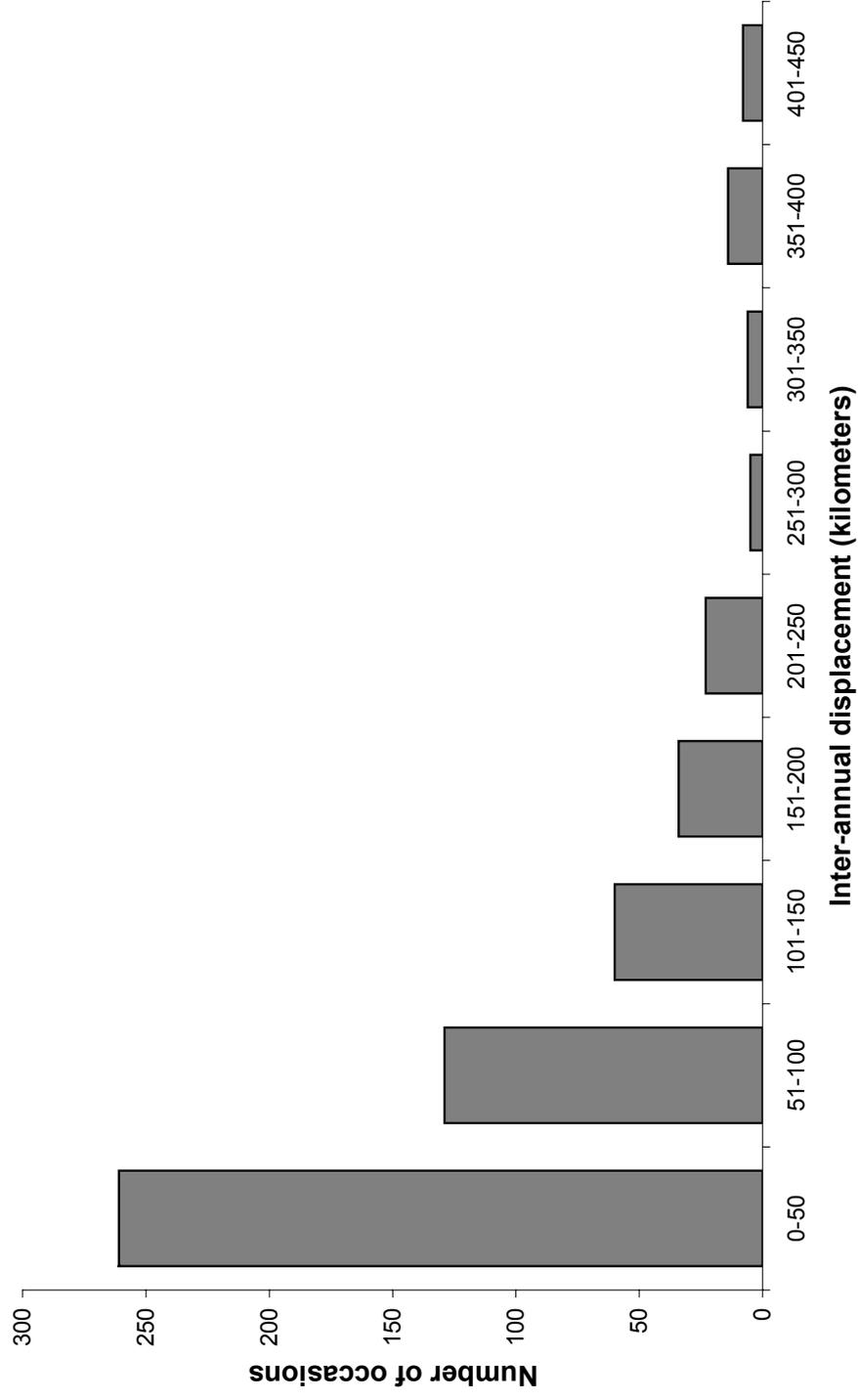


Figure 2.6: Inter-annual displacements from SBNMS (striped area) to other GOM areas, 1989-2005. Lines represent direction of exchange, not a route travelled between areas. Shaded areas indicate primary aggregation sites shown in Figure 2.1. Arrows indicate direction of exchange, but were omitted for clarity in some cases.

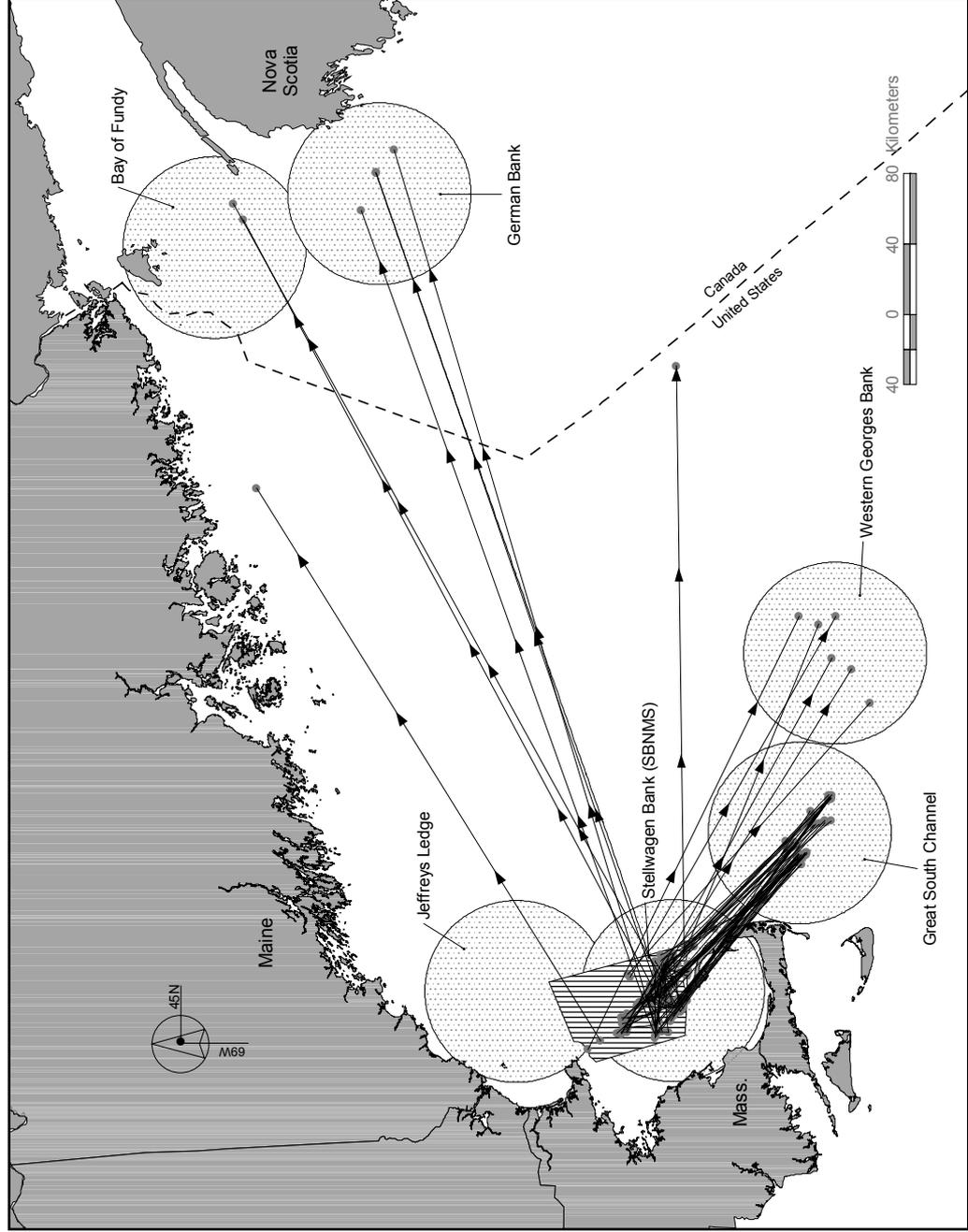
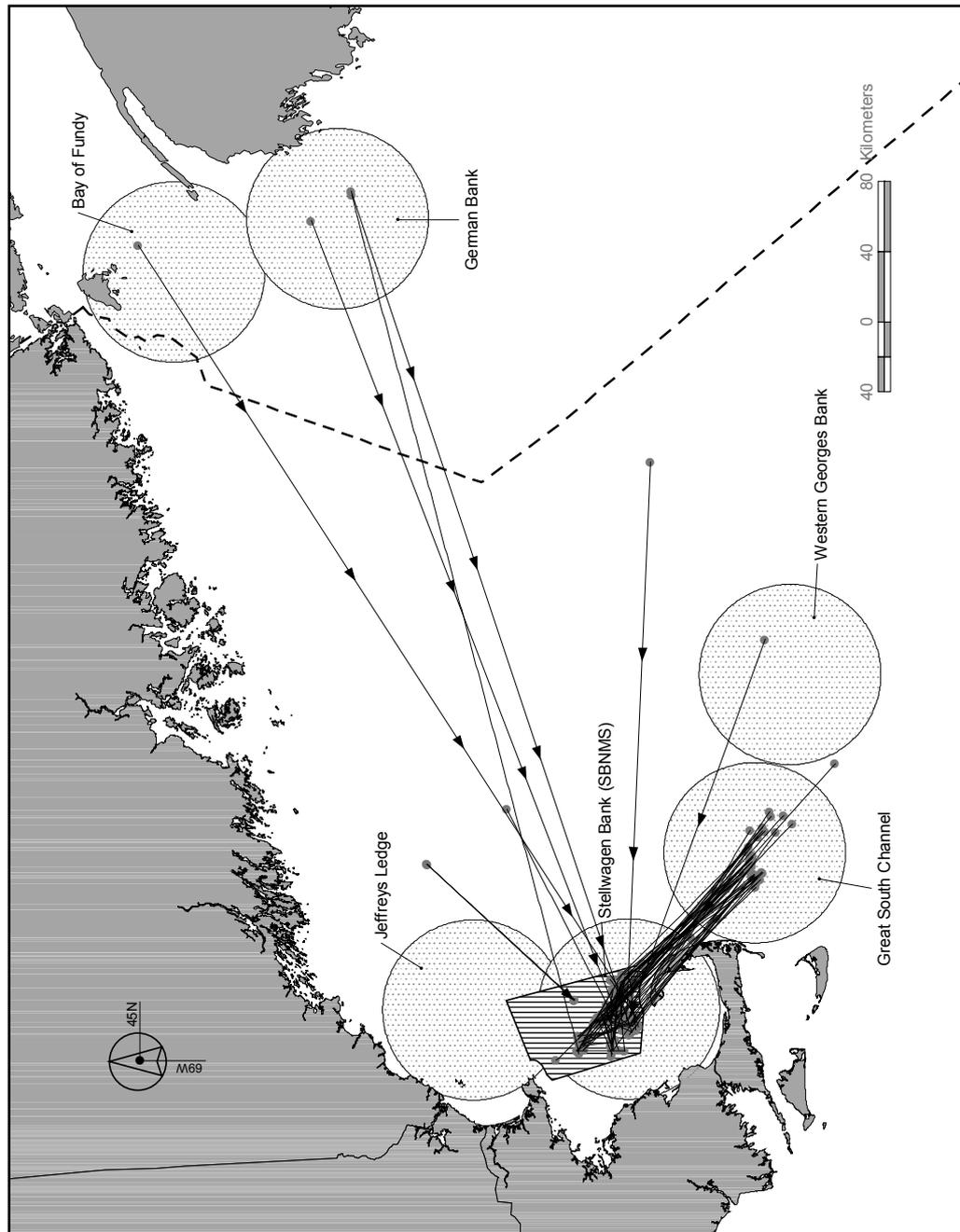


Figure 2.7: Inter-annual displacements to the SBNMS (striped area) from other GOM areas, 1989-2005. Lines represent direction of exchange, not a route travelled between areas. Shaded areas indicate primary aggregation sites shown in Figure 2.1. Arrows indicate direction of exchange, but were omitted for clarity in some cases.



2.4 Discussion

2.4.1 Habitat stratification

All demographic classes were found in each of the GOM areas studied, but juveniles and mature females were significantly more likely to be encountered in southern areas. Juveniles were most prevalent at Stellwagen Bank and the Great South Channel where females tended to dominate the adult population. They were least common in the Bay of Fundy where adult males were favoured. Several studies have found mothers to have a different pattern of distribution than other whales on both their feeding and breeding grounds (Goodale, 1982; Perkins *et al.*, 1985; Smultea, 1994; Steiger and Calambokidis, 2000; Ersts and Rosenbaum, 2003). Otherwise, habitat stratification has not been reported in this species.

Demographically stratified habitat use is common in social, sexually dimorphic species, like ungulates, where it may result from different nutritional needs, energetic requirements, social dynamics or differential risk of predation (see reviews by Main *et al.*, 1996; Loe *et al.*, 2006). Dietary differences have also been confirmed in a number of cases (Shank, 1982; Oakes *et al.*, 1992; Weckerly, 1993; Jenks *et al.*, 1994; duToit, 1995; Bleich *et al.*, 1997). Le Boeuf *et al.* (2000) and Breed *et al.* (2006) reported sex-based habitat partitioning in seals, which are sexually dimorphic but lack the social structure that complicates interpretation of underlying causes in ungulates. Breed *et al.* (2006) attributed habitat stratification in grey seals to competition reduction and concluded that it might also be common in other sexually dimorphic marine species. Humpback whales have neither persistent social bonds after weaning (Weinrich and Kuhlberg, 1991; Clapham, 1993), nor strong sexual dimorphism. The present study indicates that differential habitat use can also occur in the absence of both.

Mothers may occupy shallower waters on their breeding grounds in order to reduce male harassment or risk of predation (Smultea, 1994). However, neither is known to be a concern by the time of arrival in the GOM (Clapham, 1996; Clapham, 2001). On the feeding ground, humpback whale distribution has been shown to be sensitive to the availability of primary prey species (Payne *et al.*, 1986; Payne *et al.*, 1990; Weinrich *et al.*, 1997). Individuals of different sizes, sexes or reproductive states are expected to have different caloric requirements. If each prey species require differential effort or skill to capture, or have a different caloric value, then there is a potential for diet to vary between classes. Mature baleen whale females, especially those that are lactating, are thought to

have a higher energetic burden than other animals (Lockyer, 1984). Stevick *et al.* (2006) reported that females were more likely to make extreme movements on an oceanic scale, but otherwise few studies exist to differentiate foraging effort between the sexes. In this study, neither inter-annual movement nor inter-area exchange explained the differences in distribution observed between adult males and females within the GOM. This suggests that demographic stratification is more a product of habitat preference than sex-specific differences in foraging range, as is known to occur in some odontocete species (e.g., Hooker *et al.*, 2002). Adult female use of southern sand lance habitats may reflect their own preference for that prey species, perhaps because substrate dependence makes sand lance more reliable to locate and/or capture. Alternatively, females may favour sand lance habitats because their offspring are more successfully weaned or more likely to survive after weaning. Whereas natal dispersal is common in terrestrial mammals, it does not appear to play an important role in the distribution of humpback whales during their juvenile years. Rather, juveniles make smaller inter-annual displacements than adults, and so persist in areas where they were first brought as calves.

Differential habitat use by age, sex or reproductive status has been reported in several other baleen whale species, including minke, fin, right and bowhead whales (Wada, 1989; Agler *et al.*, 1993; Bérubé *et al.*, 2001; Brown *et al.*, 2001; Cosens and Blouw, 2003). However, the underlying factors in those cases have also yet to be determined. It is noteworthy that Agler *et al.* (1993) reported spatial differences in the apparent reproductive rates of North Atlantic fin whales, a sympatric species within the GOM. They did not have the demographic data to discriminate between lower female fecundity and fewer females in northern areas. If, like humpback whales, female fin whales are preferentially distributed in the southern GOM, then a comparative study could help to clarify the specific underlying cause.

Habitat stratification has the potential to bias estimates of age structure, vital rates and abundance if it is not recognised and accounted for (Härkönen *et al.*, 1999). Previously published reproductive rates for the GOM (Clapham and Mayo, 1990; Barlow and Clapham, 1997) were based on data obtained primarily at Stellwagen Bank and the success of those studies was likely due to preferential habitat use by adult females. However, spatial heterogeneity may play a role in inconsistencies detected between populations, both within and between oceans. Stratification is one potential explanation of low apparent reproductive rates among humpback whales off of California (Steiger and

Calambokidis, 2000). Calves were seen in all areas surveyed, but the crude birth rate varied regionally from 0.6% to 6.7%. By contrast, the average calving rate among mature females (0.47) was comparable to findings from other humpback feeding areas. Low reproductive rates were unexpected in that population and the authors theorised that the calving rate might be biased upwards. However, they did not consider that the crude birth rate might be biased downward by a preponderance of males or juveniles in their sample.

2.4.2 Inter-area exchange

The GOM is a relatively small feeding ground, and this study confirmed exchange between all of the areas studied. However, spatial structure was also indicated by the tendency of individuals to return to the same site and by an unequal probability of movement between sites. Fidelity to single sites has previously been established in the GOM and elsewhere, but simultaneous studies of more than one area within a feeding ground are only starting to emerge (Weinrich *et al.*, 1997; Weinrich, 1998; Calambokidis *et al.*, 2001; Straley *et al.*, 2002; Larsen and Hammond, 2004; Stevick *et al.*, 2006). In all of the GOM areas we studied, adults were more likely to remain than to move to another area, although the probability of remaining was higher at some sites than others. Multi-state models estimate transitions between areas conditional on survival and on being present among the areas sampled. This was reasonable for this analysis because over 80% of sightings occurred in six areas over the course of the study. Nevertheless, if individuals in some areas were more likely to move to an un-sampled area, then site fidelity would be over-estimated. This may partially explain high estimates of site fidelity at western Georges Bank and German Bank, as sampling was more limited in the offshore areas east of those locations and did not extend beyond the GOM (Figure 2.1). Areas in the vicinity of Stellwagen Bank were well-sampled and so we had little reason to suspect that site fidelity was over-estimated in that case. Rather, results indicate individual preferences among adult humpback whales for the Stellwagen Bank area, despite substantial inter-annual variability in its attractiveness to the population as a whole.

Although this study clarified relationships between GOM areas in terms of exchange, it did not identify a covariate that adequately explained those patterns. This was likely due to our inability to model time variation and incomplete knowledge of area-specific prey species and availability. Inter-annual variability in habitat use was considerable and our inability to model this with the available data may have obscured

meaningful patterns in the data. Furthermore, sightings were allocated to relatively large areas and so inter-area distances may not have accurately characterised individual movements. In the future, modelling that categorises individuals by actual distance moved, in addition to area, may prove more effective.

As part of an ocean-basin-wide study, Stevick *et al.* (2006) compared movement between “northern”, “southern” and “offshore” GOM areas defined by sub-regional categories used in the management of the North Atlantic Humpback Whale Catalog. “Northern” areas included the Bay of Fundy and German Bank, “southern” areas included Jeffreys Ledge and Stellwagen Bank, and “offshore” areas included the Great South Channel and western Georges Bank. Stevick *et al.* (2006) found high probabilities of movement between all three areas, but fewer between “offshore” and “northern” areas. The only other studies of exchange and differential habitat use within the GOM focussed exclusively on Stellwagen Bank and Jeffreys Ledge (Weinrich *et al.*, 1997; Weinrich, 1998), and used methods that did not consider survival and area-specific re-sighting probabilities. Jeffreys Ledge is occasionally an important aggregation site for humpback whales and exchange does occur with Stellwagen Bank. Nevertheless, we found Jeffreys Ledge to be the least persistent summer aggregation site of those studied. It exhibited less exchange with Stellwagen Bank than to western Georges Bank, an area twice as far away. Previous studies that looked exclusively at Stellwagen Bank and Jeffreys Ledge, or grouped them into a single “southern” area, may have over-estimated the importance of exchange between them. However, as autumn spawning sites for herring, both Jeffreys Ledge and the western Georges Bank area may have a greater importance as aggregation sites for GOM humpback whales than our summer study would suggest.

2.4.3 Implications for the SBNMS

Peer-reviewed studies supporting MPA site selection, development and evaluation are still relatively uncommon, including for cetacean species (Halpern and Warner, 2002; Gerber *et al.*, 2003). Knowledge of the biology, range and habitat requirements of cetacean species is often poor enough that any documented use of an area may be adequate justification for MPA designation (Hoyt, 2005). However, once a sanctuary is established there may be a tendency, if not a mandate, to limit management attention to the area that has been specified. Where wide ranging species are concerned, broad scale studies are

also critical for placing the subset of the population that can be managed into a larger context.

Aerial surveys performed from 1979 through 1982 indicated that humpback whales were typically concentrated in south-west and north-east GOM areas, including Stellwagen Bank (CeTAP, 1982). However, commercial fish exploitation had caused a dramatic decline in Atlantic herring abundance by the 1970s, and a corresponding increase in sand lance abundance (Meyer *et al.*, 1979; Overholtz and Friedland, 2002). It was hypothesised that high density aggregations in the south-west GOM had been brought about by increases in sand lance and a corresponding shift of humpback whales from coastal Maine (Payne *et al.*, 1986). When sand lance abundance subsequently declined at Stellwagen Bank in the mid-1990s, Weinrich *et al.* (1997) speculated that GOM humpback whales would return to a historical pattern of distribution less centred upon sand lance habitat. However, the present results indicate that the large scale distribution of the population has remained relatively unchanged. Thus, the SBNMS lies at and adjacent to persistent aggregation sites for humpback whales in the region.

The SBNMS is also well-situated in that it was established in an area used preferentially by juveniles and mature females. These classes typically play important roles in large mammal population dynamics, the first because of its sensitivity to environment and/or population density and the second because of its importance to population growth. Humpback whales presently have broad legislative protection in the U.S. waters of the GOM. However, MPAs provide an opportunity for focussed management, including monitoring and more practical enforcement. It appears that initiatives targeting those key classes could therefore be implemented from within the SBNMS. Population monitoring efforts have previously focussed on the SBNMS, but it was not known whether those data were representative of the population overall. As discussed in Chapter 5, reproductive rate estimates based on data from the south-west GOM data appear to be comparable to those obtained by GOM-wide sampling. Given the importance of high re-sighting rates in mark-recapture analyses, an effective monitoring strategy for reproduction might continue to maximise effort in south-west GOM areas, like the SBNMS.

Despite the appropriateness of its location, the size of this MPA does not encompass the range of any individual humpback whale. Proposals have been made to extend the SBNMS in the future or to create additional MPAs at Jeffreys Ledge and/or

the Great South Channel. Humpback whales are only one species of management interest and so those decisions would likely depend on many factors. However, this research indicates that the choice of areas would not have equal results where humpback whales are concerned. Adults move between all of the GOM areas studied, but the areas of particular importance to SBNMS whales in this study were the Great South Channel and western Georges Bank. An extension to the south would incorporate the most common alternate summer habitat of SBNMS humpback whales, as well as an important habitat for juveniles and an area of routinely high humpback whale density. Extension to the north would encompass fewer humpback whales, but a slightly different demographic than is presently observed in the sanctuary. Thus, although both areas lie adjacent to the SBNMS, the relative importance of each area should also be considered when establishing management priorities.

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Chapter 3:

Seasonal population structure and migratory behaviour of Gulf of Maine humpback whales

3.1 Introduction

Humpback whales, *Megaptera novaeangliae*, migrate annually between discrete high latitude feeding areas and shared low latitude breeding areas. This species migrates farther than any other mammal (Stone *et al.*, 1990) and forgoes feeding while on the breeding range with few exceptions (Baraff *et al.*, 1991). This apparent trade-off between feeding and breeding opportunities has the potential to cause migratory behaviour to differ among individuals and demographic classes.

The most detailed demographic data on humpback whale migration comes from the Southern Hemisphere, where coastal migrating populations attracted intense commercial whaling. Scientific study of whaling catches indicated that migrating populations were not homogenous, but rather varied distinctly by sex, age and reproductive status (Chittleborough, 1965; Dawbin, 1966, 1997). Mature females nearing the end of lactation were first to migrate toward the breeding ground, followed by independent juveniles of both sexes, mature males, “resting” females (neither pregnant nor recently lactating), and finally females in late pregnancy. This pattern was roughly reversed on the return migration, with pregnant and resting females leaving first for their feeding grounds and females with new calves leaving last.

Northern Hemisphere humpback whales do not appear to be coastal migrants (CeTAP, 1982; Mate *et al.*, 1998; Reeves *et al.*, 2004) and so insight into this behaviour comes mainly from their migratory destinations. In the North Pacific, apparent breeding ground arrivals and departures suggested a pattern similar to what has been reported for the Southern Hemisphere (Nishiwaki, 1959; Craig *et al.*, 2003). However, a recent North Atlantic breeding ground study found that males arrived earlier on average than all classes of females (Stevick *et al.*, 2003a). Migration distances vary substantially among populations migrating to the same North Atlantic breeding site (2300-8080-km, Stevick *et al.*, 2003a) and Craig *et al.* (2003) hypothesised that this could have obscured other patterns. The North Atlantic study also could not discriminate among migrants based on their maturational class, a potentially important factor in migratory timing. However,

there was considerable heterogeneity in both the Southern and Northern Hemisphere data, suggesting that other factors influence migratory timing in all oceans. A comparable study focussing on a single, well-studied feeding population may help to resolve this discrepancy.

Individuals of all ages and both sexes have been encountered on migration (Dawbin, 1966, 1997), and yet the apparent sex ratio on migration routes and breeding grounds is typically male-biased (Chittleborough, 1965; Brown *et al.*, 1995; Palsbøll *et al.*, 1997). Females also do not reproduce in all possible years and this has led some to hypothesise that as many as half do not undertake or complete migration to the breeding ground each year (Brown *et al.*, 1995; Craig and Herman, 1997; Craig *et al.*, 2003). “Conditional” migration has also been offered as an explanation for annual variability in the numbers of humpback whales migrating along the eastern Australian coastline (Chaloupka *et al.*, 1999) and for discrepancies between feeding and breeding ground abundance estimates (IWC, 2006). In fact, humpback whales are sporadically encountered in mid- to high-latitude waters between late autumn and early spring (Ingebrigtsen, 1929; Matthews, 1937; Mackintosh and Brown, 1956; Williamson, 1961; CeTAP, 1982; Sigurjónsson and Gunnlaugsson, 1990; Straley, 1990; Christensen *et al.*, 1992; Clapham *et al.*, 1993a; Weller *et al.*, 1996; Clapham *et al.*, 1997; Gregr *et al.*, 2000; Charif *et al.*, 2001; Barco *et al.*, 2002; Frantzis *et al.*, 2004; Thiele *et al.*, 2004; Kemper, 2005). However, it has yet to be determined whether such sightings constitute evidence of significant non-migration and whether females are preferentially involved.

The Gulf of Maine (GOM) is the site of the southern-most humpback whale feeding population in the North Atlantic. Individuals exhibit high rates of annual return and summer occupancy which are thought to be maternally directed (Martin *et al.*, 1984; Clapham and Mayo, 1987; Katona and Beard, 1990). Sightings are common in the GOM from mid-April through October (CeTAP, 1982; Katona and Beard, 1991; Clapham *et al.*, 1993a). The few studies undertaken in other months indicate that humpback whales can also be present between late autumn and early spring (CeTAP, 1982; Clapham *et al.*, 1993a), but the specific demographic pattern of migratory arrivals and departures has not been established. Three months or more may elapse between the first and last migrant in each direction (Dawbin, 1997). If this is the case in the GOM, then accurate population monitoring may depend on an understanding of the period of migratory closure.

We used aerial surveys and photo-identification data to clarify the seasonal dynamics of the GOM humpback whale population. In particular, we sought to a) characterise the demographic pattern of migration, b) to identify months in which population composition was influenced by migration and c) to evaluate the hypothesis that significant numbers of humpback whales do not undertake or complete migration each year.

3.2 Methods

3.2.1 Data sources

Individual humpback whales were identified from their natural markings, especially the ventral pigmentation of the flukes and the shape and size of the dorsal fin (Katona and Whitehead, 1981). In the GOM, photographs of identifying features were obtained by research vessels engaged in photo-identification (photo-ID) surveys and by naturalists aboard commercial whale watching vessels. Photo-ID surveys targeted known humpback whale aggregation sites in the south-west GOM from 1983 through 1988, and throughout the geographic GOM from 1989 through 2005 (Figure 3.1, Table 3.1). Surveys were performed year-round, but were less frequent from November through May and logistically limited to south-west GOM areas. Whale watching vessels operated on a near-daily basis in the south-west GOM from mid-April through October, 1979-2005. Humpback whales were the primary species of interest and an effort was made to photo-ID every individual encountered. Selected data through 1988 were previously presented by Clapham *et al.* (1993a).

Winter sightings outside the GOM were obtained from the Provincetown Center for Coastal Studies (PCCS), the Northeast Fisheries Science Center (NEFSC) and the North Atlantic Humpback Whale Catalog (NAWHC). These data stemmed from various research projects and opportunistic sources and were used primarily to identify “migrants” in our GOM data. When estimating the composition of GOM whales on the West Indies (WI) breeding ground, we focused on data obtained during the Years of the North Atlantic Humpback Whale (YONAH) project, January through March, 1992-1993. YONAH was a mark-recapture study intended to estimate population size and structure across the North Atlantic (Palsbøll *et al.*, 1997; Smith *et al.*, 1999; Stevick *et al.*, 2003a; Stevick *et al.*, 2003b). Humpback whale behaviour on the breeding ground varies with sex and reproductive state and YONAH protocols were designed to minimise and evaluate sampling bias (Smith *et al.*, 1999). We therefore considered these to be the best existing

Figure 3.1: Study area, winter aerial survey effort, winter sightings and summer distribution of humpback whales in the Gulf of Maine.

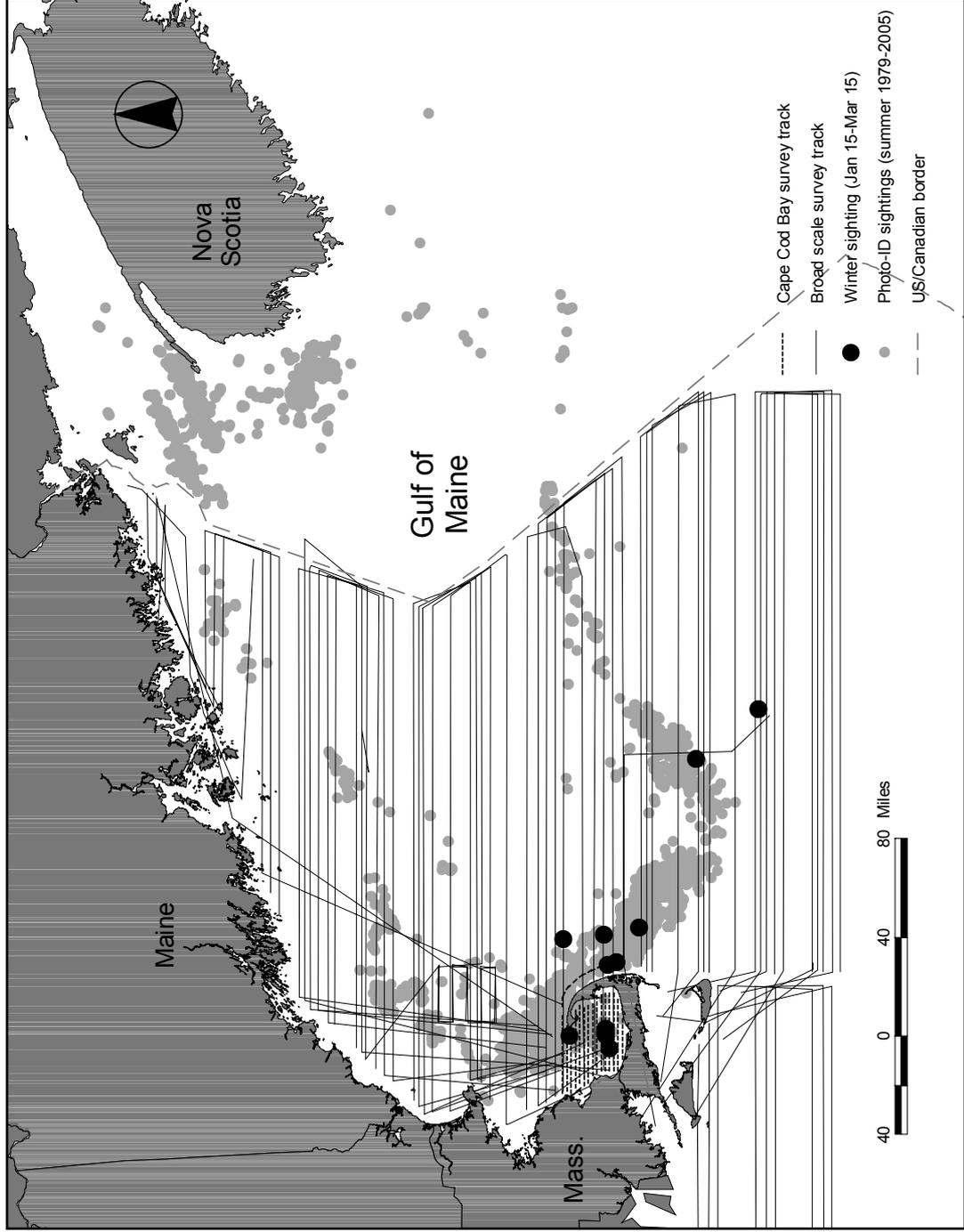


TABLE 3.1: Summary of sampling effort by season, region and institution. We discriminated between sampling that was limited to the south-west Gulf of Maine (SW GOM) and sampling that spanned GOM areas.

INSTITUTION	REGION	YEARS	EFFORT(days)				Total
			Winter (Jan-Mar)	Spring (Apr-Jun)	Summer (Jul-Sep)	Autumn (Oct-Dec)	
PCCS	SW GOM	1979-2005	182	2,381	2,436	710	5,709
PCCS*	GOM	1989-2005	3	8	283	20	314
		Vessel:	185	2,389	2,719	730	6,023
PCCS	SW GOM	1998-2005	170	73	0	6	249
NEFSC	GOM**	2005-2006	52	29	32	20	133
		Aerial:	222	102	32	26	382

*One winter survey was also performed by NEFSC, effort is not shown

**Limited to U.S. GOM waters

data for assessing breeding ground population composition. WI data were obtained primarily at Silver Bank, a breeding aggregation located approximately 70 miles north of the Dominican Republic. Individuals were matched to the GOM population by photo-ID or molecular genetic matching on six microsatellite loci (Palsbøll *et al.*, 1997).

Given the low frequency of vessel surveys in the GOM in winter, we used data from systematic aerial surveys for insight into relative seasonal humpback whale abundance and distribution. Aerial surveys were designed for North Atlantic right whales (*Eubalena glacialis*), but all marine mammal species were recorded when sighted. PCCS conducted aerial surveys in and adjacent to Cape Cod Bay, a critical right whale habitat, between December and May, 1998-2005 (Figure 3.1, Table 3.1). Although humpback whales can be found in Cape Cod Bay, this is not their principal habitat in summer and their winter distribution is not well defined. We therefore also used humpback whale sightings from NEFSC broad scale aerial surveys conducted between January 2005 and March 2006 and spanning U.S. GOM waters (Figure 3.1, Table 3.1). The latter had the potential to detect humpback whales in offshore areas more commonly used in summer months (Figure 3.1). Aside from these differences in survey coverage, the two programs followed equivalent survey and sighting protocols as described in Brown *et al.* (2007).

3.2.2 Trait assignment

Demographic data for individuals were obtained from the Gulf of Maine Humpback Whale Catalog curated by PCCS. Humpback whales are not strongly sexually dimorphic and there is no outward evidence of age or maturational state, except for mothers accompanied by a dependent calf. Animal sex was therefore determined by molecular genetic analysis of a skin sample (Palsbøll *et al.*, 1992; Bérubé and Palsbøll, 1996a, b) or a photograph of the genital slit (Glockner, 1983). Tissue samples for molecular genetic analyses were obtained by biopsy techniques (Palsbøll *et al.*, 1991) or by the collection of naturally sloughed skin (Clapham *et al.*, 1993b). Once a sex determination was made, it was applied to all other sightings of that individual.

Exact age was known for individuals first observed as calves. Calves were identified in the field by their close, consistent association with a single animal at least twice their size. They exhibited stereotypical positioning and behaviours that are not observed in older animals and photo-identification confirmed that they were new to the catalogued population. Humpback whale calves remain with their mothers until at least the autumn of

their first year (Clapham and Mayo, 1987; Baraff and Weinrich, 1993). Although many GOM whales were first documented as calves, others were not encountered until after weaning and some were born before cataloguing began in the 1970s. When an independent animal was confirmed to be new to the catalogued population, it was at least one year old (its minimum age), but could have been older.

We allocated individuals to classes based on patterns of survival and reproduction. Female GOM humpback whales produce their first viable calf between the ages of five and 13 (Clapham, 1992; Barlow and Clapham, 1997, also see Chapter 5). Males reach puberty at approximately the same age as females (Chittleborough, 1965), although it is not known when they begin to successfully reproduce. Both sexes achieve adult survival rates by age five (see Chapter 4). Based on this information, “juveniles” were defined as individuals of either sex that were first seen as calves and known to be 1-4 years old. Males were potentially mature if known to be at least five years old, but no further discrimination was possible. Females were considered “sub-adults” when they were at least five years old, but without a documented calving history. They were “adults” after first reproduction and “mothers” when a calf was in tow. Adult females were classified as pregnant retrospectively if re-sighted with a calf the following year. Females seen without a calf had either not been pregnant or had lost the calf prior to observation. The remaining individuals could not be reliably assigned to a maturational class. These “unknowns” were hypothesised to be juveniles missed in a recent calf year. However, any individual with a low detection probability could have fallen into that category, regardless of age. Dependent calves (less than one year old) provided information about the reproductive state of the mother, but were not otherwise included in analyses.

3.2.3 Data analyses

Monthly humpback whale encounter rates were calculated from aerial survey data as the number of humpback whales sighted per nautical mile surveyed. Migration timing was inferred from the first and last sighting dates of photo-identified individuals averaged within demographic classes (Dawbin, 1997; e.g., Craig *et al.*, 2003; Stevick *et al.*, 2003a). The average first sighting date was based on individuals seen at least once between 15 March and 30 June, and the last sighting date was based on individuals seen between 1 September and 31 December. For each month, we also calculated the relative frequency of each demographic class based on the characteristics of sighted individuals. Each was

counted once per month per year, regardless of how many sightings occurred, and months were summed across the years of the study. Months were allocated to calendar seasons as follows: winter (January-March), spring (April-June), summer (July-September) and autumn (October-December).

An individual observed in the GOM in winter could have over wintered, left late or arrived early. We discriminated among these possibilities based on a combination of sighting data and minimum likely migratory transit times. The only mark-recapture based estimate of migration between the GOM and the WI was 34 days (Clapham and Mattila, 1988), but this was likely an over-estimate of actual travel time. Using maximum likely migration speeds for this species (114 km/day, Gabriele *et al.*, 1996), the time to travel a great circle route to the closest breeding area (Silver Bank, 2300 km) was 20 days. When an individual was seen in the GOM between January and March with no gaps exceeding 40 days, it was assumed to have over wintered at high latitudes. This was conservative because it assumed no period of residency on the breeding ground and because individuals with sparse sightings in the GOM may still have over wintered.

If some demographic classes were consistently less likely to migrate, then they should have been under-represented in the WI relative to the GOM. We compared the age and sex structure of migrants to the GOM population during the peak of summer when the population was most likely to be closed to migration. We also compared apparent fecundity of migrants to GOM females not known to have migrated. Females were either a) seen on the breeding ground in winter or b) seen only on the feeding ground later in summer and so not known to have migrated, although they might have done so unobserved. Analysis was limited to females that did not initially have a calf in tow. Fecundity was then measured as the percentage of females with a calf the next calendar year, out of the total re-sighted. Re-sightings were limited to GOM data to standardise the potential effect of neonatal mortality on fecundity comparisons.

Means were reported with their standard deviation (*s*), unless otherwise noted. Categorical comparisons were made by G-test and means were compared by t-test or ANOVA with a post hoc Scheffé procedure ($\alpha=0.05$, Sokal and Rohlf, 1981).

3.3 Results

3.3.1 Gulf of Maine

Humpback whales were encountered in the GOM in all months, but 96.4% (n=672) of broad-scale aerial sightings occurred between May and October (Figure 3.2). Encounter rates were highest in July and August, and lowest in February when only three humpbacks were seen. Most winter broad-scale survey sightings occurred in early January or late March and the few sightings that occurred were in areas typically used by humpback whales in summer (Figure 3.1). Humpback whales were also uncommon in Cape Cod Bay in February (n=3), but detection rates there were consistently low from late January through early March (Figure 3.3). We focused on this peak winter period for insight into over wintering.

Twenty-one individuals were photo-identified during vessel surveys at the peak of winter, 1984-2005. None were confirmed to have migrated; however, sightings were rarely made at both high and low latitudes in the same winter season. Winter sightings were predominantly known or suspected juveniles (61.9%, n=13) and sexed animals favoured females (71.4%, n=15, $G=8.84$, $p=0.02$). None were seen in multiple winters, but nearly all (n=18) were re-sighted in other years. Over wintering was indicated for no fewer than 28.6% (n=6). These were seen on an average of 5.8 days ($s=0.98$) with mean sighting intervals of 13.5 days ($s=3.51$). Over wintering whales were primarily juvenile females. Two were known to be two- or three-years old and two additional did not reproduce for at least eight subsequent years of observation, providing strong evidence that they were also juvenile when sighted. The only male was still of juvenile length (<34 ft) when he died two years later. The remaining individual was of unknown age and sex.

Mature males were not encountered at the peak of winter, but eight mature females were seen. One late pregnant female was encountered on 18 January and re-sighted with a calf on 20 June. This primiparous five-year-old could have migrated to give birth, although sighting data were inconclusive in this regard. Five adult females were encountered in a single offshore aggregation on 28 February. At least four had weaned calves from the previous season and at least three did not produce calves the following year. Sighting data were insufficient to determine whether or not they had migrated, but their reproductive state did not require it.

The average first sighting of photo-identified individuals varied significantly among demographic classes ($F_{3,1532}=31.19$, $p<0.001$, Table 3.2). Juveniles and unknowns were

Figure 3.2: Mean monthly humpback whale encounter rates by broad-scale survey in the U.S. waters of the Gulf of Maine, January 2005 through March 2006. The error bars represent the standard error and the total number of sighted animals are shown in parentheses.

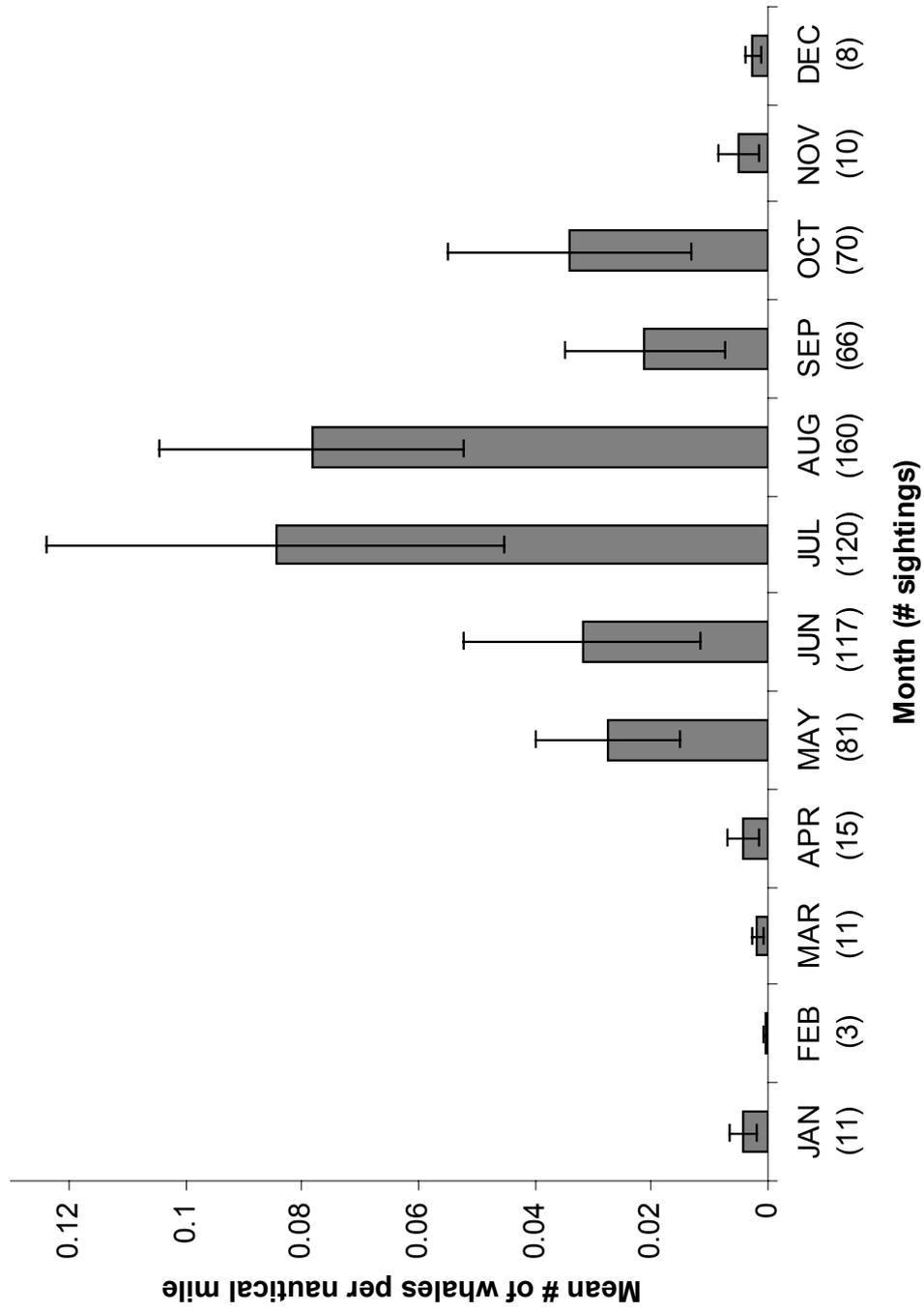


Figure 3.3: Winter humpback whale encounter rates in Cape Cod Bay (PCCS, 1998-2005) and the Gulf of Maine (NEFSC, 2005-2006). Numbers in parentheses indicate total sightings by survey program and error bars represent the standard error of the mean. Humpback whales were rarely encountered in winter, especially from mid-January through mid-March.

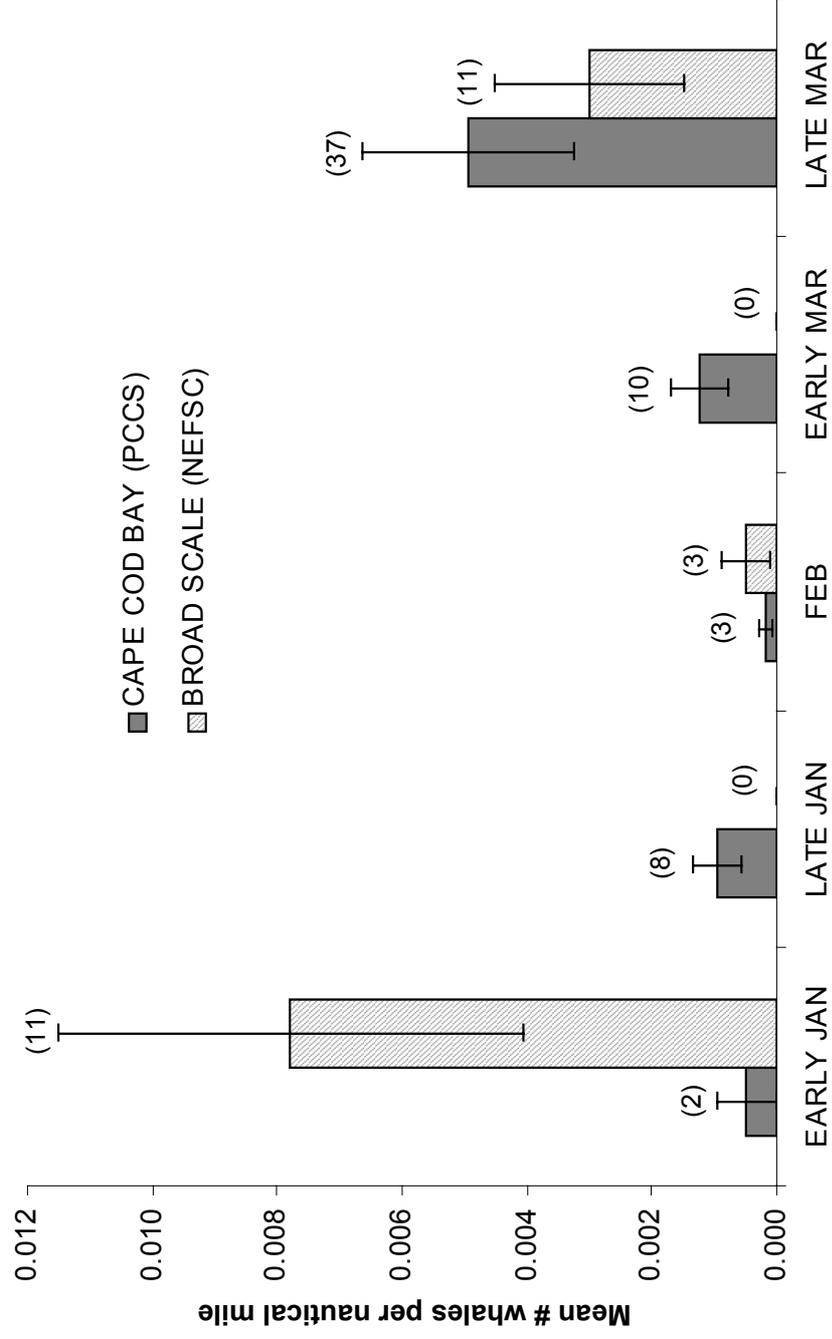


TABLE 3.2: Spring sighting characteristics by demographic class, 1 March through 30 June. Juveniles and unknowns were seen earliest on average. Mature males and mothers were seen significantly later than other classes. As a group, females were encountered significantly earlier than males.

Class	Mean First Sighting Day (From 1 Mar)	Arrival Order (Days from earliest mean)	Standard deviation (Days)	Earliest First Sighting Date		N	Spring Sample Composition (%)
				All whales	Confirmed migrants		
Unknown	71.99	0	23.80	01 Mar	20 Mar	865	30.0
Juvenile	72.68	0.69	23.64	03 Mar	10 May	377	13.1
Sub-adult female	76.00	4.01	23.50	02 Mar	03 May	223	7.7
Pregnant female	77.08	5.09	26.17	04 Mar	03 May	254	8.8
Adult female	79.19	7.20	24.72	18 Mar	13 May	255	8.8
Male	84.69	12.70	23.49	18 Mar	19 Apr	620	21.5
Mother	87.97	15.98	21.47	04 Apr	18 Apr	285	9.9
Female	77.75	5.76	24.25	01 Mar	20 Mar	1606	61.7
Male	81.00	9.01	24.47	03 Mar	19 Apr	997	

first on average, but not substantially earlier than pregnant females. By contrast, Scheffé tests indicated that males and mothers arrived later than juveniles, unknowns and pregnant females. “Resting” adults arrived earlier than mothers, but were not later than juveniles, nor earlier than males. Trends in monthly composition also suggested a steady increase in mature whales through the spring (Figure 3.4). When individuals were not stratified by age or reproductive status, females were significantly earlier on average than males ($F_{1,260}=10.99$, $p<0.001$). The vast majority of individuals were first encountered by June, and fewer than 10% were first encountered after July (Figure 3.5).

The earliest GOM sighting of a confirmed migrant occurred on 20 March. One of the last GOM mothers seen in the WI (8 March) arrived in the GOM on 18 April, after no more than 41 days (2,466 km, 59.7 km/day). However, some northbound migrants were encountered at Bermuda in mid- to late April (Stone *et al.*, 1987), placing them more than 1,200-km south of the GOM at a time when many whales have already completed the migration. Of those identified at Bermuda, five were male, two were female and one was of unknown sex. Two (one male, one female) arrived in the GOM no later than 20 and 25 May, respectively. These had been seen after 95% of other sightings at Bermuda (Stone *et al.*, 1987), and so were likely at or near the end of the migratory stream. The only GOM mother seen passing Bermuda (on 15 April) was not re-sighted that year. Assuming a 114 km/day transit speed, she could have arrived in the GOM before the end of April. If travelling at the slower, likely under-estimated, speed of the mother described above, she still could have arrived in the GOM by mid-May. Thus, whales still on the breeding range in March and those still on migration in late April can complete the northbound migration before June.

The earliest known southbound migrant was seen off the U.S. mid-Atlantic states on 01 December after a prior GOM sighting on 11 November. However, the first sighting of a GOM whale on the breeding ground was 1 January (Silver Bank), indicating a departure no later than December 10. The demographic effects of migration were less pronounced in autumn than in spring (Figure 3.5, Table 3.2). There were no significant differences in the average last sighting date among classes ($F_{3,1232}=0.35$, $p=0.79$) or between sexes ($F_{1,2118}=0.051$, $p=0.82$). Mature females were under-represented from September onward, but with mothers more prevalent than other adults (Figure 3.4). Mature males were initially under-represented but later encountered in the same proportion as they had been

Figure 3.4: Monthly composition of individuals identified in the southwest Gulf of Maine, relative to the peak feeding season. Mature males and females were under-represented in winter and spring, while juveniles and animals of unknown age were over-represented at those times.

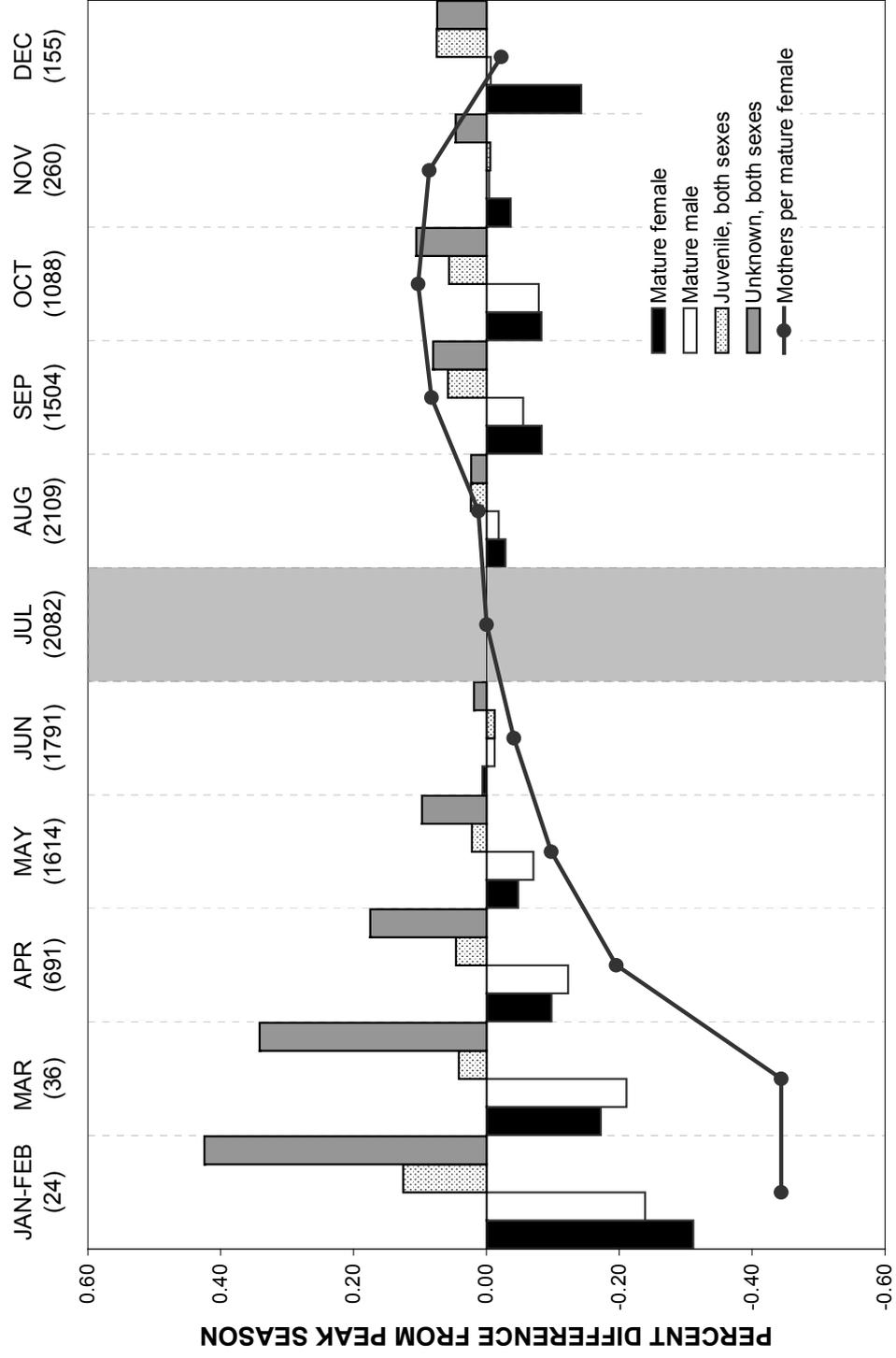


Figure 3.5: Cumulative photo-identification rate in the south-west Gulf of Maine in years of high local humpback whale density ($n > 250$ individuals). Fewer than 10% of individuals were first encountered after July.

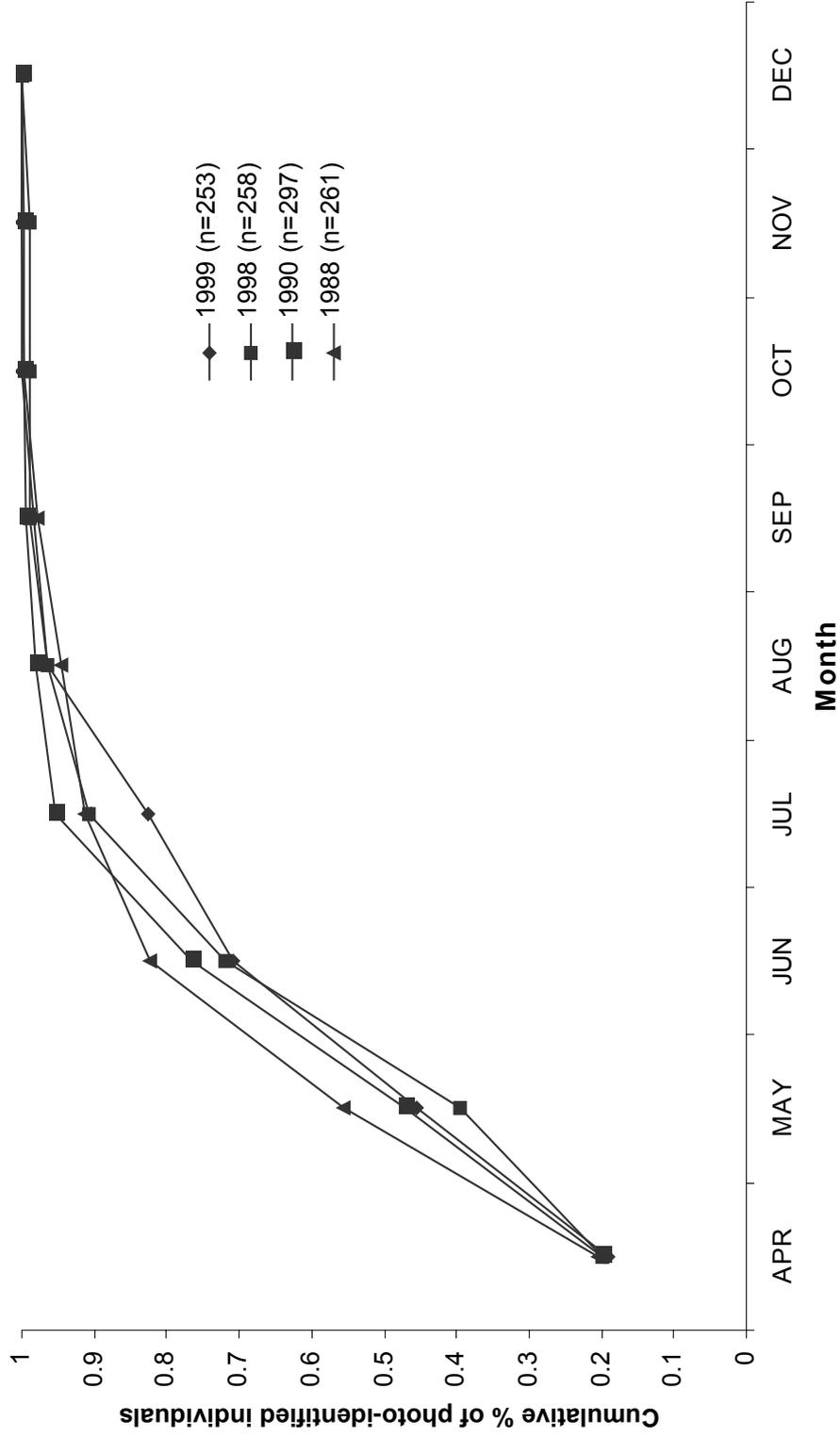


TABLE 3.3: Autumn sighting characteristics by demographic class, 1 September through 31 December. Differences between classes and sexes were not statistically significant.

Class	Mean Last Sighting Day (From 1 Sep)	Departure Order (Days from earliest mean)	Standard deviation	Latest Last Sighting Date		N	Autumn Sample Composition (%)
				All whales	Confirmed migrants		
Adult female	38.51	0	28.43	22 Dec	19 Dec	271	11.7
Male	38.72	0.20	30.52	22 Dec	09 Dec	449	19.4
Sub-adult female	38.76	0.25	29.48	19 Dec	06 Dec	190	8.2
Juvenile	38.90	0.39	27.00	29 Dec	01 Nov	346	14.9
Mother	39.43	0.91	28.20	22 Dec	19 Dec	268	11.6
Unknown	40.56	2.05	27.35	31 Dec	09 Dec	619	26.7
Pregnant female	41.24	2.73	28.02	19 Dec	16 Nov	173	7.5
Female	39.12	0.60	27.92	31 Dec	19 Dec	1237	58.3
Male	39.42	0.91	29.17	29 Dec	09 Dec	885	

in summer months. All classes were still represented in December (Table 3.3), including individuals confirmed to have subsequently migrated. As a group, the 36 confirmed autumn migrants were not demographically different from other animals encountered ($G=8.02$, $p=0.16$, $df=5$). Finally, the latest sightings of confirmed migrants involved females expected to be at the opposite extremes of the migration. One mother had recently weaned a calf when seen in the GOM on 19 December and conceived another calf, presumably later that winter. The other was already pregnant when seen on 19 December and returned with a calf on 5 June.

3.3.2 West Indies

A total of 236 GOM whales were encountered in the WI, half of which were seen during the YONAH project. The average sighting date of mature males was slightly earlier than females, but this approached significance only when mothers were excluded ($F_{1,152}=3.63$, $p=0.059$). A higher percentage of whales in the YONAH sample were mature (80%, $n=91$) than expected from the composition of the GOM population in the same years ($X^2=7.865$, $p=0.005$, $df=1$, see Chapter 4). Independent juveniles ($n=12$) were primarily yearlings ($n=4$) or animals approaching sexual maturity (age 4, $n=5$). The two three-year olds (one male, one female) were singletons when seen or associated with one or two other whales. GOM individuals ranged from one to at least 19 years old in both areas, but WI whales were 1.3 years older on average (7.3 years, $n=33$, $t_{463}=3.2$, $p=0.001$). Whereas yearlings were present at the expected frequency, two- and three-year olds were under-represented.

Migrants were not significantly more likely to produce a calf (66%, $n=12$) than GOM females not directly observed on the breeding ground (43.8%, $n=21$, $G=2.71$, $p=0.100$). Sub-adults encountered in the WI rarely produced a viable calf (18.2%, $n=2$), despite their confirmed presence on the breeding ground.

3.4 Discussion

3.4.1 Migration timing

In the Southern Hemisphere, mature females lead and terminate the flow of migration in both directions (Dawbin, 1966; 1997). Although a similar pattern has been found in the North Pacific (Nishiwaki, 1959; Craig *et al.*, 2003), the average male was reported to arrive earlier in winter in the West Indies (Stevick *et al.*, 2003a). Ecological factors could

cause migratory behaviour to differ among oceanic populations (Alerstam and Hedenstrom, 1998), and one low-latitude feeding population is thought to forgo migration altogether (Mikhalev, 1997). In this study, we re-examined this question for one discrete segment of the West Indies breeding population.

Mature GOM males and mothers exhibited significantly later return in spring than other demographic classes, comparable to what has been described in other oceans. These are the only classes hypothesised to preferentially benefit from extended residency at low latitudes. The humpback whale mating system is polygynous (Cerchio *et al.*, 2005) and so males can potentially increase their reproductive success by maximising encounters with receptive females. In the West Indies in particular, males may increase opportunities to mate with females from more distant feeding grounds the longer that they extend their stay at low latitudes (Stevick *et al.*, 2003a). Maternal preference for warm, shallow waters for an extended period after birth may increase the probability of neonate survival, although the specific mechanisms are not clear (e.g., Corkeron and Connor, 1999; Clapham, 2001).

The autumn migration toward the breeding ground provided the strongest signal in Southern Hemisphere data, but we found less support at that time for staggering by class (Dawbin, 1997) or by sex alone (Stevick *et al.*, 2003a). Photo-ID sample sizes were smaller in autumn because prevailing weather was less conducive for vessel-based research, and this may have reduced our ability to detect differences among classes. This study was also conducted on a subset of the feeding range and abrupt changes in water temperature and nutrient distribution in autumn may have disrupted humpback whale distribution patterns and obscured true migratory movement. However, there may also be more variability in the timing of the southbound migration. Whereas the timing of departure from the breeding ground is likely driven by intrinsic factors, feeding ground departures may be influenced by variability in high latitude prey abundance and distribution. Such variability may be less of a consideration in the Southern Hemisphere where a single plankton species (Antarctic krill, *Euphausia superba*) dominates the diet. However, even in the Southern Hemisphere, differences among demographic classes were marked by wide confidence intervals. Thus, it is likely that factors other than demographic class shape the pattern of humpback whale migration within any given ocean.

Overall, our results were most consistent with the demographic pattern described by Dawbin; we found little evidence that males undertook an earlier southbound migration

(Stevick *et al.* 2003). Nevertheless, the arrival of females before males on the breeding ground, termed “protogyny”, is an uncommon behaviour in polygynous migrating animals (Morbey and Ydenberg, 2001). Furthermore, it is perplexing in light of current knowledge of the mating system of this species, which is polygynous with attributes of a lek (Clapham, 1996), albeit with relatively little male reproductive skew (Cerchio *et al.*, 2005). It is generally assumed that males attempt to maximise reproductive opportunities on the breeding ground, whereas adult females return to their feeding ground promptly after conception. If this is the case, then one might expect males to arrive with, or in advance of, the class of females that is most likely to come into oestrus. Craig *et al.* (2003) theorised that males might arrive later to maximise their overlap with both adult females and mothers. However, males should seek out the category of breeder that yields the highest probability of paternity and only 2% of mothers appear to conceive after parturition and carry that pregnancy to term (Chittleborough, 1965, also see Chapter 5). Alternatively, early arriving adult females may be less desirable to males for other reasons. Most will have weaned a calf before or shortly after their arrival on the breeding ground. If the probability of weaning increases over time, then females that arrive the earliest may have completed that process most recently. There is little information on oestrus in this species, but if there is an obligate hiatus after late lactation, then early arriving females may initially be unreceptive. Delayed male arrival may simply reflect the best balance between feeding and breeding opportunities, rather than an effort to split investment between adult females and mothers.

Dawbin (1966, 1997) assumed that all classes travel at equal speed during migration and this was integral to his inference of staggered migration. However this has yet to be confirmed and mothers, in particular, may migrate more slowly due to the presence of a calf (Lockyer, 1984). Until recent satellite telemetry studies, migration speeds of free-ranging mothers had not been documented. Mate *et al.* (1998) estimated a migration rate of 150 km/day for a mother in the North Pacific, but was only able to track the first 4.5 days of her spring migration. More recently, Zerbini (2006) estimated the autumn migration rate for one Southern Hemisphere mother at 92 km/d. Like all such estimates, our mark-recapture based transit time of 59.7 km/day was likely an underestimate. However, it is the minimum transit speed on record for a mother in the North Atlantic and within the range previously reported for other demographic classes (Clapham and Mattila, 1988).

3.4.2 Do all whales migrate?

Whaling biologists interpreted the male bias in low latitude catch data to be an artefact of legal protection afforded to mothers (Matthews, 1937; Chittleborough, 1965). Chittleborough (1965) referred to the near-parity catch sex ratio at Albany, Australia where females were still in late pregnancy and so could legally be taken. However, Brown *et al.* (1995) found a male-biased sex ratio among free-ranging whales on the eastern Australian migration route that they did not believe was the result of sampling bias. They concluded that 50% of females, likely those still sexually immature, did not undertake migration every year.

Subsequent authors have interpreted their own sex-skewed breeding ground data to reflect an absence of adult females (Craig and Herman, 1997; Craig *et al.*, 2003). Humpback whales produce a calf every 2-3 years on average (Clapham and Mayo, 1990; Glockner-Ferrari and Ferrari, 1990). In a two-year calving interval, pregnancy follows immediately upon the weaning of a calf, whereas a three-year interval indicates a “resting” year in which pregnancy either did not occur or failed. Craig and colleagues (Craig and Herman, 1997; Craig *et al.*, 2003) proposed that adult females do not migrate in these “resting” years. Alternatively, they suggested that some might mate on their southbound migration and return to the feeding ground before reaching the breeding ground. They provided compelling reasons as to why mature females might forgo or attempt to reduce the costs of migration in the short term in order to increase their lifetime reproductive success. However, in order to explain a sex skew at low latitudes, both theories require that a substantial number of adult females be present outside of the breeding ground during winter. The first theory requires that the fecundity of migrants be high enough to compensate for non-migrating females. The second requires that some of the females observed at high latitudes in winter be pregnant.

There have been numerous reports of humpback whales outside the breeding grounds between late autumn through early spring (Ingebrigtsen, 1929; Williamson, 1961; Sigurjónsson and Gunnlaugsson, 1990; Straley, 1990; Christensen *et al.*, 1992; Clapham *et al.*, 1997; Stefansson *et al.*, 1997; Gregr *et al.*, 2000; Charif *et al.*, 2001; Thiele *et al.*, 2004; Kemper, 2005). In most cases, however, reports are insufficient to determine whether the animals were early to arrive, late to depart or over wintering. Our results confirm the suspicion of Clapham *et al.* (1993a), that some of the individuals they detected

in the GOM in winter were over wintering. It is, nevertheless, a relatively uncommon phenomenon. Broad-scale aerial surveys made only three humpback whale sightings during the peak of winter in the GOM, despite an estimated summer population size in the high hundreds (Clapham *et al.*, 2003). The clearest evidence of over wintering in the GOM involved juvenile females and was consistent with an under-representation of GOM juveniles on the breeding grounds. Adult females were detected in the GOM in winter, but were not in the majority. Not all migrating females produced a calf and their fecundity was not significantly higher than other females. The few adults observed at high latitudes in winter did not appear to have returned to the GOM early because they were already pregnant.

The GOM population has a shorter migration to its breeding ground than any other North Atlantic feeding population and so our results may not be representative of over wintering in all high latitude areas. For example, the few whaling catches made at South Georgia near the peak of the breeding season appeared to have favoured females (Matthews, 1937). Humpback whales caught throughout winter in coastal areas of Norway included mature females, although they were in early and late stages of pregnancy and the demographic composition of other whales was not specified (Ingebrigtsen, 1929; Sigurjónsson and Gunnlaugsson, 1990; Christensen *et al.*, 1992). Otherwise, we were unable to find a consistent bias toward mature females in published accounts. Acoustic monitoring in the eastern North Atlantic led Charif *et al.* (2001) to theorise that some mature males over wintered off the British Isles because singers would not have had time to complete migration during the normal breeding season. Catches of mature animals of both sexes occurred in the vicinity of the GOM as late as November (Nova Scotia, Mitchell, 1973), although our results indicate that animals observed as late as December can complete the migration. In the only systematic study of free-ranging whales in winter in the North Pacific, Straley (1990) found humpback whales of both sexes and ages and no direct evidence of over-wintering. Finally, no more than 2.6% (n=49) of the total commercial whaling catch off California between 1919 and 1926 occurred in January and February. Winter catches ranged from only 1 to 22 whales per year, the sex ratio was parity and body lengths were consistent with a combination of juvenile and adult animals (Clapham *et al.*, 1997).

By contrast, winter sightings outside of typical humpback whale feeding and breeding grounds appear to favour juvenile animals of both sexes. In the Northern Hemisphere,

juveniles from the GOM and eastern Canada are found off the U.S. mid-Atlantic states in winter (Barco *et al.*, 2002). Sporadic sightings of humpback whales also occur off the Atlantic coast of Florida (Tom Pitchford, PCCS unpublished data), in the Gulf of Mexico (Weller *et al.*, 1996) and the Mediterranean Sea (Frantzis *et al.*, 2004). The stock identity of the latter is not yet known and demographic data stem primarily from stranding records which may not be representative of the free-ranging populations. Furthermore, it remains unclear whether these animals also visit the breeding ground.

If both sexes are equally likely to be absent from the breeding ground, then overwintering can not explain the male skew typically observed at low latitudes. However, a skewed sex ratio is not, in and of itself, evidence of female absence from the breeding ground. For example, a biopsy-based, sex-stratified abundance estimate for the West Indies, found males to exceed females by 43% (Palsbøll *et al.*, 1997). This result has previously been misinterpreted as evidence that a large portion of the female population does not migrate in alternate years (Craig and Herman, 1997; Craig *et al.*, 2002; Craig *et al.*, 2003). However, individual females would have to be absent in two consecutive years produce this effect (P. Palsbøll, pers. comm.), and that behaviour would be inconsistent with calving rate data. Smith *et al.* (1999) and Palsbøll *et al.* (1997) offered another potential explanation for their sex skewed results: that females were less likely to be sampled when present on the breeding ground. Mattila *et al.* (2001) proposed that the shorter average breeding ground residency by adult females (Gabriele, 1992) could account for this effect. Craig and Herman (1997) discounted this possibility without analysis, but Friday *et al.* (2001) confirmed through modelling that a shorter female residency could cause a male sampling skew on the order of what has been observed. Garrigue *et al.* (2004) subsequently found males and females to be equally abundant on one low density Southern Hemisphere breeding ground. They attributed this finding to higher female sampling probabilities in low population density and across a broad sampling season.

In conclusion, animals of all age classes and both sexes are found outside the breeding ground in winter. However, the available data suggest that juveniles are the most likely to be systematically missing. Even if they do not overwinter in large numbers on their feeding ground, they may still fail to complete the migration to the breeding ground. This poses a potential problem for abundance estimates of wintering populations, as the alternate habitats used by juveniles in winter may be difficult to identify and sample

systematically. Furthermore, for most populations, the age of free-ranging whales is not known. Visual size estimates have not been tested in this regard and are likely more accurate for the smallest and largest individuals. For example, Craig *et al.* (2003) suspected that the animals that they classified as “juveniles” on the breeding ground were primarily yearlings. Molecular genetic ageing techniques now in development for humpback whales (Dennis, 2006) may help to assess the magnitude of bias in such estimates.

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Chapter 4:

Age structure and survival of Gulf of Maine humpback whales

4.1 Introduction

Large whale species are cryptic, wide-ranging, difficult to age, and known to live beyond 100 years in at least one case (George *et al.*, 1999). These characteristics pose a challenge for all demographic research, but especially for estimates of age structure and age-specific survival. The age structure of a population can provide insight into population status and trend, particularly in conjunction with independent estimates of vital rates or abundance (Coulson *et al.*, 2001; Holmes and York, 2003; Manly *et al.*, 2003). Several types of data can be used to estimate the mature fraction of a population, including exact age, physical size or evidence of maturational state. However, all are difficult to sample systematically in free-ranging baleen whale populations. Unless an individual is observed as a calf, its age can only be determined after death (e.g., Chittleborough, 1959; Lockyer, 1984; George *et al.*, 1999), and only if the carcass is recovered in adequate condition. Photo-identification programs monitor individual cetaceans, often from their year of birth, and are already in place in many areas to study other aspects of large whale demography (Hammond *et al.*, 1990). However, longitudinal data have only been used to estimate age structure in one baleen whale species to date (Hamilton *et al.*, 1998).

Modern statistical approaches have improved estimates of survival in the common situation in which individuals are encountered sporadically (e.g., Lebreton *et al.*, 1992). These techniques have been applied more frequently to humpback whales (*Megaptera novaeangliae*) than to any other large whale species (Buckland, 1990; Barlow and Clapham, 1997; Chaloupka *et al.*, 1999; Rosenbaum *et al.*, 2002; Clapham *et al.*, 2003; Larsen and Hammond, 2004; Mizroch *et al.*, 2004). However, most studies estimate “non-calf” survival because only dependent calves can be discriminated from older whales with certainty. Mammals are not expected to achieve prime age survival immediately upon weaning, and juvenile survival tends to be more annually variable than that of adults (Caughley, 1966; Gaillard *et al.*, 1998; Gaillard *et al.*, 2000; Eberhardt, 2002; Gaillard and Yoccoz, 2003). If “non-calf” estimates are a variable mixture of juvenile and adult

survival rates, then survival trends over time and differences between populations may be difficult to interpret.

In the only study of juvenile humpback whale survival to date, Rosenbaum *et al.* (2002) found sexually immature females to have lower survival (0.7022) than mature females (0.9638, 95% CI: 0.9463-0.9758). They did not find age-specific survival among juveniles although this was not the primary focus of research and aspects of age-specificity may have been obscured by study design. For example, survival was estimated across a wide study period (1979 through 1995) and a combination of cohort and annual variation could have obscured age-specific differences. Furthermore, survival was estimated for females only and some individuals were sexed retrospectively. Females can be reliably sexed once they begin to reproduce, but those that die before reproducing will be excluded from a sex-stratified estimate. Retrospective sexing may therefore have produced an upward bias that minimised age-specific differences (Buckland, 1982; Nichols *et al.*, 2004).

The Gulf of Maine (GOM) is the southern-most summer feeding ground for humpback whales in the North Atlantic. Individuals can be identified from their natural markings and data on birth year and sex have been catalogued annually since the 1970s. Here, these data are applied to the first systematic study of age structure and age-specific survival in a free-ranging humpback whale population.

4.2 Methods

4.2.1 Data collection

Individual humpback whales were identified from their natural markings, especially the ventral pigmentation of the flukes and the shape and size of the dorsal fin (Katona and Whitehead, 1981). In the GOM, photographs of identifying features were obtained by research vessels engaged in photo-identification (photo-ID) surveys and by naturalists aboard commercial whale watching vessels. Photo-ID surveys targeted known humpback whale aggregation sites in the south-west GOM from 1983 through 1988, and throughout the GOM from 1989 through 2005 (Figure 2.1). The latter “GOM-wide” surveys targeted all known humpback whale aggregation sites and sampling effort was expended proportional to observed whale density. The only exceptions were between 1994 and 1996, when surveys were logistically limited to western Gulf of Maine areas. Whale

watching vessels operated on a near-daily basis in the south-west GOM from mid-April through October, 1979-2005. Humpback whales were the primary species of interest and an effort was made to photo-ID every individual encountered.

Demographic data for sighted individuals were obtained from the PCCS Gulf of Maine Humpback Whale Catalogue (Massachusetts, USA). Exact age was known only for whales that were dependent calves at first encounter. Calves were classified in the field based on their physical size, stereotypical behaviours and close, consistent association with a mature female. They were assumed to range from 3 to 9 months old when first observed and typically remained dependent until at least October of their first year (Clapham and Mayo, 1987; Baraff and Weinrich, 1993). Individuals that were independent when first catalogued prior to October were therefore at least one year old, but could have been older. Sexes were based on the external morphology of the genital slit (Glockner, 1983) or molecular genetic analysis of a skin sample obtained by biopsy sampling techniques (Palsbøll *et al.*, 1991; Palsbøll *et al.*, 1992; Bérubé and Palsbøll, 1996a, b). Females known only from their calving histories were considered unsexed in this study, in order to prevent a bias toward females that lived to reproduce. Only 2% (n=38) of catalogued individuals were recovered after death, most during a single unusual mortality event (Geraci *et al.*, 1989). Given the sparseness of these data, they were not incorporated into the modelling process.

Humpback whale calves do not present their flukes consistently and approximately 5% of individuals undergo moderate to major pigmentation changes in their first few years (Carlson *et al.*, 1990). The quality of calf fluke documentation determines whether an aged whale will be recognised upon re-sighting and so is an important consideration for age-specific survival estimates. Quality of documentation was categorised based on image clarity, contrast, and angle (Friday *et al.*, 2000). In high quality images, the flukes filled at least one quarter of the frame and were visible to at least the midpoint such that both sides of the upper half were clearly visible. The angle was roughly perpendicular to the flukes and the image was in good focus. Only calves with documentation meeting all of these criteria were included in age-specific survival estimation. When investigating time variation within an age category, analysis included individuals with documentation that failed to meet one quality criterion but was nevertheless considered adequate for matching. Fluke distinctiveness was not assessed because it is primarily a concern when photographic documentation is poor (Friday *et al.*, 2000). Once an individual was well

documented at least once, photo-quality was no longer considered an important source of bias for age-specific estimates.

4.2.2 Data analyses

4.2.2.1 Population age structure

Population age structure was estimated annually based on individuals identified during GOM-wide surveys. Individuals were allocated to maturational classes based on the length of their sighting histories and the earliest age at sexual maturity. Female GOM humpback whales reproduce no earlier than age five (Clapham, 1992; Barlow and Clapham, 1997). Males reach puberty at approximately the same age as females (Chittleborough, 1965), although it is not known when they begin to successfully reproduce. Individuals were therefore assigned to one of three age classes: dependent calves (<1 year old), independent juveniles (known to be 1-4 years old), and potentially mature animals (5+ years). Means across years were reported with standard deviation (s) and a G-test ($\alpha=0.05$) was used to examine the significance of inter-annual variation ($\alpha=0.05$, Sokal & Rohlf, 1981).

Although many GOM humpback whales were of exact known age, it was not possible to limit age structure estimates to that group. A large portion of the extant population was born before cataloguing began in the mid-1970s and excluding those animals would have biased the mature fraction downward. However, when the year of birth was not known, maturational class could not be reliably assigned until at least four years had passed since their first sighting. Animals with shorter sighting histories were often suspected to be young based on their apparent size in the field, and their deterministic transition to the mature class after four years increased the likelihood that remaining unassigned animals were juveniles. However, any animal with a lower than average likelihood of detection could also have fallen into this category, regardless of age. The proportion of these animals that was likely mature was investigated by comparing spatial distribution, association patterns and vital rates to animals of known age.

4.2.2.2 Survival analyses

When individuals are not encountered in all sampling periods, their apparent survival reflects a combination of true survival, fidelity to the study area and probability of detection when present. Open mark-recapture population models such as the Cormack-Jolly-Seber (CJS, Cormack, 1964; Jolly, 1965; Seber, 1965) estimate survival in light of

these confounding factors. The standard CJS model assumes that survival within groups varies only over time, but its structure can be modified to accommodate other biological hypotheses (Lebreton *et al.*, 1992). We selected a mark-recapture model containing all parameters of biological interest, evaluated the goodness of fit (GOF) of this “global” model to the data and then examined support for reduced models and explanatory factors, as described below.

For a given period of interest, individuals were considered “marked” in the first year that they were photo-identified. Binary encounter histories were constructed for each individual reflecting whether or not it was re-sighted in each subsequent year. Although analysis focused on individuals of known exact age, two other categories of individuals were also of interest. The first were at least 25 years old in the period of interest, but of unknown exact age. These were older than nearly all aged whales and so actuarial senescence was expected to be most evident in this group. The second group had short sighting histories that could not be reliably assigned to a maturational class. These were studied to evaluate the assumption that they were demographically similar to independent juveniles.

Mark-recapture models produce valid estimates only when the underlying data meet model assumptions. Individuals within groups or strata are expected to have an equal but independent probability of detection on the study site as well as an equal probability of survival to the next sampling period. Emigration is permitted from the study area, but it must be random and temporary. Finally, the sampling period should be brief relative to mortality processes, and individuals must be successfully recognised if re-encountered. In consideration of these concerns, annual sightings were limited to a four-month window (June-September) when sampling effort was greatest in both sampling programs. This was considered to be adequately short in light of the high survival rates of this species (Hargrove and Borland, 1994), and the importance of maximising marked sample sizes (O'Brien *et al.*, 2005). Sex-stratified survival estimates were limited to individuals sexed prior to the period in question to prevent a bias toward those that lived to be sampled later in life (Buckland, 1982; Nichols *et al.*, 2004). Age-specific estimates focused on individuals with high quality documentation because failure to successfully recognise an individual is then typically quite low (Stevick *et al.*, 2001). Calves that emigrated from the south-west GOM, either temporarily or permanently, could have been re-encountered during photo-ID cruises during GOM-wide surveys. Although individuals

can emigrate from the GOM to other North Atlantic feeding areas (Katona and Beard, 1990; Clapham *et al.*, 2003), only four known-age whales have been documented to do so and three have subsequently returned. Permanent emigration was not expected to be an important consideration for animals first observed as calves.

Program U-CARE (version 2.2.5, Choquet *et al.*, 2005) was used to detect and diagnose other sources of heterogeneity that could violate model assumptions. U-CARE performs tests that evaluate within-group differences in survival (Test 3.Sr and Test 3.Sm) and re-sighting probabilities (Test 2.Ct and Test 2.Cl). Test 3 components indicate differences in apparent survival that could be due to age-specific effects, transients or other factors. Transients are individuals that are seen once and subsequently leave the study area so that they have no chance of being re-encountered (Pradel *et al.*, 1997). These cause a downward bias in CJS estimates of survival because permanent absence can not be differentiated from death. Individuals first seen as calves were GOM residents by definition. However, if transients were present among “unassigned” or “old” whales, an age-structured model would limit downward bias to the first survival estimate after marking. U-CARE Test 2 components diagnose heterogeneity in re-sighting probabilities for individuals known to have survived. Trap-dependence refers to the situation in which an individual that is present is more or less likely to be seen if seen previously (i.e., trap-happy or trap-shy, Sandland and Kirkwood, 1981; Pradel, 1993). By contrast, Markovian temporary emigration occurs when individuals are more or less likely to remain in the study area (Schaub *et al.*, 2004). When Test 2.Ct was significant, the CJS model was generalised to multiple states (Arnason, 1973; Lebreton and Pradel, 2002) to specifically account for re-sighting heterogeneity. Individuals were either seen (1) or not seen (0) at a given occasion and re-sighting probabilities were modelled as the transitions between those fixed states (e.g. Gimenez *et al.*, 2003; Frederiksen *et al.*, 2004; Crespin *et al.*, 2006). In those cases, it was assumed that the probability of survival did not depend on the state of departure (i.e., whether or not the individual was seen on that occasion).

U-CARE assumes that survival varies only with time within groups, and this was not always the case in this study. Furthermore, even after adjusting the model for likely sources of heterogeneity, residual over-dispersion can cause estimates to be artificially precise (Burnham *et al.*, 1987). We re-examined the fit of our modified global model with the median c-hat technique in program MARK (version 4.3, Cooch and White, 2006) and used an estimated variance inflation factor (c-hat) to account for residual over-dispersion.

To be conservative, analysis followed Nisbet & Cam (2002) and used the estimated value of \hat{c} even when it indicated very mild over-dispersion. Model selection was then performed in MARK based on Akaike's Information Criterion (Burnham and Anderson, 2002). Akaike's Information Criterion (AIC) evaluates the relative fit of each candidate model in light of the number of parameters necessary to achieve that fit. We used QAICc, a form that accounted both for small sample sizes and the inclusion of a variance inflation factor. The model with the lowest QAICc value was considered to have the most support from the data, and all other models were evaluated based on their distance from the preferred model (Δ QAICc). Those within 2 units were considered equally likely, whereas a model that differed by 10 units or more was inferred to have no support (Burnham and Anderson, 2002). The ratio of normalised QAICc weights of two models was used as an indication of relative strength of support. Model averaging was performed within program MARK to obtain parameter estimates in cases of model selection uncertainty.

Re-sighting probability

Analysis sought the most parsimonious model for re-sighting probability before examining reduced parameter models for survival (Lebreton *et al.*, 1992). A previous study on GOM females found that a two age class model without time effects was the most parsimonious for juvenile re-sighting rates, whereas annual variation provided the best fit for all females above the age of five (Rosenbaum *et al.*, 2002). No rationale was given for modelling re-sighting probability as a function of age in that study; however, we expected juveniles to differ from adults due to their smaller apparent range of movement (see Chapter 2). We explored full age specificity as well as time effects through age five. We also expected sex-specific differences in re-sighting probability given greater sampling effort in the southern GOM where females are more frequently encountered (Chapter 2).

Age-specific survival

Age-specific survival was estimated for 2000 through 2005, a subset of available years in which the widest range of ages were available for comparison. Although a more narrow window would have been desirable to eliminate simultaneous time effects (e.g., Nisbet and Cam, 2002), this was not feasible given our annual sample sizes. Even within the specified period, birth cohorts were too small to be analysed individually. Instead, individuals were grouped by the age at which they were first encountered and constraints were imposed within program MARK to equate true age across cohorts. Time variation

was modelled in a separate step (see below) once age-specific patterns were identified. The age-structured model was too complicated to incorporate sex as a factor and so we ran the same suite of models on the full data set and then separately for males and females.

Model selection examined hypotheses ranging from full age specificity (ϕ_a) to no age effects on survival (ϕ). We fit linear (ϕ_A) and quadratic (ϕ_A^2) models to examine support for constant or accelerating effects of age. We also investigated models in which the slope of the trend changed at sexual maturity (McDonald *et al.*, 1996). This was either set at age five, the earliest average age of sexual maturity (Clapham, 1992), or age eight, the average maximum age at female sexual maturity between 2000-2005 (Chapter 5). Reduced models were constructed in which ages were grouped into *a priori* classes. Independent juvenile survival was modelled as age-specific or constant, but in either case different from older whales. We also theorised that “old” whales of unknown exact age would have a lower and more variable average survival than younger, known age, adults. Finally, we examined support for the “non-calf” adult survival rate commonly modelled for this species out of logistical necessity. We systematically removed younger ages from the “non-calf” estimate to find the minimum age that maximised adult survival. This was intended to inform adult survival estimation in populations where only time since first sighting is known.

Time variation and explanatory factors

Time variation and explanatory factors were studied for individuals born across an 17-year period, 1988-2003. When annual variation was supported, we separated true “process” variation from sampling variation using the variance components technique in program MARK (Burnham and White, 2002). We attempted to explain this variation with factors known or suspected to influence survival, as described below. Group covariate data were modelled infra-structurally in program MARK in a linear modelling framework. If a particular covariate was not available in all years, we standardised the values so that missing data would not influence the results (Cooch and White, 2006). We used model selection to identify the factor(s) that best explained temporal variation.

Low prey abundance is thought to have been responsible for large-scale distribution shifts in the GOM (Payne *et al.*, 1990) and increased emigration probabilities (Stevick *et al.*, 2006). In this study, we investigated the influence of prey abundance on annual survival probability. Humpback whales are generalists that feed on a variety of schooling fish species and euphausiids. Four species are known or assumed to be

important in the GOM: sand lance, *Ammodytes* spp. (Overholtz and Nicolas, 1979; Hain *et al.*, 1982; Hays *et al.*, 1985; Payne *et al.*, 1986; Payne *et al.*, 1990; Hain *et al.*, 1995), Atlantic herring, *Clupea harengus* (Hain *et al.*, 1982; Paquet *et al.*, 1997; Weinrich *et al.*, 1997), Atlantic mackerel, *Scomber scombrus* (Mitchell, 1973; Geraci *et al.*, 1989) and euphausiids, *Meganyctiphanes norvegica* (Paquet *et al.*, 1997). Abundance indices for fish species were obtained from the Northeast Fisheries Science Center (Woods Hole, MA) based on data from stratified bottom trawl resource surveys conducted twice annually from the GOM to North Carolina. The sand lance index was based on the mean number of individuals caught per standard tow (1988-2003), whereas biomass estimates were available for herring (1988-2005) and mackerel (1988-2004). We hypothesised that the annual abundance of these fish species, whether singly or in combination, had the potential to affect apparent survival to the next year. In the case of calves, we also examined prey abundance after weaning. We hypothesised that calves would be less affected by prey abundance during the period of maternal care, but strongly affected when they began to forage independently. In the latter case, they might be more likely than older whales to die in spring before they could be re-encountered alive.

No data were available to characterise euphausiid abundance, and the relative importance of each fish species in the GOM humpback whale diet was not known. However, we hypothesised that adult movement patterns were sensitive to preferred prey availability and so used net inter-annual displacement as a more general indicator of the quality of the feeding environment. Net inter-annual displacement was calculated as the shortest distance between sighting positions in two consecutive GOM-wide surveys. When an individual was seen on multiple days in a given year, the position of the earliest sighting was used. The distance between annual sightings was calculated using the “Distance and bearing between matched features extension” for ArcView GIS 3.2 (Jenness 2002) and averaged across individuals within a given year. Large inter-annual displacement distances by adults were hypothesised to reflect more effort spent searching for food in the second year. By contrast, small displacement distances were taken as evidence that little additional searching was required.

Finally, we investigated the demographic impact of an “unusual mortality event” (UME) declared by the U.S. National Oceanic and Atmospheric Administration (NOAA) in 2003. This event took place in the GOM during summer, but because of the remote, offshore distribution of the carcasses and their advanced level of decomposition, none of

the individuals could be identified and their demographic characteristics were unknown. Furthermore, the number of detected carcasses represented an unknown fraction of actual deaths. We attempted to characterise the ages or age classes affected by this event and the magnitude of impact. Because the UME occurred in summer, its effects could have been reflected in annual survival estimates for 2002 and/or 2003.

4.3 Results

4.3.1 Population age structure

GOM-wide surveys produced annual sample sizes ranging from 57 (1991) to 405 (2003) individuals. Fewer than half (41%, $n=1,117$) of sampled individuals were known age, but most of the rest (76% $n=1,479$) were at least five years old when sampled. Several characteristics of unassigned whales supported suspicions that they were young. Although encountered throughout the GOM, unassigned whales had a similar distribution to juvenile animals. Like juveniles, they were found preferentially in southern areas (80.0%, $n=369$) where effort was highest (Figure 4.1). They associated with documented juveniles at more than twice the frequency (64.0%, $n=134$) expected for mature animals (25%, as calculated from Clapham, 1993 - Table 3). Only 4.7% ($n=8$) of females were encountered with a calf while still unassigned. In the few cases that an unassigned animal had been seen as a calf by other researchers, the majority (85.2%, $n=23$) were yearlings or two year olds at the time of our first sighting. The remaining 14.3% ranged from five to eight years old. We used the latter as a rough estimate of the maximum percentage of unassigned whales that were at least five years old.

After correcting for unassigned animals, the annual mature fraction averaged 68.7% ($s= 8.1\%$) across the 17-year period. Estimates ranged from 52.3% (95% CI: 44.7-59.8%) to 83.2% (95% CI: 72.6-91.0%) and inter-annual variation was significant ($G=73.97$, $d.f.=16$, $p<0.001$). The highest estimates were obtained between 1994 and 1996, when sampling was limited to western GOM areas and suspected to have been biased (Figure 4.2). The proportion of calves in the sample did not vary significantly between years ($G=21.44$, $d.f.=16$, $p=0.162$) and so we evaluated inter-annual variation in light of time-varying juvenile survival rates (see Section 4.3.3).

Figure 4.1: Regional encounter rates of unassigned whales compared to mature whales and juveniles. Like juveniles, unassigned whales were more frequently encountered in the south where sampling effort was high (also see Chapter 2).

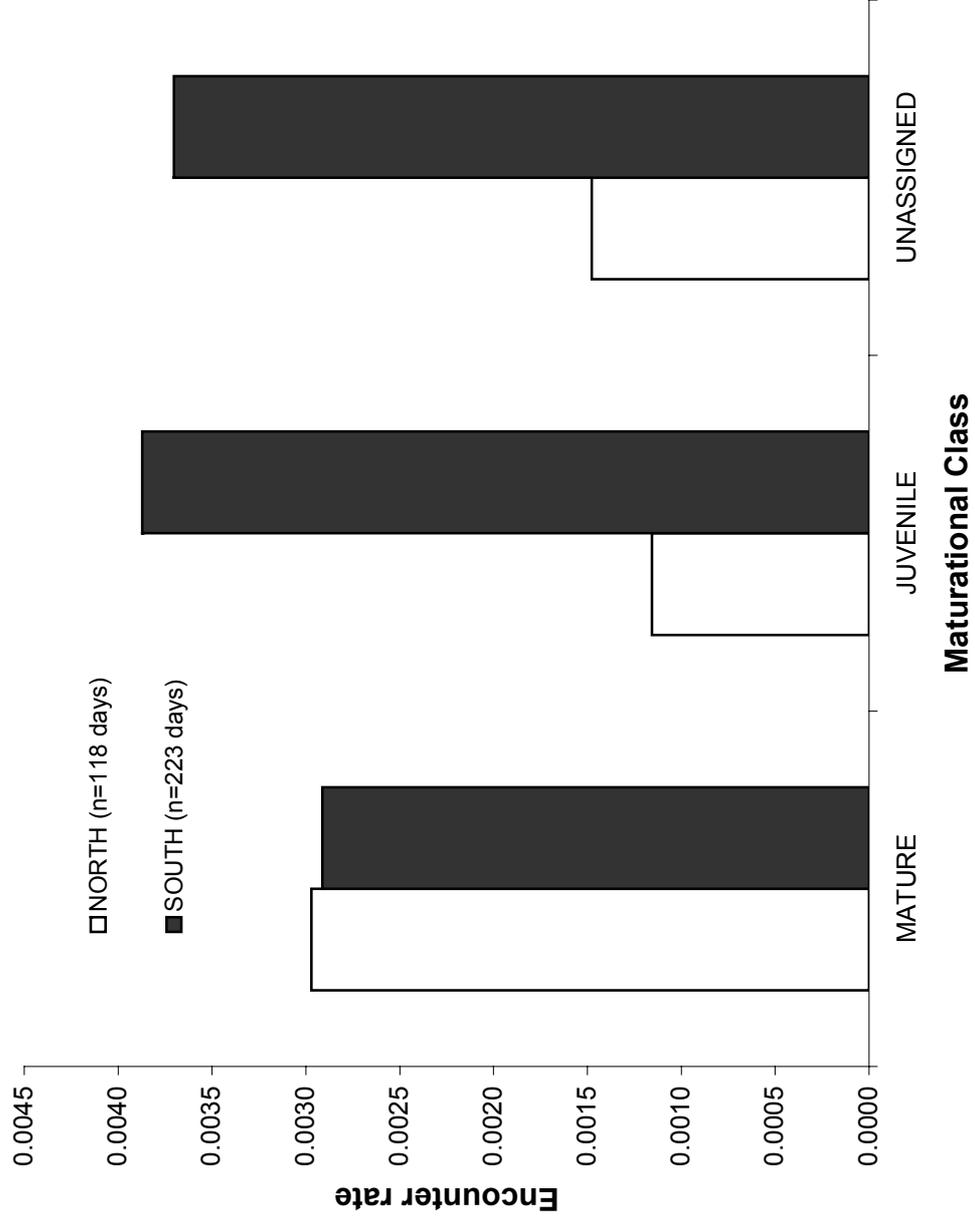
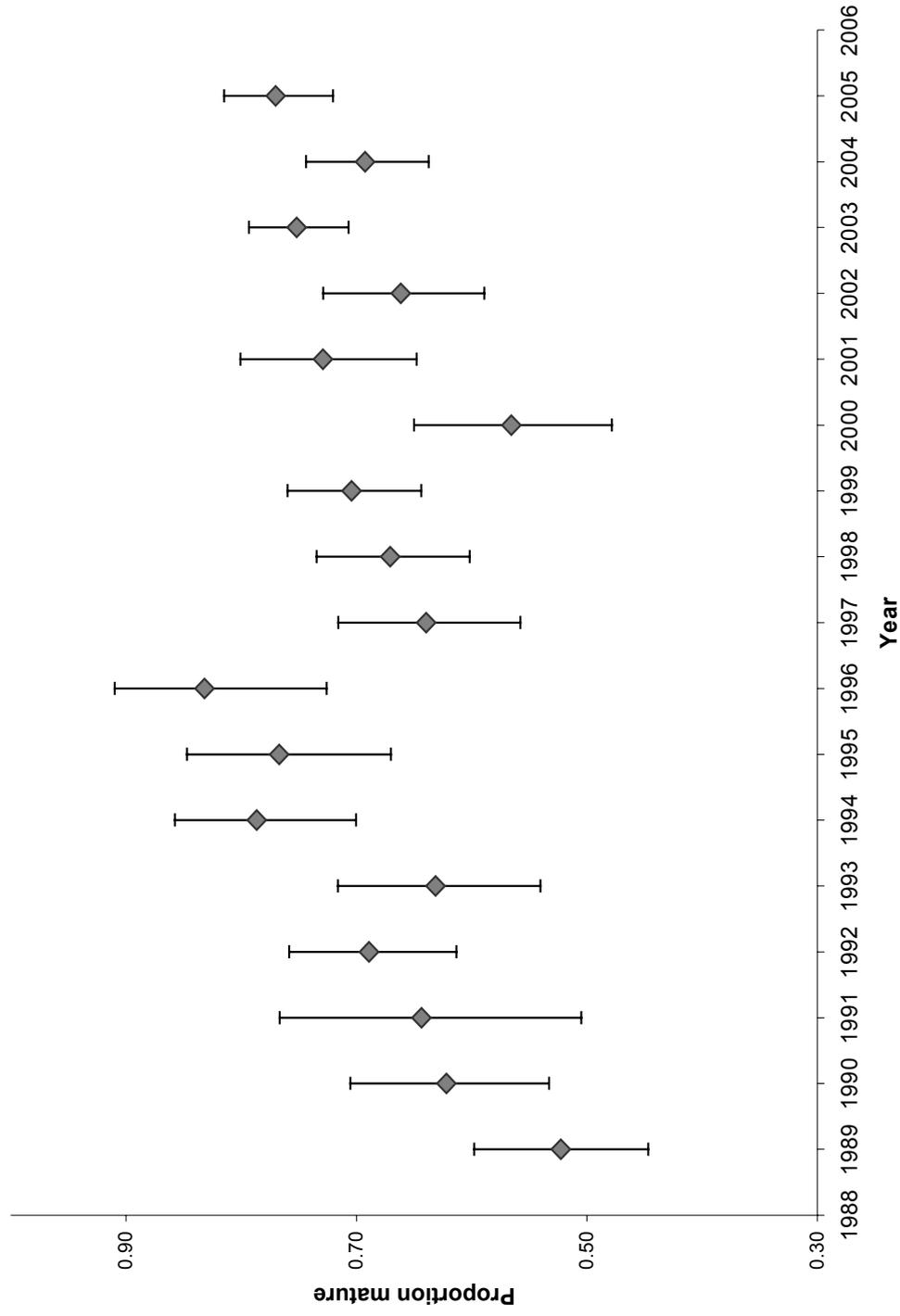


Figure 4.2: Annual estimates of the proportion of humpback whales that were potentially sexually mature (ages 5+), 1989-2005. Estimates were based on GOM-wide survey data, June through September and error bars indicate 95% confidence intervals. High estimates in 1994-1996 corresponded to years in which sampling effort was limited to western GOM areas.



4.3.2 Age-specific survival

Between 2000-2005, there were 711 annual sightings of 261 well-documented individuals ranging in age from <1 year (calves) to 28 years. Fifty-eight additional “old” individuals were at least 25 years old during the same period, and 132 “unassigned” whales were first encountered as independent animals, preventing us from allocating them to a specific age class. Goodness of fit testing indicated that the standard CJS model was not an appropriate starting point for these data (Table 4.1). There was significant heterogeneity in survival (U-CARE Test 3), as well as in directional tests for transience for individuals entering the study prior to age five. Once the model was modified to include an effect of age on survival, the median \hat{c} procedure indicated minor residual over-dispersion (Table 4.1). We proceeded to model selection taking the estimated variance inflation factor into account.

The most parsimonious model for re-sighting probability was a three age class model in which re-sighting probabilities were lower for yearlings and two-year olds than for ages 3+. In the full data set and for males, adult re-sighting rates varied over time. However, the most parsimonious model for females had a constant adult re-sighting rate. “Unassigned” animals exhibited re-sighting probabilities most similar to yearlings.

Survival varied with age in all three data sets, but trend and age class models were more preferred over full age specificity (Table 4.2). No single model had unanimous support from the data, but all indicated lower survival prior to the earliest average age at first reproduction (Figure 4.3). In the full data set, model averaging indicated calf survival at 0.664 (95% CI: 0.517-0.784). “Non-calf” adult survival models were not well supported by the data (Table 4.2) and the “non-calf” point estimate of 0.925 (95% CI: 0.891-0.950), was lower than the best model for known age adults (0.991, 95% CI: 0.919-0.999) after excluding animals aged four years or less. The survival rate of unassigned individuals was most consistent with animals that entered the sample as independent juveniles. Contrary to expectations, “old” whales exhibited high mean survival rates although confidence intervals were wide (Figure 4.3).

Upon running the same suite of models on males and females separately, different age-specific patterns of survival emerged. As shown in Table 4.3, the top models for males suggested that survival was roughly equal among juveniles and then increased to a higher “adult” survival rate at approximately age 5 (Figure 4.4). By contrast, model selection indicated that female survival reached its maximum value closer to age ten and

Table 4.1: Goodness of fit test results from program U-CARE and the median c-hat procedure in program MARK. U-CARE tests the fit of the CJS model to the data and the p-value from the X^2 test is shown along with the deviance c-hat (X^2/df). Test components indicating significant heterogeneity are in bold. The median c-hat procedure was performed on a modified global model incorporating age structure (for Test 3 failures) and multiple states (for Test 2 failures).

Analysis	U-CARE test results					Estimated	
	Test3.SR	Test3.SM	Test2.Ct	Test2.CI	Deviance c-hat (X^2/df)	Median c-hat	Median c-hat
Age (2000-2005)	<0.001	<0.001	0.145	0.849	6.88	1.044	1.044
Males only	<0.001	<0.001	0.322	0.828	3.00	1.027	1.027
Females only	<0.001	0.310	0.774	1.000	3.00	1.019	1.019
Time (1988-2005)	<0.001	<0.001	<0.001	0.077	3.75	1.194	1.194

Table 4.2: Model selection for apparent survival probability (full data set). Ages were discrete when separated by a comma or an ellipsis (for a sequence of ages). They were pooled when separated by a dash. Exact ages ranged from calves (C) through age 25. Linear (A) and quadratic (A²) trend models were applied to ages specified in parentheses. Linear trend models provided the best fit to early ages, although a trend across all ages was also supported. Models with constant survival above the age of sexual maturity were preferred.

Model type	Model	Δ QAICc	QAICc Weights	# Parameters
Trend	A(C..25)	0.000	0.266	13
	A(C..8), 9-25	0.497	0.207	14
	A(C..4), 5-25	1.448	0.129	14
	A ² (C..25)	2.061	0.095	14
	A(C..8), A(9..25)	2.165	0.090	15
	A(C..4), A(5..25)	3.069	0.057	15
Age class	C, 1-4, 5-25	3.095	0.057	14
	C, 1-8, 9-25	11.302	0.001	14
	C-4, 5-25	2.601	0.072	13
	C-8, 9-25	14.322	0.000	13
Age-specific (juvenile)	C..4,5-25	6.972	0.008	17
	C..3,4-25	9.716	0.002	16
	C..2,3-25	18.606	0.000	15
	C,1,2-25	33.897	0.000	14
Non-calf	C,1-25	39.547	0.000	13
Unconstrained	C..25	43.628	0.000	39

Table 4.3: Top models for apparent survival probability stratified by sex. Models shown are the subset of those run (see Table 4.2) with $\Delta\text{QAICc} \sim 2$. The top model for females indicated an increasing linear trend (A) in survival from the calf year (C) through age 8 and a subsequent linear decline. Top models for males indicated two age classes for survival and constant survival by age five. Models that pooled “old” whales (ages 25+) with known age adults were better supported for males than for females.

Sex	Top models	ΔQAICc	QAICc Weights	# Parameters
Female	A(C..8), A(9..25)	0.000	0.762	10
	A(C..8), 9..25+	2.227	0.200	8
Male	C-4, 5-25+	0.000	0.381	12
	C-4, 5-25	0.982	0.233	13
	A(C..4), 5-25	2.711	0.098	14

Figure 4.3: Estimated age-specific survival probabilities. The solid line reflects model averaged age-specific survival estimates and the dashed lines bound the 95% confidence interval of those estimates. Diamonds are unconstrained estimates from the fully age specific model. The solid triangle is the model averaged estimate of survival in “old” whales (ages 25+) with 95% confidence intervals shown.

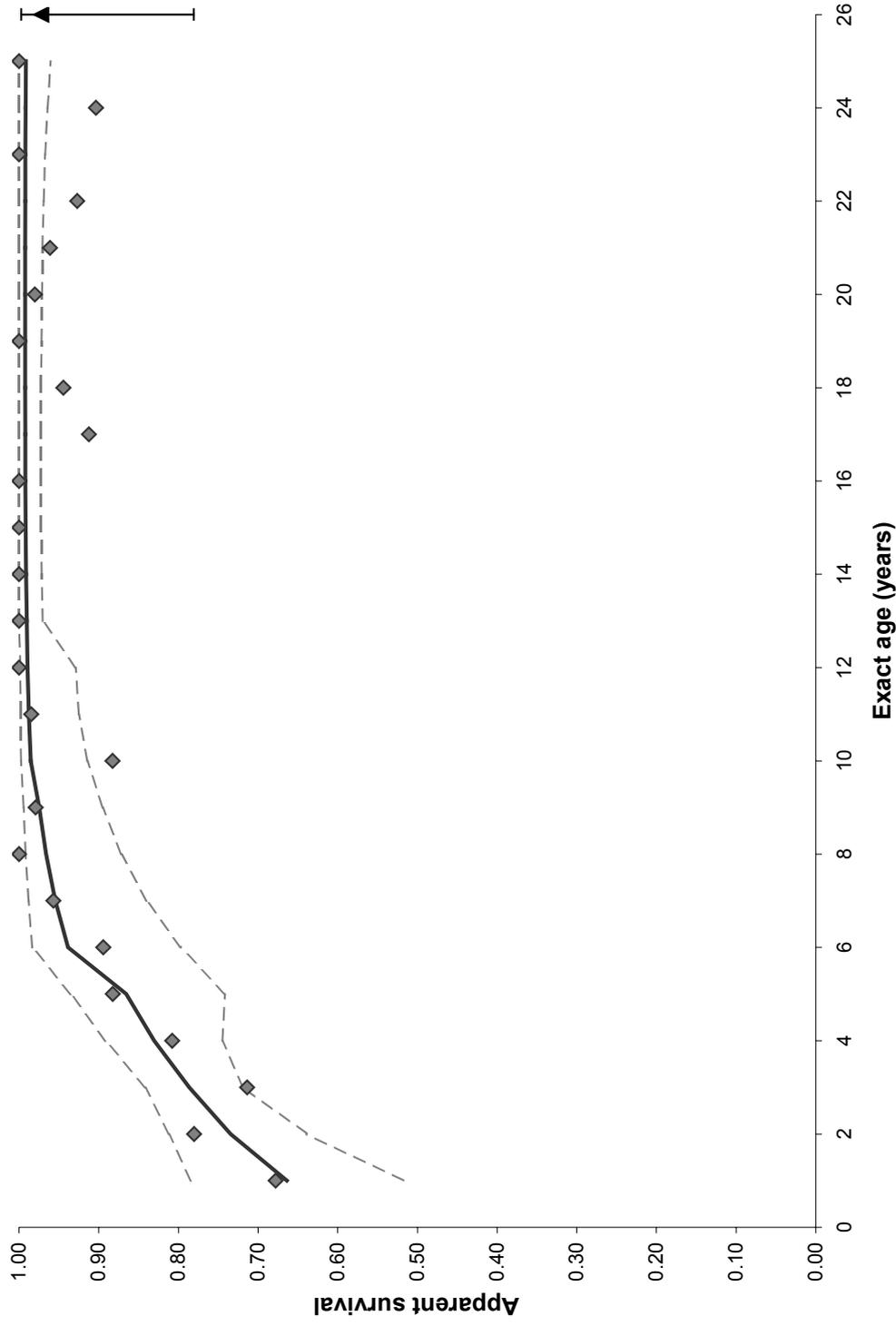
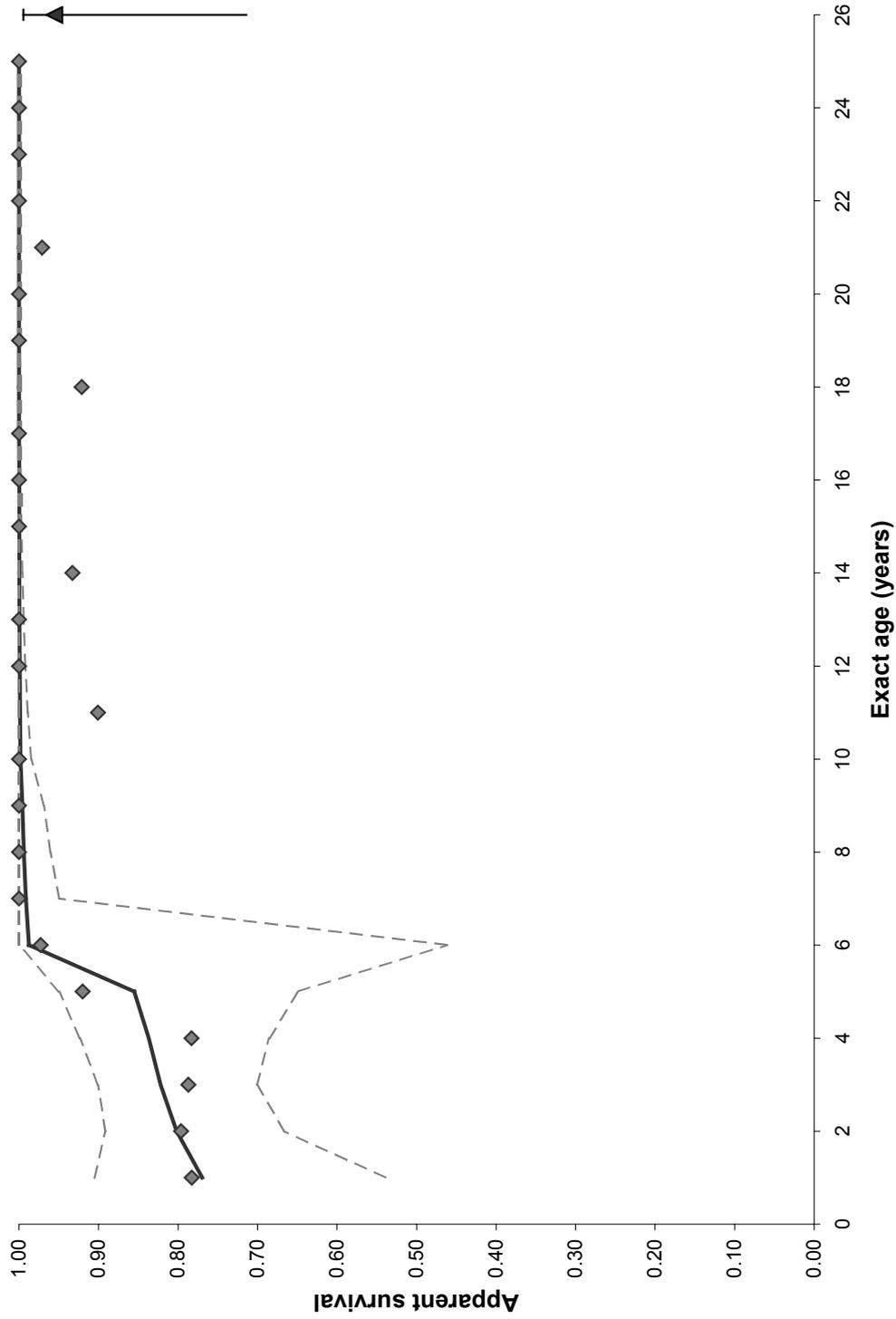


Figure 4.4: Estimated age-specific survival probabilities for males. The solid line reflects model averaged survival estimates and the dashed lines bound the 95% confidence interval of those estimates. Diamonds are unconstrained estimates from the fully age specific model. The triangle represents the model averaged estimate for “old” males (ages 25+) with 95% confidence interval shown.



then declined slightly with exact known age (Table 4.3, Figure 4.5). Similar estimates were obtained for “old” males (0.977, CI: 0.577-0.999, Figure 4.4) and “old” females (0.975, CI: 0.611-0.999, Figure 4.5). Pooling known age and “old” adult females was not as well supported by model selection (Table 4.3), but yielded a total adult female estimate of 0.975 (95% CI: 0.908-0.997). The point estimate of “non-calf” survival was higher for males (0.954, 95% CI: 0.900-0.979) than for females (0.911, 95% CI: 0.867-0.941), although confidence intervals were overlapping.

4.3.3 Time variation and explanatory factors

Annual variation in survival was estimated for 366 calves born from 1988 through 2004. The CJS model fitted these data poorly (Table 4.1). We accounted for heterogeneity by incorporating age structure for survival and by generalising the CJS model to multiple states for re-sighting probability. With this starting model, the median \hat{c} technique indicated an acceptable level of residual over-dispersion (Table 4.1). We incorporated the specified value of \hat{c} and proceeded with model selection.

As in the previous analysis on the full data set, the most parsimonious model for re-sighting probability included three age classes with constant re-sighting probability for yearlings and two-year olds, and time varying re-sighting probabilities for ages 3+. In light of age-specific survival results, we focused temporal analysis on four age groups: calves, independent juveniles (ages 1-4), young, possibly mature animals (5-8 years) and adults (9+ years). Of these, only calves exhibited annually varying survival (Table 4.4). A model in which calves and independent juveniles exhibited the same time-varying survival rates (per Rosenbaum *et al.* 2002) was not well-supported (Table 4.4). Potential explanations for annual variation in calf survival were explored as described below. Both independent juveniles and young adults exhibited lower survival proximal to the “unusual mortality event” (UME), but only for 2003. Support for a survival effect was equivocal for juveniles, but the survival of young adults was lower in 2003 (0.888, 95% CI: 0.543-0.981) than in any other year. Adult survival was estimated to be constant and averaged 0.978 (95% CI: 0.901-0.995) across the study period.

Annual calf survival estimates ranged from 0.200 (95% CI: 0.021-0.742) to 0.933 (95% CI: 0.018-0.999, Figure 4.6). However, mean calf survival was estimated at 0.756 with a standard error from process variance of 0.039. Approximately 27.5% of the total standard error was due to sampling variance. Sand lance and/or mackerel abundance in

Figure 4.5: Estimated age-specific survival probabilities for females. The solid line reflects model averaged survival estimates and the dashed lines bound the 95% confidence interval of those estimates. Diamonds are unconstrained estimates from the fully age specific model. The triangle represents the model averaged estimate for “old” females (ages 25+) with 95% confidence interval shown.

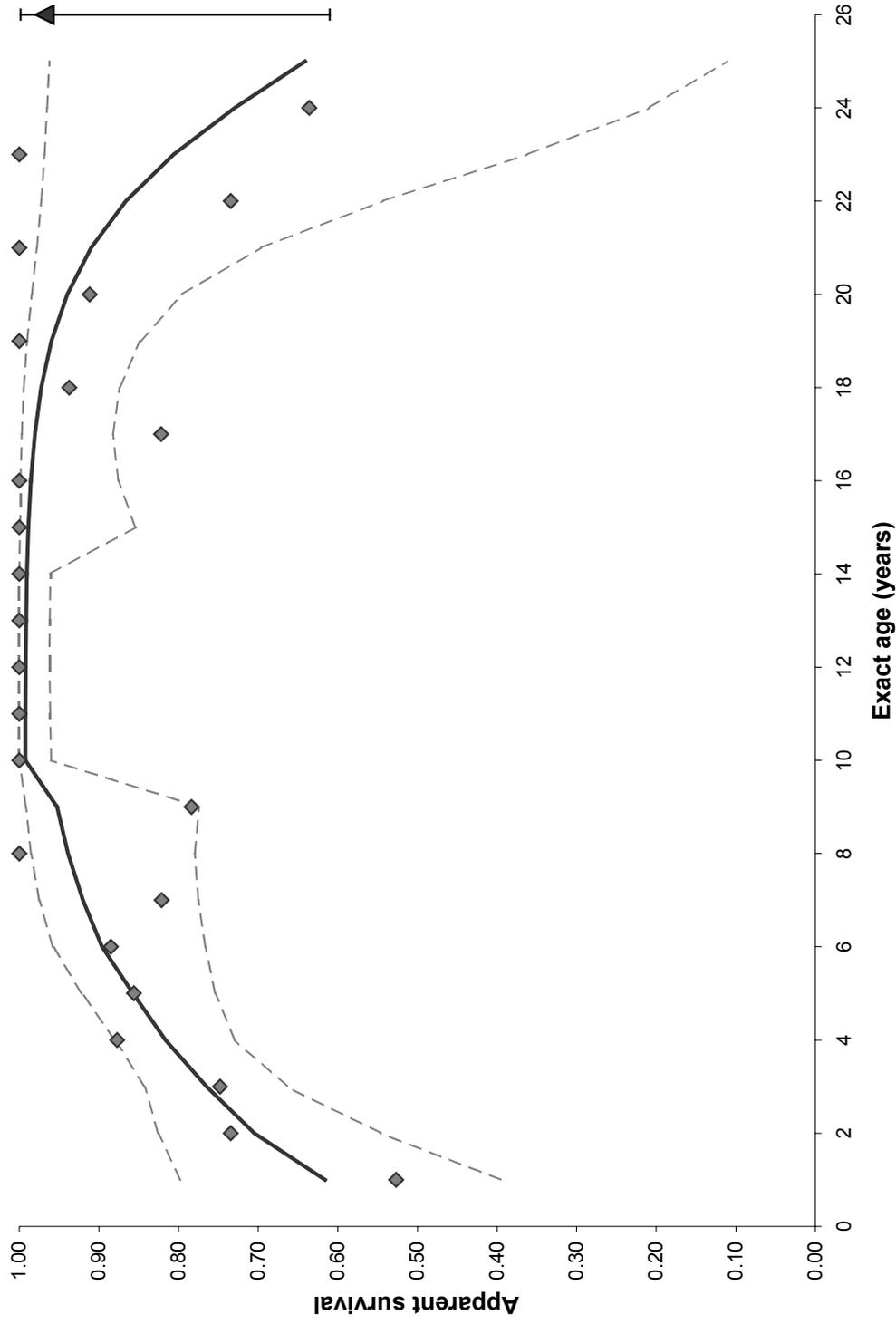
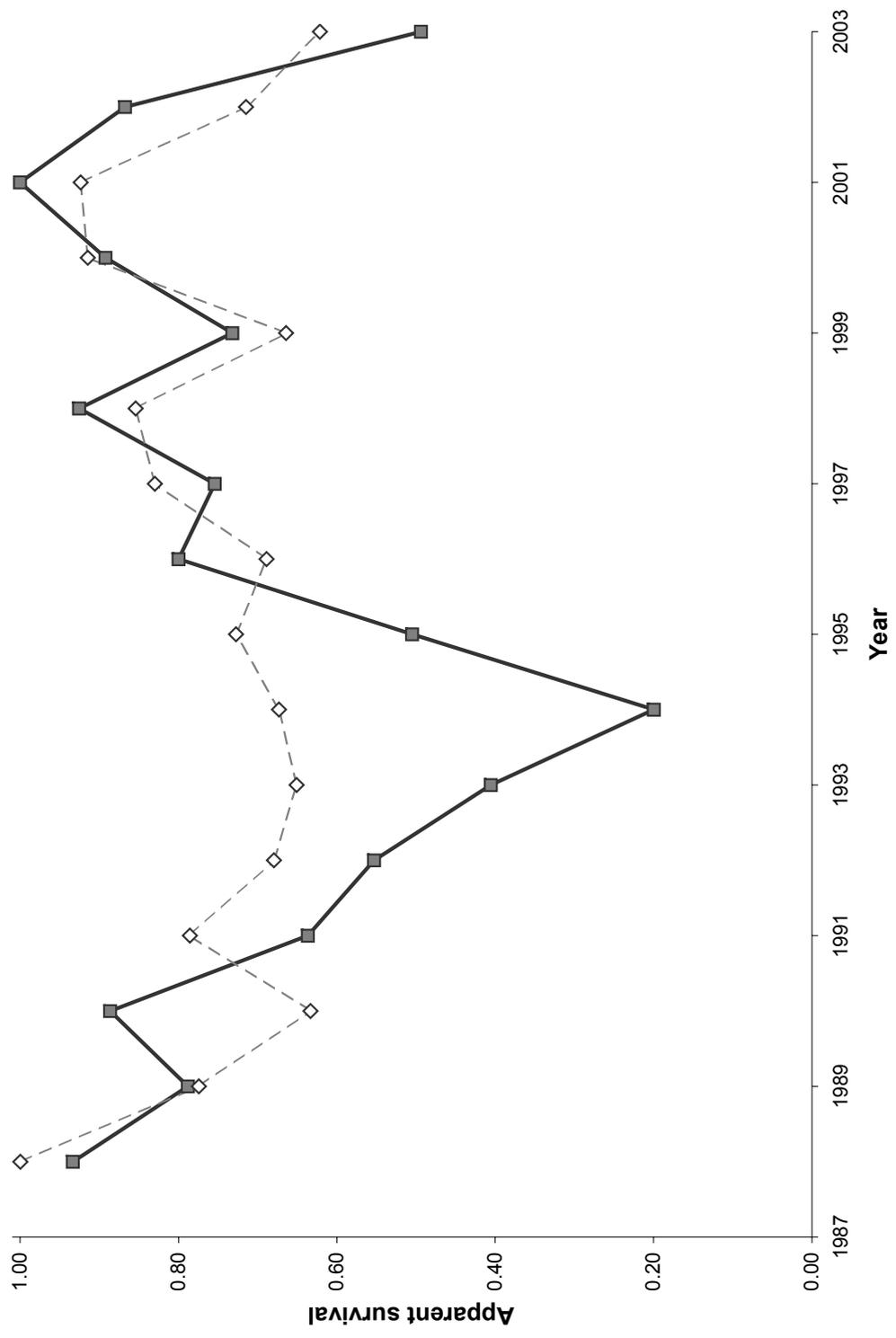


Table 4.4: Model selection for annual variation in apparent survival probability, by age category. Re-sighting probability for all models was a three age class model with constant re-sighting probabilities in the first two years and time-varying thereafter. Models examined annual variation (t), linear trend over time (T), the effects of a unusual mortality events in one (UME₁) or two years (UME₂) and constant survival (.). We also examined support for equal time-varying survival among calves and independent juveniles per Rosenbaum *et al.* (2002). Top models with equal support from the data are shaded. Annual variation was only supported for calves. Whereas UME effects were equivocal for juveniles, young adults exhibited lower survival in 2003 than in other years. Adults exhibited constant survival.

Calf (<1)	Model structure, by age category			Δ QAICc	QAICc Weights	# Parameters
	Juvenile (1-4)	Young adult (5-8)	Prime adult (9+)			
t	.	UME ₁	.	0.000	0.412	54
t	UME ₁	UME ₁	.	1.816	0.166	55
.	.	UME ₁	.	2.165	0.139	38
UME ₁	UME ₁	UME ₁	.	3.845	0.060	40
t	UME ₂	UME ₁	.	4.039	0.055	56
.	UME ₁	UME ₁	.	4.047	0.054	39
T	.	UME ₁	.	4.325	0.047	39
UME ₂	UME ₁	UME ₁	.	5.254	0.030	41
UME ₁	UME ₁	UME ₁	UME ₁	6.002	0.020	41
T ²	.	UME ₁	.	6.493	0.016	40
		UME ₁	.	7.728	0.009	53
- t -				20.844	0.000	68
t	t	UME ₁	.	21.405	0.000	69
t	t	UME ₂	.	23.664	0.000	70
t	t	t	.	42.512	0.000	79
t	t	t	UME ₁	44.859	0.000	80
t	t	t	UME ₂	46.160	0.000	81
t	t	t	t	53.331	0.000	86

Figure 4.6: Apparent survival of humpback whale calves, 1988-2004. The solid line reflects unconstrained parameter estimates and the dashed line represents the estimates from a model in which calf survival was fit to sand lance abundance in the season following weaning.



the season following weaning were the factors that best explained annual variation (Table 4.5). Support for a sand lance effect was 1.62 times greater than for mackerel. By contrast, the abundance of these prey species in the calf year were not good predictors of survival. Neither Atlantic herring abundance, nor adult net displacement adequately explained patterns of calf survival.

Age structure estimates provided a marginal fit to survival data when estimates from all years were included ($\Delta\text{QAICc}=2.793$), but not otherwise (Table 4.5). High estimates of the mature fraction between 1994-1996 were consistent with particularly low calf survival rates from 1993-1995 (Figure 4.6).

4.4 Discussion

4.4.1 Population age structure

Age structure has not previously been estimated for a free-ranging humpback whale population. Size structure estimates are more common in studies of large whales as data can be obtained by aerial photogrammetry (Withrow and Angliss, 1992; Zeh *et al.*, 1993; Cosens and Blouw, 2003) or underwater videogrammetry (Spitz, 1999), often in conjunction with other research. Those techniques would not have been feasible for this study because humpback whales can not be individually identified from the air and underwater visibility in the GOM does not permit underwater observations. However, a combination of longitudinal monitoring (for age data) and GOM-wide sampling (for annual composition) produced estimates that appeared to be consistent with other demographic data. In some species, age or stage structure data are more easily obtained and so may improve inference from vital rates or abundance estimates (Coulson *et al.*, 2001; Holmes and York, 2003; Manly *et al.*, 2003). In our case the opposite was true; survival estimates provided independent support for our inference that “unassigned” animals were largely juveniles and helped to discriminate between potential bias and true inter-annual variation in age structure estimates.

Age structure data are not particularly informative about population dynamics in isolation because several different processes can combine to produce the same effect. However, this information can be quite valuable to other areas of research. As discussed by Cerchio *et al.* (2005), data on population age structure would have helped to clarify the

Table 4.5: Factors examined to explain annual variation in calf survival. Top models with equal support from the data are highlighted. The best fit was provided by abundance of sand lance and/or Atlantic mackerel in the season following weaning. Atlantic herring abundance and adult displacement patterns did not reliably predict calf survival. Independent age structure estimates were marginally consistent with trends in calf survival.

Factor	Δ QAICc	QAICc Weights	# Parameters
Prey abundance (after weaning)			
Sand lance	0.000	0.277	41
Mackerel	0.961	0.171	41
Sand lance + mackerel	1.476	0.132	42
Sand lance + herring	2.154	0.094	42
Mackerel + herring	2.436	0.082	42
Sand lance + mackerel + herring	3.472	0.049	43
Herring	7.957	0.005	41
Prey abundance (calf year)			
Mackerel	3.705	0.043	41
Sand lance	4.267	0.033	41
Herring	7.126	0.008	41
Sand lance + mackerel + herring	7.193	0.008	43
Population age structure			
All annual estimates	2.793	0.069	41
Excluding 1994-1996	6.500	0.011	41
Net inter-annual displacement (adults)	4.899	0.024	41
Linear trend over time			
Unconstrained annual variation	7.363	0.007	41
	13.409	0.000	54

low apparent skew in paternity that they observed among North Pacific humpback whales. In Chapter 3, GOM age structure data were used to clarify the demographic pattern of migration to the West Indies breeding ground.

4.4.2 Adult survival

Adult female survival is an important benchmark for population monitoring in light of its typically strong contribution to population growth rate. In mammals, adult females are expected to maintain high, near-constant rates of annual survival and even small declines may be of management concern. Thanks to advances in mark-recapture statistical techniques, survival estimates can be obtained for species that are cryptic and/or spatially heterogeneous. However, in the case of large whales, the inability to allocate individuals to meaningful age classes may confound interpretation when estimates change or differ between populations. In this study, “non-calf” survival estimates were approximately 6% lower than adult survival, despite the fact that adults comprised 68.7% of the population on average. Maximum adult survival was achieved by excluding individuals known to be less than four years old.

Exact age is rarely known in other populations, but a comparable approach would be to stratify estimates among individuals based on the length of their *prior* sighting histories. For example, Mizroch *et al.* (2004) produced estimates of survival for North Pacific humpback whales from a database in which more than 1,400 individuals were observed in five or more years, including 456 seen in more than 10 years. Survival estimates generated from those data ranged from 0.937 (95% CI: 0.921-0.950) to 0.984 (95% CI: 0.954-0.995), depending on the data and method used. If adult survival is the vital rate of interest, then limiting estimates to individuals seen at least four years prior has the potential to improve inference, provided that adequate sample sizes can be maintained. At a minimum, sensitivity testing could be performed to determine the effectiveness of this approach for a given data set.

In mammals, survival is expected to be lowest among juveniles, high during an extended “prime” period followed by senescent decline (Caughley, 1966). Whereas we confirmed an extended period of lower juvenile survival, we did not find evidence of actuarial senescence, at least through age 25. Theoretical expectations of senescent decline in late life are difficult to test in long-lived organisms, especially those that can only be aged as young (Promislow, 1991; Gaillard *et al.*, 1994). Sample sizes diminish as

individuals die at each age and temporal variation can confound comparison of different cohorts (McDonald *et al.*, 1996). Long-term studies using appropriate statistical techniques have confirmed actuarial senescence in a variety of long-lived species, including one of three seal species examined (Beauplet *et al.*, 2006). The age at which senescence might begin is also a topic of debate, but has been hypothesised to be birth, sexual maturity or even twice that age (Promislow, 1991). Even if it were the latter, then effects could have been detected among the ages studied here. Model selection supported declining survival in adulthood for females of known age, but the same was not true for males and the average survival of “old” animals of both sexes was high, albeit with wide confidence intervals. We therefore suspected that other factors were responsible for reduced survival among females (see Section 4.3.3 and Chapter 5).

Although prime adult survival is thought to be buffered against typical environmental variation (Gaillard and Yoccoz, 2003), unusual events can have significant effects (Gaillard *et al.*, 2000). GOM humpback whales are vulnerable to periodic “unusual mortality events” (UMEs), the first of which was occurred from November 1987 through early January 1988. Sixteen carcasses were recovered close to shore and in good condition, and so were known to consist of both sexes and a wide range of ages. A second event occurred in summer 2003 in a remote offshore location near the eastern edge of the GOM. Carcasses were not found proximal to death and so individual identity, demographic characteristics, numbers affected and cause of death were not known. Because of their location at the extreme edge of the region, it was also not certain that the carcasses were part of the catalogued population. However, adults dominate in offshore areas and so there was a potential for preferential impact to that component of the population.

If the GOM population was exposed to the 2003 UME, then the results of this study suggest that those reaching sexual maturity (ages 5-8) were preferentially affected. If so, the deaths may not have occurred in the offshore waters where the carcasses were detected, as animals in this age category are less commonly encountered there. In 2003, animals aged 5-8 were primarily encountered in inshore waters, and especially at the Great South Channel (Figure 2.1). The cause of this event remains unknown, but a third humpback whale UME was recently designated by NOAA for summer 2006. If the two are related, then this new information may help to focus research efforts.

4.4.3 Juvenile survival

Juveniles differ from sexually mature animals in physical size (Chittleborough, 1965; Stevick, 1999), association patterns (Clapham, 1993), distribution (Chapter 2), habitat use (Weinrich *et al.*, 1997) and migratory behaviour (Chapter 3). Thus, it is reasonable to assume that they do not reach adult survival immediately upon weaning. However, few robust estimates of juvenile survival are available for this or other large whale populations. Barlow and Clapham (1997) approximated GOM calf survival at 0.875 (S.E.~0.047) for the period 1979-1991 based on a combination of return rates (0.828, 1979-1991) and the square of the adult female survival rate (maximum survival, 0.922), following Barlow and Boveng (1991). More recently, Rosenbaum *et al.* (2002) estimated mean juvenile survival by maximum likelihood techniques (0.7022, 1979-1995), but pooled calves with independent juveniles. In our study, a comparable model had less support than those in which survival increased to the earliest age at sexual maturity.

Estimates of first year calf survival were substantially lower than those approximated by Barlow and Clapham (1997) and more similar to the “juvenile” survival rate of Rosenbaum *et al.* (2002). They were also similar to recent findings for western gray whale calves (0.701, 95% CI: 0.492-0.850, Bradford *et al.*, 2006). This was of interest because western gray whales are at low levels of abundance and calf survival is an issue of management concern. We specifically addressed potential sources of downward bias in calf survival estimates by limiting estimates to calves with high quality documentation to ensure reliable re-identification. Whereas nearly all prior demographic studies on this population were limited to south-west GOM areas (e.g. Clapham and Mayo, 1987; Clapham and Mayo, 1990; Barlow and Clapham, 1997; Rosenbaum *et al.*, 2002), our survey methods also allowed individuals to be detected if they lived but moved to other GOM areas after weaning. We also modified model structure to account for age-specific heterogeneity in re-sighting probabilities. Based on these facts, we do not believe that our results substantially underestimate GOM calf survival from six months onward. Nevertheless, they do under-estimate calf survival from birth because an unknown number of calves die before they can be documented in the GOM. In the North Pacific, mortality prior to weaning was estimated at 0.182 (95% CI 0.023-0.518) based on a small sample of mothers identified on their breeding and feeding grounds in the same year (Gabriele *et al.*,

2001). However, even that estimate does not account for deaths that occurred on the calving ground before a calf was detected.

Of the factors examined, sand lance and/or Atlantic mackerel abundance provided the best explanation for the observed patterns of annual variation in calf survival. In the GOM, sand lance are primarily distributed in southern areas where calves and yearlings are also preferentially encountered (see Chapter 2). By contrast, the primary piscine prey species in the northern GOM is thought to be Atlantic herring. The better fit of sand lance versus herring abundance to calf survival is therefore consistent with the demographic stratification described in Chapter 2. A previous study concluded that Atlantic mackerel was not likely to be an important prey species for GOM humpback whales because other prey species were better predictors of emigration probabilities (Stevick *et al.*, 2006). However, those results may not apply equally to juvenile animals in light of their smaller range of movement (Chapter 2). Unfortunately, trends in sand lance and mackerel abundance were quite similar over the course of this study. Thus, the importance of Atlantic mackerel as a prey source for humpback whale calves after weaning is unclear. The potential for an interaction between adult fecundity and first year calf survival is investigated in Chapter 5.

4.4.4 Sex-specific survival

This is the first study to investigate sex-specific differences in the survival of free-ranging humpback whales. Male survival increased at approximately the average minimum age at sexual maturity and then remained high and constant with age. By contrast, female survival increased more slowly with age and declined slightly among known age adults (but not old whales). Sex-specific survival effects were previously considered unlikely in light of even sex ratios *in utero* (Chittleborough, 1965), among neonates (Palsbøll *et al.*, 1997; Smith *et al.*, 1999) and among calves after their first northbound migration (Clapham *et al.*, 1995). Biopsy-based sampling in the GOM also indicated an equal sex ratio among independent juveniles (1-4 years) and a pooled sample of adults (ages 5+, Clapham *et al.*, 1995). Nevertheless, the sexes have different habitat use patterns in the GOM suggesting reliance on different prey resources (Chapter 2). Females are also larger than males of the same age and invest differently in reproduction. It is conceivable that these factors could result in different schedules of age-specific mortality.

Both males and females are thought to reach sexual maturity at an average age of five (Chittleborough, 1965). The humpback whale mating system is polygynous (Cerchio *et al.*, 2005) and males compete physically for access to females (Tyack and Whitehead, 1981; Baker and Herman, 1984). Males as young as five years old have been observed in competitive groups (Clapham *et al.*, 1992), although it is unknown when they begin to successfully reproduce. Agonism between males on the breeding ground is thought to cause mainly minor physical injuries, despite the fact that one death has been observed (Tyack and Whitehead, 1981; Baker and Herman, 1984; Pack *et al.*, 1998). Age-specific survival estimates in this study also provide little indication that reproduction becomes costly to males at any particular age. By contrast, the average female humpback is slightly larger than a male of the same age (Chittleborough, 1955) and provides all parental care to her offspring. She is capable of producing her first viable calf by age five (Chittleborough, 1965; Clapham, 1992), but physical growth does not end until approximately 8-10 years after sexual maturity (Chittleborough, 1965). Reproduction poses a potential hazard to mothers if resources must be diverted from somatic growth and maintenance toward foetal growth and development (Stearns, 1992). This may be particularly true for primiparous females, and in years of environmental adversity. Over the course of this study, the age at first birth doubled in the GOM (Chapter 5). If this change was associated with an increased cost of breeding, then the patterns we observed might reflect mortality among females that did not delay reproduction. Evidence for costs of female reproduction are examined in Chapter 5.

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Chapter 5:

Patterns, determinants and costs of reproduction among Gulf of Maine humpback whales

5.1 Introduction

Humpback whales, *Megaptera novaeangliae*, are long-lived, iteroparous breeders that depend entirely on maternal reserves to support themselves and a single offspring during its first few months after birth. Lactation is costly while fasting on the breeding ground (Oftedal, 1993) and may still account for as much as 41% of caloric intake when feeding resumes in the spring (Lockyer, 1986). Gestation lasts approximately one year (Chittleborough, 1958) and the patchy and variable nature of feeding resources may have unexpected impacts on maternal condition by the time of parturition. If resources are insufficient for lactation, then there may be a cost in the form of reduced fitness or survival for mother and/or offspring (Williams, 1957). Reproduction may be more risky for young mothers due to their smaller body size, relative foraging inexperience and because energy could be diverted from their own physical growth and development (Eberhardt and Siniff, 1977). At the other extreme, old females are expected to increase their maternal investment as their residual reproductive value declines (Williams, 1966). They may therefore be less likely to survive if more inclined to reproduce when conditions are not favourable (Festa-Bianchet *et al.*, 1998).

Predictors and costs of reproduction are poorly understood in large whales, primarily because of the difficulty of obtaining adequate data. The Gulf of Maine (GOM) humpback whale population has previously been an important source of information on humpback whale reproduction. In the 1980s, the average GOM female gave birth to her first calf at an age of six years (Clapham, 1992) and produced a single offspring every 2 to 3 years thereafter (Clapham and Mayo, 1987b; Clapham and Mayo, 1990; Barlow and Clapham, 1997). Annual reproduction is rare in the GOM and elsewhere (Chittleborough, 1958, 1965; Clapham and Mayo, 1987b; Clapham and Mayo, 1990; Glockner-Ferrari and Ferrari, 1990; Barlow and Clapham, 1997). However, most previous GOM studies were conducted within a small geographic area and over a single decade of observation. It has not yet been determined whether those findings are spatially or temporally representative of the overall population.

Average age at first birth is expected to vary over time and between large mammal populations (Stearns, 1992). Although its plasticity makes it informative for population dynamics monitoring, this parameter is difficult to estimate in free-ranging whales because females must be observed annually from birth until their first viable calf is produced. As individuals drop out of the study due to missed years and death, the small remaining sample may be biased toward precocious females and those whose sex is known only because they reproduced. To date, estimates for humpback whales have been based on sample sizes of only 10-12 females born over one or two decades (Clapham, 1992; Gabriele *et al.*, 2007).

Adult humpback whale fecundity does not require continuous observation, but is commonly estimated by naïve techniques, such as the interval between births, the number of calves per mature female, or the number of calves per total individual encountered (Baker *et al.*, 1987; Clapham and Mayo, 1987a, b; Clapham and Mayo, 1990; Glockner-Ferrari and Ferrari, 1990; Clapham, 1992; Rosenbaum *et al.*, 2002). These approaches do not account for differences in detection probabilities or survival among females. Maximum likelihood techniques have been used to model inter-birth intervals in GOM humpback whales for the purpose of estimating population growth rate (Barlow and Clapham, 1997; Clapham *et al.*, 2003). However, it has yet to be determined whether reproduction varies significantly over time or age in this species, and what factors might be responsible.

Multi-state models offer a robust alternative for studies of reproduction (Nichols *et al.*, 1994), but have not yet been applied to cetacean species. In this study, multi-state modelling techniques were used to study humpback whale recruitment and adult breeding probabilities over a 27-year period in the GOM.

5.2 Methods

5.2.1 Data collection

Individual humpback whales were identified from their natural markings, especially the ventral pigmentation of the flukes and the shape and size of the dorsal fin (Katona and Whitehead, 1981). In the GOM, photographs of identifying features were obtained by research vessels engaged in photo-identification (photo-ID) surveys and by naturalists aboard commercial whale watching vessels. Photo-ID surveys targeted known humpback whale aggregation sites in the south-west GOM from 1982 through 1988, and throughout

the geographic GOM from 1989 through 2005 (Figure 2.1). The latter “GOM-wide” surveys targeted known humpback whale aggregation sites and sampling effort was expended proportional to observed whale density. The only exceptions were from 1994 through 1996, when surveys were limited to western GOM areas. Data were also collected from whale watching vessels operating on a near-daily basis in the south-west GOM from mid-April through October, 1979-2005. Humpback whales were the primary species of interest and an effort was made to photo-ID every individual encountered.

Demographic data for sighted individuals were obtained from the PCCS Gulf of Maine Humpback Whale Catalogue (Massachusetts, USA). Exact age was known only for whales that were dependent calves at first encounter. Calves were classified in the field based on their physical size, stereotypical behaviours and close, consistent association with a mature female. They were assumed to range from 3 to 9 months old when first observed and typically remained dependent until at least October of their first year (Clapham and Mayo, 1987b; Baraff and Weinrich, 1993). Individuals that were independent when first catalogued prior to October were at least one year old at first sighting, but could have been older. Calves provided information about the reproductive state of the mother, but were not otherwise included in analyses. “Juveniles” were defined as individuals that were first seen as calves and known to be 1-4 years old. Females were “sub-adults” when at least five years old, but without a documented calving history. They were “adults” after first reproduction and “mothers” when a calf was in tow. Females seen without a calf had either not been pregnant or had lost the calf prior to observation. Females were sexed based on the external morphology of the genital slit (Glockner, 1983) or molecular genetic analysis of a skin sample obtained by biopsy sampling techniques (Palsbøll *et al.*, 1991; Palsbøll *et al.*, 1992; Bérubé and Palsbøll, 1996a, b).

5.2.2 Apparent age at first birth

Apparent age at first birth (AFB) was defined as the age at which a female was observed with her first calf. For females observed continuously, it was also likely to have been the first calf produced. In this study, a sighting history was considered continuous if a female was seen every year from the earliest documented age at first parturition (age 5, Clapham 1992). Females that were only missed the year prior to the first confirmed calf were also included in analysis, as annual reproduction was considered unlikely. When one or two other years were missed, the minimum AFB was the earliest age after four that a calf may

have been missed. The maximum AFB assumed that the first documented calf was the first one produced. Females missed in more than two years were excluded from analysis. We also estimated a minimum AFB for females that were observed continuously but had not yet reproduced. The estimate assumed that these gave birth at the next opportunity, although this was not necessarily the case. Mean AFB estimates were reported with their standard deviations (s) and the statistical significance of difference between means was determined using the Mann-Whitney U test where $\alpha=0.05$ (Sokal and Rohlf, 1981). Humpback whales have an 11-12 month gestation period (Chittleborough, 1965) and so the maximum age at sexual maturity was approximately one year prior to AFB.

5.2.3 Statistical modelling

Free-ranging females must survive and be re-sighted before their reproductive state in a given year can be known. If reproduction impacts survival, or if some females are more likely to be encountered in one reproductive state than another, then estimates of fecundity may be biased. Multi-state mark-recapture models estimate transitions between finite, exclusive states after accounting for apparent survival and detection probabilities (Arnason, 1972, 1973; Hestbeck *et al.*, 1991; Brownie *et al.*, 1993; Schwarz *et al.*, 1993; Lebreton and Pradel, 2002). The technique is a generalisation of the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) and can be implemented in modern statistical software, such as program MARK. Program MARK also facilitates study of explanatory factors by allowing covariate data to be modelled infra-structurally in a linear modelling framework. This approach is therefore highly appropriate for studying patterns and costs of reproduction in species with incomplete individual detection, survival and breeding probabilities.

Individuals were considered “marked” in the first year that they were documented within a period of interest. An encounter history was constructed for each indicating its annual sighting status and reproductive state when observed. Analysis was based on the Arnason-Schwartz (AS) multi-state model which assumes that the probability of making a transition depends only on the present state, provided that the individual survives (Arnason, 1972, 1973; Schwarz *et al.*, 1993). We identified all parameters of biological interest, evaluated the goodness of fit (GOF) of this “global” model to the data and then examined support for reduced models and explanatory factors. The complexity of multistate models rapidly increases with the number of states included in the model. For this reason, we modelled recruitment separately from adult fecundity, as described below.

5.2.3.1 Recruitment

For females first seen as calves, we estimated the probability of becoming a breeder at a given age or year (Pradel and Lebreton, 1999; Cam *et al.*, 2005). Females do not reproduce prior to age five in this species and including younger animals would have introduced unnecessary survival heterogeneity into the model (see Chapter 4). Analysis was therefore limited to females that survived to at least age five, excluding all earlier sightings. Age at entry was standardised by inserting a dummy record for all individuals at age four, regardless of whether or not a sighting occurred in that year. Capture probability can not be estimated at first encounter and no earlier breeding transition was possible. Consequently, this approach was not expected to affect other parameters in the model. The resulting estimates reflect the probability of becoming a breeder at a given age or year, conditional on having survived to that age and on not having given birth previously.

Transitions were estimated between three states: sub-adults, first-time breeders and adults. At a given age or year, a sub-adult could remain in that state or become a first-time breeder. All first-time breeders transitioned to adults and all adults remained in that state for the duration of the study. Reverse transitions (first-time breeder to sub-adult, or from adult to either sub-adult or first-time breeder) were impossible and so constrained as such in the model. Unlike some recruitment studies, female humpback whales were regularly encountered while still sub-adult. Re-sighting probabilities were permitted to vary over time and survival was assumed to be time-invariant but allowed to differ between states. The transition from sub-adult to adult was allowed to vary with time and/or age. To investigate costs of early reproduction, we compared females known to have bred for the first time by age seven (“early recruits”) to all other first-time breeders (“late recruits”).

5.2.3.2 Adult fecundity

Once a female was observed with a calf, her subsequent fecundity was measured as the probability of transition between calving and apparently non-calving states. This was measured at the population level using encounter history data from GOM-wide surveys, 1989-2005. Analysis then focussed on the south-west GOM, using all sources of encounter history data, 1984-2005, to investigate local trends and explanatory factors. Adult survival was allowed to vary with breeding state and time, depending on the

analysis. Re-sighting and transition probabilities for adults were investigated with respect to time.

In a separate analysis, we examined evidence for age-related differences among adults using a subset of available years, 2000-2005. Analysis was limited in this manner because of the potentially confounding effect of time when investigating age-specific differences, as discussed in detail in Chapter 4. The present analysis used the same data for females as in Chapter 4, but in this case limited analysis to reproductive adults and differentiated between them based on their breeding state. With the exception of one female that bred by age five, the youngest adults in that period ranged from 10-15 years old. The five year old was excluded for clarity and the remaining females were compared to adults of unknown age, but with prior sighting histories of at least 20 years.

5.2.3.3 Goodness of fit and model selection

Mark-recapture models produce valid estimates only when the data meet model assumptions. Individuals within groups or strata are expected to have an equal but independent probability of detection on the study site as well as an equal probability of survival to the next sampling period. Emigration is permitted from the study area, but it must be random and temporary. The sampling period should be brief relative to mortality processes, and individuals must be successfully recognised and assigned to the correct state if re-encountered. Program U-CARE (version 2.2.5, Choquet *et al.*, 2005) was used to detect and diagnose heterogeneity in survival (Test 3G.Sr and Test 3G.Sm) and re-sighting probabilities (Test M.ITEC and Test M.LTEC, Pradel *et al.*, 2003). Survival heterogeneity was expected to be minimal because a three-month sampling window (July-September) is short relative to life span in this species (Hargrove and Borland, 1994). This window was also expected to reduce the potential for bias due to migration and weaning effects. Mothers return from the breeding ground later than other adults, but should have been equally available for sampling after June (Chapter 3) and weaning was not expected prior to October (Baraff and Weinrich, 1993). Mothers could also be misclassified due to calf mortality prior to observation. The calf mortality rate prior to weaning has been estimated at 0.182 (95% CI 0.023-0.518) in the North Pacific (Gabriele *et al.*, 2001), but data were insufficient to specifically account for it in this study. Retrospective sexing can cause bias mark-recapture estimates of survival by creating a bias toward individuals that lived to be sexed later in life (Buckland, 1982; Nichols *et al.*,

2004). However, only five individuals remained unsexed by their first sub-adult sighting and so age of sexing was not considered a concern for this study.

Heterogeneity was a potential concern for re-sighting probabilities because some analyses were based on sampling that was limited to south-west GOM areas. In the multi-state case, U-CARE Test M components diagnose heterogeneity in re-sighting probabilities for individuals known to have survived. Trap-dependence refers to the case in which an individual that is present is more or less likely to be seen if seen previously (i.e., trap-happy or trap-shy, Sandland and Kirkwood, 1981; Pradel, 1993). By contrast, Markovian temporary emigration occurs when individuals that are seen are more or less likely to remain in the study area (Schaub *et al.*, 2004). A significant Test M result was addressed by modelling re-sighting probability with an individual, time-varying covariate which specified whether or not the individual was seen in the previous sampling period.

Program U-CARE assumes time variation in transition probabilities which was not the most general model when age effects were of interest. Furthermore, even after adjusting model structure for specific sources of heterogeneity, residual over-dispersion can cause estimates to be artificially precise (Burnham *et al.*, 1987). The fit of the global model was therefore also evaluated using the median \hat{c} technique in program MARK (version 4.3, Cooch and White, 2006). The variance inflation factor (\hat{c}) generated by the latter was included in the modelling process to account for residual over-dispersion, even when it was estimated to be mild (Nisbet and Cam, 2002). However, the median \hat{c} procedure does not accommodate models with individual covariates. When these were required to address trap dependence, the procedure was performed on an equivalent model without individual covariates, given that the latter served to improve the fit of the model to the data.

Model selection was performed in program MARK, based on Akaike's Information Criterion (Burnham and Anderson, 2002). Akaike's Information Criterion (AIC) evaluates the relative fit of each candidate model in light of the number of parameters necessary to achieve that fit. We used QAICc, a form that accounted both for small sample sizes and the inclusion of a variance inflation factor. The model with the lowest QAICc value was considered the most parsimonious, and all other models were evaluated based on their distance from the preferred model (Δ QAICc). Those within 2 units were considered equally likely given the data, whereas a model that differed by 10 units or more was inferred to have no support (Burnham and Anderson, 2002). The ratio

of normalised QAICc weights of two models also provided an indication of relative strength of support. In most cases, model selection sought the most parsimonious fit for re-sighting, apparent survival and transition parameters, in that order. However, when cost of breeding was of interest, apparent survival was prioritised above transition probability. Parsimony was attempted by reducing model parameters, starting with interactions (*), additive effects (+) and finally main effects. Model averaging was performed within program MARK to obtain parameter estimates in light of model selection uncertainty. True “process” variation was separated from sampling variation by applying the variance components technique in program MARK to the global model (Burnham and White, 2002).

5.2.3.4 Time variation and explanatory factors

When annual variation was supported by model selection, we attempted to explain those results with covariate data. Re-sighting probability was modelled as a nuisance parameter; we attempted to achieve parsimony by modelling it as a function of the number of individuals successfully identified in a given year (Mizroch *et al.*, 2004). Explanations for variation over time were primarily of interest when modelling fecundity. As this was measured as the transition to a calving state, females that made the transition would have been pregnant when encountered. Therefore, models that constrained transition probability to a covariate measured in the same season investigated the probability of carrying an existing pregnancy to term. By contrast, a covariate measured one year prior investigated an influence on the probability of conception. Other lag periods and cumulative covariate effects were possible but not examined.

Low local prey abundance is thought to have been responsible for large-scale distribution shifts in the GOM (Payne *et al.*, 1986; Payne *et al.*, 1990; Weinrich *et al.*, 1997) and increased emigration probabilities (Stevick *et al.*, 2006). Apparent adult survival does not appear to vary substantially from one year to the next (Chapter 4), but we were interested in a potential trade-off with respect to reproduction. As described in detail in Chapter 4, abundance indices for key fish species were obtained from the Northeast Fisheries Science Center (Woods Hole, MA). They were based on data obtained during stratified bottom trawl resource surveys conducted twice annually from the GOM to North Carolina. The sand lance (*Ammodytes* spp.) index was based on the mean number of individuals caught per standard tow (1988-2003), whereas biomass estimates were available for Atlantic herring (*Clupea harengus*, 1988-2005) and Atlantic

mackerel (*Scomber scombrus*, 1988-2004). Given uncertainties about prey preference and availability, we also used adult humpback whale movement patterns as a more general indicator of the quality of the feeding ground environment. Above-average inter-annual displacement distances (Chapter 2) were hypothesised to reflect more effort spent searching for food from one year to the next. Below average inter-annual displacements were taken to indicate that resources were adequate in the location in which they were found the previous year. Finally, we investigated correlation between female fecundity and first year calf survival (Hastings *et al.*, 1999). The latter is annually variable (see Chapter 4) and so likely incorporates biologically meaningful environmental effects that we could not otherwise quantify.

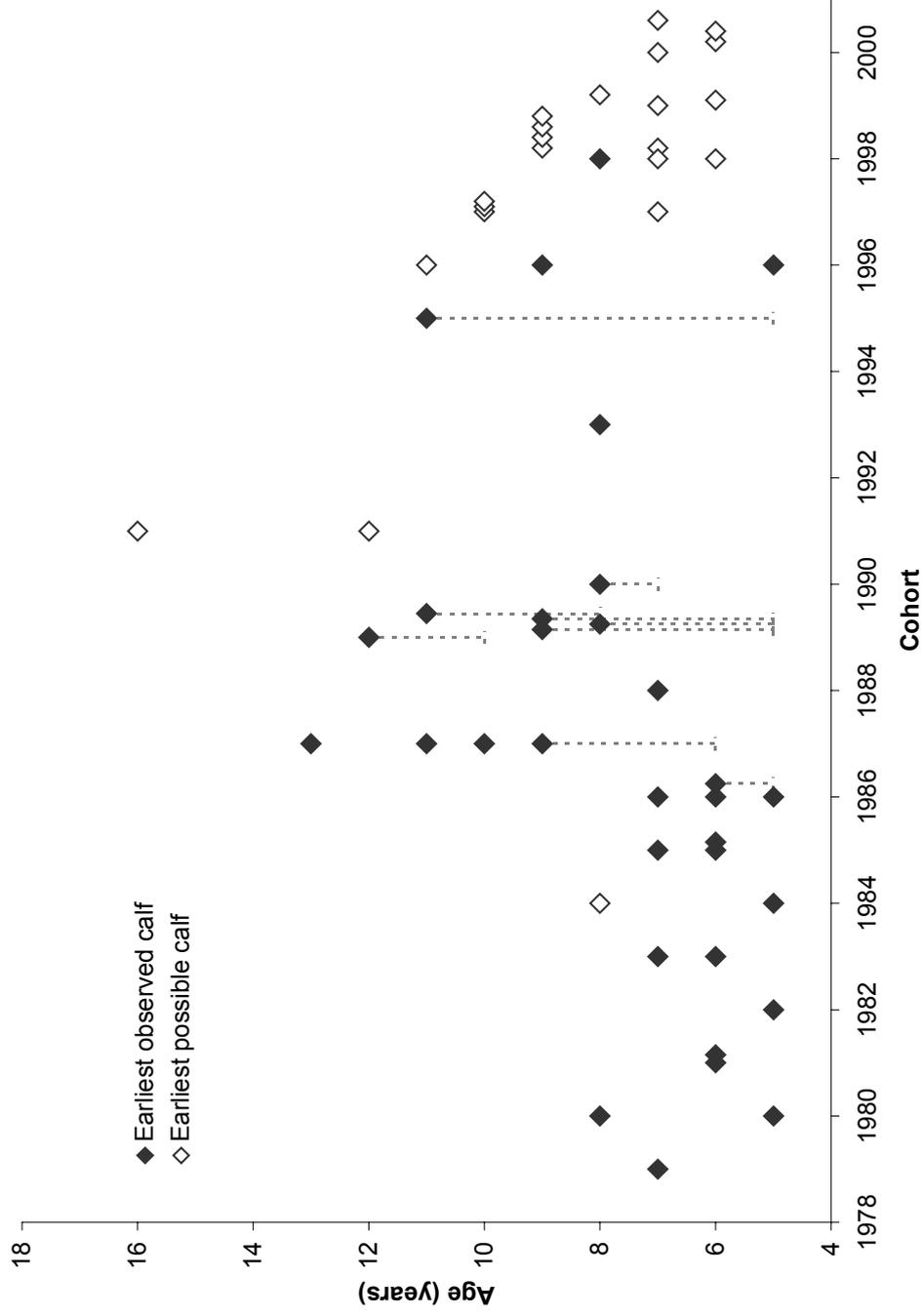
If a particular covariate was not available in all years, we standardised the values so that missing data would not influence the results (Cooch and White, 2006). Model selection was used to identify covariates that improved the fit of the model to the data.

5.3 Results

5.3.1 Apparent age at first birth

Of 591 calves documented between 1979 and 2000, 181 were known to have been female. Only 25 were observed continuously from age five until they first reproduced (Figure 5.1), and their mean apparent AFB was 7.08 years ($s = 2.00$). Clapham (1992) previously estimated AFB for the subset of GOM females born through 1987 at 5.92 years, but four females were still sub-adult at the end of that study. Adding those individuals increased the mean slightly to 6.13 years ($s=0.89$, $n=16$). By contrast, half of the calves born later (1987-2000) recruited at 9-13 years ($n=4$) resulting in a significantly higher overall for the later period (8.78 years, $s = 2.33$, $U=135.5$, $p=0.002$). Six additional females were missed in one or two sub-adult years and the first observed calf was likely the first produced. Inclusion of these females increased the maximum average apparent AFB to 9.21 years ($s = 2.08$, $n=14$) for the later period. Finally, 21 females born since 1987 were observed continuously from age five without producing a calf (Figure 5.1). As of 2005, their earliest possible mean age at first birth would be 8.52 years ($s=2.46$, $min=6$, $max=16$), assuming that they reproduced at the next opportunity. These results provided additional support for an increase in AFB during the later period.

Figure 5.1: Observed age at first birth (solid diamonds), by cohort. Dashed lines and terminal bar indicate the difference between the minimum and observed age at first reproduction. Minimum possible age at first birth for females not yet observed to reproduce is also shown. The latter assumes that reproduction occurs the season after the most recent sighting.



5.3.2 Statistical modelling results

5.3.2.1 Recruitment

Between 1979-2005, 91 females of known age were re-sighted at least once after age four. Goodness of fit testing confirmed trap dependence, but no other significant departures from model assumptions (Table 5.1). The median \hat{c} procedure performed on a global model incorporating age structure indicated minor over-dispersion ($\hat{c}=1.138$). Sub-adult and adult re-sighting probabilities were subsequently fitted with time-varying individual covariates to account for trap dependence. Model selection favoured models in which re-sighting probability varied with recruitment status. Sub-adults exhibited a lower probability of detection than adults, and late recruits were seen less frequently as adults than early recruits. Survival appeared to be highest among sub-adults and lowest among first time breeders, but the data also supported an interpretation of equal survival (Table 5.2). However, when first time breeders were stratified by their age at first breeding, early recruits had a lower apparent survival after first birth (0.803 95% CI: 0.509-0.941) than all other females (0.988, 95% CI:0.973-0.995). Those that survived to become adults achieved an apparent survival comparable to other females.

5.3.2.2 Adult fecundity

A total of 207 adults were encountered GOM-wide on 776 occasions between 1989-2005. Goodness of fit testing revealed no major departures from AS model assumptions (Table 5.1). A variance inflation factor from the median \hat{c} procedure ($\hat{c}=1.101$) was incorporated prior to model selection. Breeding and non-breeding adults had equal probabilities of re-sighting, and the fit for both was improved when modelled as a function of photo-ID effort. There was evidence for a survival difference between breeders and non-breeders, but the top model did not include it. Fecundity varied over time, with point estimates ranging from a low of 0.073 (95% CI: 0.007-0.458) in 1993 to a high of 1.0 (95% CI: 0.020-1.00) in 1989 (Table 5.3, Figure 5.2). The average fecundity rate over the time period was 0.424 with a process variance of 0.070 (95% CI: 0.037-0.172).

Table 5.1: Goodness of fit test results for multi-state analyses of reproduction. Results are reported from program U-CARE and the median c-hat procedure in program MARK. U-CARE tests the fit of the Arnason-Schwartz model to the data and we report the p-value from the χ^2 test for each test component. Those indicating significant heterogeneity are highlighted.

Analysis	U-CARE test results				Estimated median c-hat
	WBWA	Test 3G.SR	Test 3G.SM	Test M.ITEC	
Recruitment	0.167	0.862	0.999	0.016	1.138
Adult fecundity:					
GOM-wide	0.730	0.925	0.993	0.099	1.101
South-west GOM only	0.600	0.169	1.00	<0.001	1.062
By age**	0.079	0.396	0.721	0.410	<1.0

**Pooled groups

TABLE 5.2: Model selection for multi-state analysis of recruitment. Models with equal support from the data are shaded.

Model order	Parameter estimated			Δ QAICc	QAICc Weights	#Parameters
	Apparent Survival	Re-sighting	Transition to Breeder			
16	A/(RS)	s+m+e	T	0.000	0.324	9
17	R/(AS)	s+m+e	T	0.862	0.211	9
15	s	s+m+e	T	0.881	0.209	10
14	.	s+m+e	T	1.700	0.139	8
18	A/(SR)	s+m+e	T	2.033	0.117	9
13	s	s+m+e	.	16.611	0.000	9
12	.	s+m+e	.	17.329	0.000	7
11	s	s+m+e	age	24.974	0.000	19
10	s	s+m+e	t	25.780	0.000	29
9	.	s+m+e	t	26.203	0.000	27
8	s	s+m	age	47.513	0.000	18
7	s	s+m	t	47.914	0.000	28
6	.	s+m	t	48.091	0.000	26
5	s	s+m	age(5-7)*time	128.884	0.000	75
4	s	s+m	age*time	267.303	0.000	123
3	s	s+m	age*time	295.543	0.000	143
2	s	s*m	age*time	373.786	0.000	163
1	s	s*t	age*time	506.147	0.000	182

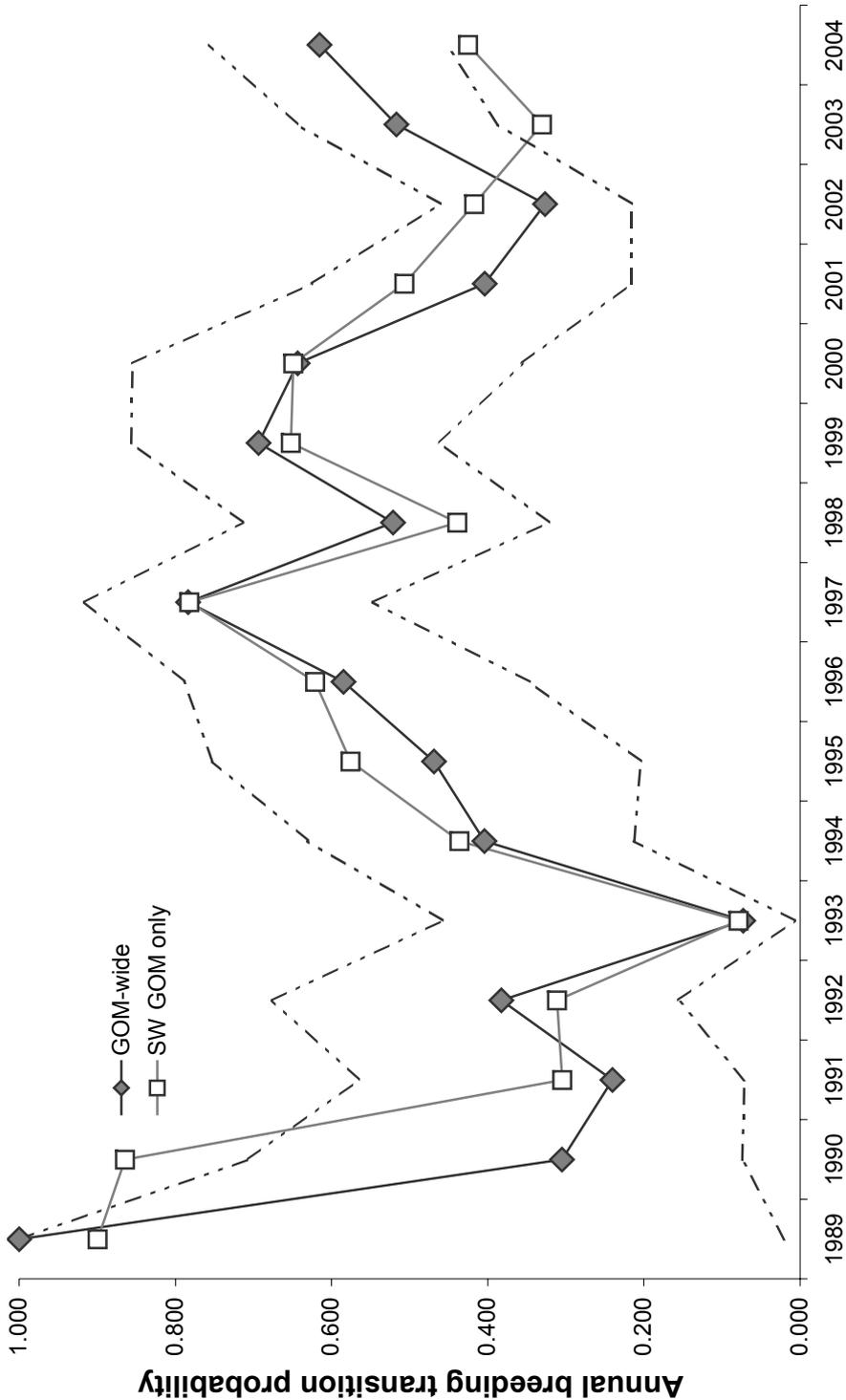
Abbreviations = constant (.), states (s), age (a, through 16 unless otherwise noted), time (t), function of effort on logit scale (e), interaction effect (*), additive effect (+). S = Subadult, R= Recruit and A= Adult. Abbreviations that are grouped with parentheses are set equal.

TABLE 5.3: Model selection for multi-state analysis of adult fecundity GOM-wide, 1989-2005. Models with equal support from the data are shaded.

Model Order	Parameter estimated		ΔQAICc	QAICc Weights	#Parameters
	Apparent Survival	Re-sighting			
11	.	effort	0.000	0.346	20
14	T	effort	0.219	0.310	21
10	s	effort	2.046	0.124	21
15	T/T	effort	2.101	0.121	22
13	.	effort	3.364	0.064	5
12	.	effort	4.666	0.034	6
9	t	effort	21.103	0.000	35
8	s+t	effort	22.479	0.000	36
6	s*t	effort	50.038	0.000	51
5	s*t	s+effort	51.850	0.000	52
3	s*t	t	64.186	0.000	65
2	s*t	s+t	64.687	0.000	66
1	s*t	s*t	91.802	0.000	81
7	s*t	.	147.264	0.000	50
4	s*t	s	147.466	0.000	51

Abbreviations = constant (.), states (s), time (t), function of photo-ID effort on logit scale (effort), interaction effect (*), additive effect (+). T/T indicates separate trend effects on each state

Figure 5.2: Annual adult breeding transition probabilities in the southwest GOM and region-wide, 1989-2004. The dashed lines bound the 95% confidence interval for the GOM-wide estimates.



In the south-west GOM, 201 unique adults were encountered on 1,110 occasions between 1984 and 2005. Goodness of fit testing revealed trap dependence which was modelled using time-varying individual covariates and retaining a variance inflation factor (Table 5.1). Re-sighting probabilities were higher than in GOM-wide sampling and breeders were more likely to be re-sighted than non-breeders. Model selection indicated lower survival of breeders versus non-breeders. We could not discriminate between constant survival for both breeding states, an increasing trend of survival among non-breeders only, or increasing survival for both. As in the GOM-wide data set, the most parsimonious model for transition probability indicated annual variation. Point estimates mirrored those of the GOM-wide sampling, with a low of 0.031 in 1993 to a high of 0.901 in 1990 (Figure 5.2). Fecundity averaged 0.565, with a process variance of 0.042 (95% CI: 0.023-0.092).

We were unable to identify an environmental covariate applied prior to conception or during pregnancy that explained annual variation in adult fecundity in the SW GOM. However, the top model was one in which fecundity was fit to offspring mortality, suggesting that females that reproduced during years of low fecundity experienced lower calf survival than those that reproduced when fecundity was high (Table 5.4). Modelling revealed no age-related differences in fecundity between adults known to be 10-15 years old (n=24) versus those known to be older (n=40). There was some evidence of slightly lower survival among breeders, especially older breeders, but it was not possible to differentiate between those possibilities with the available data (Table 5.5).

Although most analyses focussed on the probability of transitioning from a non-calf to a calving state, all indicated that less than 2% of adults were simultaneously pregnant and lactating. Only one female was of known age when she reproduced in consecutive years. She was seventeen years old when she produced her first such calf and has subsequently had at least two others (births in 1997, 1998, 2000, 2001 and 2002). Other females in the same age category were not as productive, suggesting that this was not an age-related advantage. One consecutive calf was followed to first reproduction. “Wizard” was the last of three calves born consecutive years (Weinrich *et al.*, 1993). Her subsequent age at first parturition¹ (age 8 in 1998) was within the expected range.

¹ Weinrich *et al.* (1993) incorrectly reported Wizard as male.

TABLE 5.4: Model selection for adult fecundity in the south-west GOM, 1989-2005. In the top model, time varying transition was constrained to calf survival the subsequent year. Other covariates fitted had QAICc values exceeding 10 and are not shown.

Model Order	Parameter estimated			QAICc	QAICc Weights	#Parameters
	Apparent Survival (Nonbreeder/Breeder)	Re-sighting	Transition to Breeder			
27	T/.	s+m	CALF	0.000	0.445	29
10	T/.	s+m	t	1.357	0.226	48
9	TT	s+m	t	2.172	0.150	48
7	s	s+m	t	2.605	0.121	46
11	.T	s+m	t	4.325	0.051	47
8	.	s+m	t	9.091	0.005	45
6	s+t	s+m	t	13.440	0.001	62
3	s*t	s+m	t	19.774	0.000	71
13	T/.	s+m	T	22.388	0.000	29
2	s*t	s*m	t	25.225	0.000	88
12	T/.	s+m	.	26.047	0.000	28
1	s*t	s*t	t	170.098	0.000	106
4	s*t	s	t	217.004	0.000	50
5	s*t	.	t	221.531	0.000	50

Abbreviations = constant (.), states (s), time (t), trend over time (T), function of photo-ID effort on logit scale (effort), interaction effect (*), additive effect (+), trap dependence (m), constrained to calf survival the following year (CALF). A slash separates effects on two different states.

TABLE 5.5: Model selection for adult fecundity by age category, 2000-2005. Age groups were females known to be 10-15 years versus those known to be at least 20.

Model order	Parameter estimated		ΔQAICc	QAICc	Weights	#Parameters
	Apparent survival	Re-sighting				
			From non-breeder	From breeder		
15	.	age	.	0.000	0.408	5
14	s	age	.	0.257	0.359	6
13	age	age	.	1.886	0.159	6
12	s*age	age	.	4.128	0.052	8
11	s*age	age	age	6.294	0.018	9
10	s*age	age	t	10.242	0.002	12
9	s*age	age	age*t	11.749	0.001	17
8	s*age	age	age*t	12.255	0.001	18
7	s*age	.	age*t	12.715	0.001	17
6	s*age	s	age*t	14.558	0.000	18
5	s*age	t	age*t	16.013	0.000	21
4	s*age	s+age+t	age*t	17.346	0.000	22
3	s*age	(s+t)(age*t)	age*t	24.394	0.000	27
2	s*age	(s*t)(age+t)	age*t	32.085	0.000	32
1	s*age	s*age*t	age*t	42.831	0.000	36

Abbreviations = constant (.), states (s), group(g), time (t), interaction effect (*), additive effect (+)

5.4 Discussion

5.4.1 Recruitment

Clapham (1992) reported that female humpbacks first reproduce between the ages of 5 to 7 years. No earlier age at first birth has been documented, but the present study confirms that GOM females recruit over a wider age range than previously thought. The first published estimate was based entirely on continuous observations and so could only have been biased if females had been censored, or if the spatial bias of the sampling affected the results. However, only four females were still sub-adults by the end of that study and those that survived ultimately produced calves within the published range. Furthermore, young females are now known to be preferentially distributed within the range of that study (Chapter 2). Thus, it does not appear that previous results were biased, but rather that the average age at first birth increased in this population.

Chittleborough (1965) found no inter-annual or inter-population variation in age at puberty in commercially harvested humpback whales in the Southern Hemisphere. However, his work was based on direct observation of the ovaries, in which the scars of ovulation, or “corpora albicantia,” persist for long time periods (Laws, 1961). Evidence of ovulation does not necessarily indicate birth or neonatal survival, and so caution must be exercised when comparing expectations of fecundity with the viable calving rates of free-ranging animals. Large mammal species frequently delay first reproduction beyond the age at which it is first possible. For example, in ungulates, the age at first reproduction is highly variable and often correlated with achieving a certain maternal mass (Gaillard *et al.*, 2000). Many factors can potentially influence mass gain in early life, most notably food availability and the degree of maternal investment during gestation and/or subsequent maternal care. Unfortunately, the available data on humpback whale recruitment were too sparse to model over time with covariate data. Thus, we can not report with confidence the cause of the increase in age at first birth in the GOM. However, visual inspection of cohort data suggested a rather abrupt increase in the age at first reproduction, starting with the 1987 cohort. The period of early recruitment first described by Clapham (1992) and reiterated here coincided with a period of unusually high sand lance abundance. Sand lance abundance increased steadily in the mid-1970s, peaked in the early 1980s and declined precipitously by 1985 (Fogarty *et al.*, 1991). If attainment of sexual maturity is more related to maternal reserves than age, then this temporarily abundant resource may have facilitated growth and allowed young females to mature earlier. Additional data may

help to identify the proximal factor affecting recruitment age, including the specific timing of that interaction.

The strength of the present analysis is the multi-state approach and the corresponding finding that females that recruited early exhibited lower survival than those that waited to reproduce until they were older. By assuming equal survival between breeders and non-breeders, standard methods of estimating age at first birth omit information that can potentially help to understand patterns of recruitment. For example, a similar finding of lower survival in recruiting flamingos led Tavecchia *et al.* (2001) to hypothesise that costs of reproduction were ultimately what selected for deferred breeding in that species. In our study, these costs were also evident in adult females (see below); nevertheless recruitment results should be further scrutinised as additional data become available.

Recruitment studies on humpback whales are likely to continue to be data-limited if based on observational data alone. The results reported here were based on 27 years of continuous study in a GOM area preferred by juveniles and adult females (see Chapter 2). If this research had been limited to one of the GOM areas now known to favour adults and especially males, then even fewer data would now be available. In fact, spatial heterogeneity may be one cause of the paucity of recruitment data from other well-studied populations. Given the finding that recruitment age also varies significantly over time within a single population, more data are clearly necessary to reliably study this parameter. Advances in applications of biopsy-based tissue samples may facilitate this work by allowing pregnant females to be identified before they give birth (Mansour *et al.*, 2002; Rolland *et al.*, 2005; Kellar *et al.*, 2006), or by identifying parent-offspring relationships after the calf year (Bérubé and Palsbøll, 2004) in combination with an ageing technique (Dennis, 2006).

The previously reported average age at first birth in the GOM was initially taken by Clapham (1992) as validation of a technique of ageing using alternating light and dark layers of wax accumulated in the ear (Purves, 1955). Such layers are thought to be laid down annually in either one or two pairs, now known as growth layer groups (GLGs). Using this technique and observations of ovaries in harvested specimens, Chittleborough reported that puberty in Southern Hemisphere humpback whales ranged from 2-12 years and averaged 4-5 years (Chittleborough, 1959; 1965). However, Chittleborough believed that two GLGs were deposited per year in humpbacks, whereas only one GLG appears to

be accrued annually in all other baleen whale species (Lockyer, 1984). His interpretation appeared to be supported by the recovery of a male that was less than 37 feet in length, with immature gonads and an ear plug count of 12-GLGs, five years after Discovery tagging (Chittleborough, 1960). For the reported length, an age estimate of six years is more plausible than twelve, but still not irrefutable proof of the method.

Stevick (1999) noted that North Atlantic humpback whale carcasses were smaller for their age than expected from Southern Hemisphere commercial whaling data and suggested that the discrepancy would be reduced if only one GLG were deposited per year in this species. However, ages at puberty in Chittleborough's study would then have ranged from 4-24 years and averaged 8-9 years, corresponding to a minimum average age at first birth of 9-10 years. In that event, the recruitment age in the 1980s in the GOM would have been almost half that of an actively exploited exploitation that should have been growing quickly. More recently, Gabriele *et al.* (2007) reported the age at first birth at south-east Alaska to average 11.8 years, based on 10 females observed across two decades. Their result was significantly higher than both GOM estimates and possibly even elevated relative to Southern Hemisphere catch data when one GLG is assumed. If age at first reproduction varies within and between populations (Stearns, 1992), then none of these data can be expected to validate (or invalidate) Chittleborough's assumptions. Rather, earplug readings of known aged individuals will be required.

5.4.2 Adult fecundity

As noted previously, recruiting females may suffer costs of reproduction because of their relatively small size and inexperience. However, we found reproduction to be costly for adults as well. Fecundity varied inter-annually and there was both a survival cost among breeding females and an apparent cost to their offspring, which were more likely to die when born in years that fecundity was low.

There is prior evidence that maternal condition affects both the probability of reproduction in large whales and/or the quality of offspring produced. In humpback whales, females with longer than average inter-birth intervals reportedly produced more male offspring than females, a possible reflection of superior fitness (Wiley and Clapham, 1993). By contrast, the lowest reported calving rate previously on record (0.31 calves per mature female) followed upon a winter mass mortality event in the GOM (Barlow and Clapham, 1997). Pregnant fin whales exhibited better body condition than those that were

not pregnant, although it is not known whether or not those differences were already established at the time of conception (Lockyer, 1986, 1987). Similarly, Mizroch and York (1984) found variation in female fin whale fecundity that they could not explain by density dependence, but offered fluctuations in the environment as a possible alternate cause to be explored.

Although adult fecundity varied with time in this study, we were unable to establish a trend over time, nor to find an environmental factor that adequately explained annual variation. There may be several reasons for this, the primary one being the considerable uncertainty in individual prey preferences and availability across the GOM. Furthermore, it is not possible to measure body condition directly in this species and there may not be a direct relationship between maternal resources and prey resources at a given time in capital breeders. Rather, it may be the cumulative abundance of prey over more than one season that determines maternal condition in a given year. Finally, in this study, it was assumed that all females were equally likely to transition to a calving state from a non-calving state. However, females that had not calved in two successive years may have been more likely to breed than those that calved more recently. In the future, models that allow memory of prior states (i.e., Brownie *et al.*, 1993) may improve insight into patterns of humpback whale fecundity.

Hastings *et al.* (1999) also reported higher first year mortality rate among Weddell seals born during periods of low fecundity. They tentatively concluded that the minority of females that bred when conditions were poor did not invest enough in the offspring to ensure their survival to the next year. In their case, the effect was limited to male offspring, although females are larger than males in that species. We did not investigate a correlation with offspring sex here, but Chapter 4 reported a lower average survival of female humpback whale calves during the study period. As the larger sex, it is possible that females are at a greater disadvantage when maternal investment is low; however, the specific relationship between female calf survival and maternal fecundity should be modelled directly in the future. The specific timing and mechanism for reduced maternal investment is not known, but in Southern elephant seals, maternal mass at parturition reportedly dictates the amount invested in offspring, regardless of subsequent demand (Arnbom *et al.*, 1997).

There have been no studies of survival costs of reproduction in cetaceans, but in pinnipeds there is both evidence for (Boyd *et al.*, 1995) and against it (Pistorius *et al.*,

2004; Beauplet *et al.*, 2006). Although we attempted to differentiate between breeders in two age categories, comparative studies of age-specific reproduction remain difficult without a direct means of ageing whales. The decline in fecundity among young females during the study had a strong negative effect on our ability to compare young and old breeders during a common time period. However, based on the available data, fecundity and costs of reproduction do not appear to increase significantly, nor to decline with age. There is also no evidence of a complete cessation of reproduction with age among baleen whales (Marsh and Kasuya, 1986) and the present results make a case against it for this species. Williams (1957) theorised that menopause may benefit older females in social species (humans) by allowing them to contribute to their own reproductive success by investing in their daughters' offspring. Given that there are few extended interactions between close kin in this species, reproductive senescence would not be expected from at least that fitness perspective.

The inability to identify a covariate explaining time variation also prevented us from determining the stage of that interaction. Fecundity rates are determined by either the probability of conceiving, the probability of carrying a pregnancy to term, or both. Energetic costs of pregnancy are thought to be relatively small, particularly when compared with the substantial burden of lactation (Lockyer, 1981). Foetal growth is not linear over time, but increases exponentially at approximately the fifth month of gestation, both in terms of body length (Laws, 1959) and body weight (Lockyer, 1981). Laws theorised that this timing corresponded to the return of females to their high latitude feeding grounds when resources would be adequate for the expenditure.

Lactation is costly and the last opportunity to accumulate maternal reserves is on the feeding ground during gestation. In a patchy and variable feeding environment, it may be advantageous to postpone investment into offspring until the quality of those resources can be assessed. For species with seasonally-limited mating opportunities, selection may favour the females that conceive at every occasion provided that there is a mechanism to terminate that investment should resources be inadequate to support it. In some species, females appear to mitigate impacts on survival by preventing or terminating reproduction before investment becomes too great (Gaillard and Yoccoz, 2003). Poor maternal body condition has been shown to delay or prevent ovulation in elk (Cook *et al.*, 2001) but is also associated with early pregnancy failure in caribou (Russell *et al.*, 1998). It has yet to be determined whether such processes occur in large whales.

Abortion or foetal re-absorption, should it occur in this species, could explain one perplexing aspect of the humpback whale mating system. The reproductive biology and ecology of this species appear to be geared toward annual reproduction. Females conceive, birth and wean offspring on roughly an annual schedule. Males routinely escort females with newly dependent calves on the breeding grounds despite the fact that consecutive calving is rarely documented, even in populations subjected to intensive exploitation (e.g., Chittleborough, 1958, 1965; Clapham *et al.*, 1997). If a male were to mate with a recently parturient female, most evidence suggests that a viable calf would not be produced. Yet, neonatal mortality is estimated at 15-24% in the North Pacific and is thought to occur quickly, before calves first arrive on their feeding ground (Gabriele *et al.*, 2001). Neonatal mortality represents a substantial loss to females if they must wait another year to conceive. However, if new mothers were to mate and conceive after parturition, then that pregnancy could serve as insurance against the loss of their neonate. In the event that the neonate survives, the pregnancy could fail due to the demands of lactation. However, if it the neonate were to die, then the mother could potentially reduce her loss by carrying the foetus to term. Escorting males would then sire offspring by “invisibly” replacing calves lost to neonatal mortality.

Unfortunately, few data exist with which to test this hypothesis. Lactating females were protected from commercial whaling and, in any case, small foetuses were most likely to be missed. Pregnancy testing is another potential avenue of investigation, although the technique is still under development for large whales and is likely to be most problematic for early pregnancies. To date, only one GOM female has been re-sighted the season after losing a calf and she did not produce another. In the future, a better understanding of the factors influencing reproduction, including the timing of that interaction, could provide additional insight into this question.

Finally, from a management perspective, sampling performed exclusively in south-west GOM areas produced comparable annual estimates of fecundity as those estimated from GOM-wide sampling data. This is likely due to female preference for south-west GOM areas, and suggests that local sampling in the south-western GOM, such as at the Stellwagen Bank National Marine Sanctuary, could effectively monitor this parameter (see Chapter 2).

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Chapter 6:

Stock identity of a humpback whale taken in a south-eastern Caribbean hunt¹

6.1 Introduction

North Atlantic humpback whales, *Megaptera novaeangliae*, migrate annually between shared low-latitude breeding areas and discrete high-latitude feeding areas. The principal North Atlantic breeding range lies along the Atlantic margins of the Antilles, from Cuba to northern Venezuela (Winn *et al.*, 1975; Balcomb and Nichols, 1982; Whitehead and Moore, 1982). Photo-identification research at the northern (Greater) Antilles indicates a large breeding population composed of animals from all primary feeding areas (Mattila and Clapham, 1989; Mattila *et al.*, 1989; Katona and Beard, 1990; Clapham *et al.*, 1993; Mattila *et al.*, 1994; Palsbøll *et al.*, 1997; Smith *et al.*, 1999; Stevick *et al.*, 2003a; Stevick *et al.*, 2003b). Fidelity to a specific feeding area is strong and maternally directed, such that calves born in low latitudes are recruited to their mother's stock during an extended period of maternal care (Martin *et al.*, 1984; Clapham and Mayo, 1987; Katona and Beard, 1990).

The eastern and southern (Lesser) Antilles were historically sites of a large humpback whale fishery (Mitchell and Reeves, 1983; Reeves *et al.*, 2001; Smith and Reeves, 2003), and whale density there remains comparatively low (Winn *et al.*, 1975; Levenson and Leapley, 1978; Balcomb and Nichols, 1982; Whitehead and Moore, 1982; Swartz *et al.*, 2003). Three free-ranging humpback whales have been photographically matched to high-latitude feeding areas. One was matched to West Greenland (Stevick *et al.*, 1999), a population estimated at 360 individuals (CV = 0.07, 1988-1993 Larsen and Hammond, 2004). Two others were matched to Newfoundland and Norway (Stevick *et al.*, 1999; Bérubé *et al.*, 2004). Exchange with Greater Antilles areas has also been documented (Stevick *et al.*, 1999).

St. Vincent and the Grenadines, in the Lesser Antilles, is the site of the only ongoing humpback whale hunt in the North Atlantic. Catches have been made at a rate of 0-2 whales per winter over the past two decades (IWC, 2002). In a recent Comprehensive Assessment of the North Atlantic humpback whale population, the Scientific Committee

¹ Robbins *et al.* (2006)

of the International Whaling Commission concluded that these animals were likely drawn from the same population studied at the northern end of the breeding range (IWC, 2002). However, the Committee strongly encouraged the collection of additional data with which to assess the high-latitude origin of animals taken in this hunt. Here we report the stock identity of a humpback whale caught at St. Vincent and the Grenadines based on an opportunistic photograph of the event.

6.2 Methods

We obtained images of two humpback whales landed at Petit Nevis, St. Vincent and the Grenadines, from the web site of a tourist who photographed the event on 6 March 1999. One of the images depicted the ventral flukes of the larger of two humpback whales. Individual humpback whales can be identified from the unique pattern of pigmentation on the ventral side of the flukes and the shape of the trailing edge (Katona and Whitehead, 1981). We used standard photo-identification techniques to match the image against the Gulf of Maine Humpback Whale Catalog curated by the Provincetown Center for Coastal Studies (PCCS, Massachusetts, USA). The match was subsequently confirmed by the North Atlantic Humpback Whale Catalog (NAHWC) curated by the College of the Atlantic (Maine, USA). Carcass length data and other hunt details were taken from information provided to the IWC by the government of St. Vincent and the Grenadines (IWC, 2000).

6.3 Results and Discussion

Two humpback whales were caught on 6 March 1999: one 46-foot (14 meter) female and a second female that was estimated at 20-23 feet (6-7 meters) in length (IWC, 2000). The ventral flukes of the larger animal were photographically matched to a catalogued Gulf of Maine whale known as “Haar” (NAHWC# 0694). She was first seen in July 1987 and so was at least 13 years old when she died. The PCCS catalogue contained four Gulf of Maine sightings of this animal, none of which were after 1990. The NAHWC reported no other matches to 2,542 individuals catalogued at other feeding areas through 1998.

A fluke image was not available from the second animal. However, at an estimated length of only 6-7 meters in the late breeding season, it was not likely to have been an independent, catalogued whale. Calves are estimated to range from 4.1 to 6.9 meters in length during their first winter (Spitz, 1999) and remain dependent until 8-9 meters in length (Chittleborough, 1959, 1965; Clapham *et al.*, 1999; Doroshenko, 2000).

Humpback whales are occasionally unusually large or small for the season *in utero* (Matthews, 1937; Chittleborough, 1958; Nishiwaki, 1959; Mikhalev, 1997; Doroshenko, 2000), and we are aware of one Gulf of Maine yearling that died in April at a length of only 7.2 meters (Barco *et al.*, 2002). However, based on the majority of the available length data, the small whale taken with “Haar” was likely a calf and, if so, a member of the same stock.

Nearly nine years elapsed between the most recent Gulf of Maine sighting of “Haar” and her death at St. Vincent and the Grenadines. Although sparse catalogue sighting histories are not unusual, we also considered the possibility that “Haar” was not a consistent member of the Gulf of Maine population. Low rates of exchange have been documented between the Gulf of Maine and other western North Atlantic feeding areas, including the Canadian Scotian Shelf, the Gulf of St. Lawrence, Labrador/Newfoundland and west Greenland (Katona and Beard, 1990, 1991; Clapham *et al.*, 2003). Katona and Beard (1990) hypothesised that animals from other feeding grounds may pass through this area during their northbound migration. At present, however, there is no evidence that “Haar” used another feeding area. In fact, her presence in the Gulf of Maine at the peak of at least one summer reduces the likelihood that she was simply en route to another feeding area.

This is the most south-easterly sighting of a whale with a Gulf of Maine sighting history. The Gulf of Maine population has the shortest migration to any breeding area in the western North Atlantic. However, the waters of St. Vincent and the Grenadines are at least 41% (975 km) farther than high density breeding aggregation sites at the Greater Antilles. We do not know whether Gulf of Maine whales migrate directly, or routinely, to south-eastern Caribbean waters. However, the present match suggests that this species may sometimes travel well beyond its nearest breeding area, even when that area appears to be highly attractive to conspecifics.

This is the fourth high-latitude stock identified at the Lesser Antilles, supporting the hypothesis that catches are drawn from a variety of feeding stocks. It is also the first successful match of a humpback whale from this hunt. Given the low modern abundance of humpback whales in the Lesser Antilles, catches represent an important source of information on the animals that are available to this fishery. The present match was based on photo-identification, but humpback whales can also be individually identified by molecular genetic techniques (Palsbøll *et al.*, 1997). In fact, the stock identity of one free-

ranging individual from the Lesser Antilles is known only from a genetic match to a high-latitude sample (Bérubé *et al.*, 2004). The molecular genetic archive for the North Atlantic population (CetaBase, currently housed at the University of California at Berkeley) now includes over 6,500 skin samples drawn from all known feeding and breeding grounds (P. Palsbøll, pers. comm.). Even if individuals are not successfully matched, a genetic approach potentially allows for matches to close maternal relatives, and thereby insight into stock identity. This is particularly important for carcasses, as those individuals have no opportunity to be added to the archive at a later date. We therefore encourage efforts to collect and share both types of individual identification data when hunts are performed.

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Chapter 7: Discussion

The Gulf of Maine (GOM) humpback whale population has been under continuous study since the late 1970s. This thesis used a combination of longitudinal data, broad scale sampling and mark-recapture statistical techniques to further understanding of GOM population structure and dynamics. Key findings from that work are summarised below:

- **Spatial structure**

Chapter 2 described population composition and individual exchange among six GOM sites, including a U.S. National Marine Sanctuary. It identified significant spatial and temporal structure that likely also exists on other humpback whale feeding grounds. Here, it had ramifications for a U.S. National Marine Sanctuary because demographic classes typically of management interest were preferentially distributed within and adjacent to that MPA. Therefore, despite its small size relative to the overall population, the Stellwagen Bank National Marine Sanctuary (SBNMS) appears to be an appropriate site for management initiatives targeting juveniles and adult females. By contrast, the results of this study contradict previous assumptions of a preferential exchange between Stellwagen Bank and adjacent Jeffreys Ledge and instead identify the Great South Channel as an important alternate habitat for SBNMS whales. The cause of unequal patterns of exchange could not be established, but such effects should be factored into management decisions, including potential MPA expansion.

- **Seasonal structure and migration**

In Chapter 3, I investigated the pattern of migration between the GOM and the West Indies breeding ground. Significant seasonal changes occur in the GOM in relation to the migration of this population to and from its West Indies breeding grounds. I considered the population to be closed to migratory effects between June and September, although a narrower window was imposed for the purpose of fecundity analyses in Chapter 5 to ensure that mothers would not be under-represented. Previous studies of reproduction have not imposed restrictions on the wide seasonal

range of available GOM data and so may have over-represented resting females both in spring because of their early return to the GOM and in autumn, if they weaned a calf before they were observed. Although some GOM humpback whales remained at high latitudes in winter, I found little evidence to suggest that a significant number of animals did so. Rather, there may be other behavioural explanations for male-biased sex ratios observed on most breeding grounds and migratory corridors studied. However, throughout this thesis, juveniles were found to behave differently, whether in habitat use, range of foraging movement, migratory tendencies or probability of survival. Techniques for ageing whales that allow juveniles to be reliably identified within samples should greatly advance inference with regard to population structure and dynamics.

I identified the period of migratory closure and evaluated two conflicting hypotheses about the timing of migration among demographic classes.

Finally, Chapter 6 reported the first stock assignment of a humpback whale taken in the only legal hunt in the North Atlantic. I discuss the implications of that finding for the GOM and for the management of that fishery.

- **Patterns of survival**

In Chapter 4, I investigated age structure and age-specific survival. I evaluated the effectiveness of “non-calf” estimates for monitoring within and between populations. I also reported the first estimates of male humpback whale survival and a comparative analysis of age-specific survival between the sexes. The GOM has previously been an important source of data on reproduction in free-ranging humpback whales. However, most previous work used methods that did not account for probability of detection or survival. Survival was estimated as part of several different analyses in this thesis. In each case, there was evidence of a lower survival of females relative to males. Male humpback whale survival rates have not previously been reported and this study therefore also represents the first comparison of survival between the sexes. I have interpreted lower female survival as a cost of reproduction. However, it is worth noting that in most cases, the average adult female survival rate was within the typically reported range for this species. Thus, it

was only in comparison to males and subsequently differentiating between breeders and non-breeders that this finding was uncovered. It is often the case that vital rates of males are of lesser interest in population monitoring, but in this case it led to unexpected insight. This result also suggests that un-stratified survival estimates may obscure patterns of survival in adult females that would otherwise be of management interest.

- **Patterns and costs of reproduction**

In Chapter 5, I investigated patterns of recruitment and adult fecundity, including costs of reproduction using multi-state mark-recapture techniques. In Chapter 5, I referred to a continuing question regarding the number of growth layer groups (GLGs) laid down annually in the ear plug of this species. Patterns of age-specific survival, when compared between the sexes, yielded information relevant to this question. As discussed in Chapter 4, males achieved a stable “adult” survival at approximately age five. This was consistent with the age that Chittleborough (1965) estimated for male puberty when assuming two GLGs per year, as well as the earliest known age at first reproduction in females. By contrast, the age at which females achieved maximal survival in this study was closer to the current age at first female reproduction. If there is a relationship between attainment of puberty and achieving “adult” survival rates, then these results are consistent with age thresholds reached under the assumption of two GLGs per year.

The preferential distribution of females in southern GOM areas likely facilitated previous studies of reproduction. However, even long-term research programs will have difficulty accumulating similar data if inadvertently situated in other parts of the range where females do not return reliably. For example, whale watching based research has been undertaken in several northern GOM areas for nearly as long as it has been on-going in the southern GOM. However, low population density along the coast of Maine and the prevalence of adult males in the Bay of Fundy has limited the value of these data in demographic research. Spatial heterogeneity may be difficult to identify in other populations, both because of the spatial coverage required and because of the difficulty of accumulating demographic data on the same scale. When research can not be performed at the scale of the population, studies of several

demographic parameters in combination may improve insight. For example, concurrent estimates of population sex ratio and age structure may help to clarify the potential for demographic bias in reproductive rates. Whereas sex ratio can be measured with relative ease by molecular genetic techniques, age structure data remains more difficult to obtain. Inter-area comparisons of “calves per mature female” versus crude birth rate may help identify spatial bias in the data.

Unconditional estimates of fecundity are otherwise not recommended for studies of humpback whale reproduction given evidence of heterogeneity in individual resighting and survival probabilities. In this study, multi-state analysis improved inference in a number of cases but also required a considerable amount of data. Use of this technique to study recruitment, for example, will be inconclusive if few females are observed to make that transition. Similarly, even long term studies may experience unexpected limitations when it comes to unbiased studies of age-specific reproduction and survival unless large samples can be obtained over relatively short time periods.

Several chapters described extreme “lows” in demographic parameters in the early- to mid-1990s. Adult female fecundity and first year calf survival reached record lows in 1993 and 1994, respectively. Additionally, the average age at first birth doubled and has yet to recover. Clapham *et al.* (2003) previously reported evidence for slightly lower female reproduction and a low apparent calf return rate, but could not determine whether this was a real effect or a result of sampling bias. The methods used here and the combination of effects observed suggest a true event. Eberhardt (1977) predicted a particular sequence in which populations respond to adversity, starting with reduced juvenile survival followed by increased age at first reproduction, reduced adult female reproduction and finally increased adult female survival. In this case, only adult female survival remained unaffected, unless it is manifested through costs of reproduction. In any case, it does not appear that reductions to juvenile survival and adult reproduction have persisted. An anomalous salinity event occurred along the western North Atlantic shelf during the early 1990s and is thought to have been responsible for a number of ecosystem-level changes from the Gulf of Maine north to Newfoundland (Smith *et al.*, 2001). In the

Gulf of Maine, this may have contributed to the strong, but temporary, decline in sand lance abundance in south-western GOM habitats (Weinrich *et al.*, 1997).

Although several parameters were estimated to vary over time, I was generally unable to identify covariates that explained that variation. Prey indices, for example, were rarely informative in this regard. As discussed throughout this thesis, this is likely due to the relatively poor understanding of prey preferences and availability, especially on a regional basis. I attempted to reduce this uncertainty by focussing analyses on data collected in the south-west GOM. However, studies that improve knowledge of humpback whale diet and independent methods of measuring maternal condition would greatly facilitate these types of studies.

GOM humpback whales have been intensively studied by photo-identification techniques since the 1970s. Commercial whale watching platforms have played an important role in that work by providing regular, low-cost access to near-shore cetacean habitats. Near-daily sampling effort in the south-west GOM, and especially at the Stellwagen Bank National Marine Sanctuary, has been invaluable for advancing understanding of this long lived species. However, the analyses performed herein did not take full advantage of this extensive data set. The present analyses prioritised data collected GOM-wide, as spatial bias had not previously been studied and broad-scale data were expected to provide the best foundation for mark-recapture statistical techniques. However, individuals were rarely observed on more than one occasion per year in GOM-wide surveys. Thus, when opportunistic data sets from the south-west GOM were added, their large volume of within-year re-sightings were similarly reduced to reflect only whether an individual was detected in a given year. Broad-scale surveys are both time-consuming and costly, and I found them to result in lower individual re-sighting probabilities than produced by opportunistic sampling in the south-west GOM. For cryptic species of management concern, priority must be placed on techniques that reap the maximum value from available data. Statistical techniques exist that can incorporate auxiliary data and thereby increase the precision of parameter estimates and the power of biological inference.

One such technique is Pollock's robust design (Pollock, 1982; Kendall *et al.*, 1995) which uses sightings made during short, secondary sampling events within standard (primary) sampling periods to estimate additional parameters, such as temporary emigration (Kendall *et al.*, 1995) and multi-state assignment error (Kendall *et al.*, 2003).

A particular strength of the robust design is that it can accommodate cases in which the study area does not or can not encompass the full range of individuals. This is a common situation in cetacean research, although it may not always be recognised as such. The robust design allows statistically appropriate mark-recapture studies to be conducted at smaller scales, because the probability of emigrating from the study site can be estimated. This technique may be of particular value for future research at the Stellwagen Bank National Marine Sanctuary. Sampling in the south-west GOM may be adequate for reproductive rates because of the preferential female distribution in the south (Chapter 2) and the ability to obtain large sample sizes by opportunistic techniques. Nevertheless, any such studies should use techniques that take individual probabilities of detection and survival into account. Only one study of humpback whales has employed the robust design method to date (Chaloupka *et al.*, 1999), but the method has also seen use in studies of gray whales (Bradford *et al.*, 2006) and sirenians (Kendall *et al.*, 2003). The latter is of particular interest because it paired the robust design with multi-state modelling. Mark-recapture statistical techniques are progressing toward such combined models that maximise use of available data (Barker and White, 2004). Many of these models can now be implemented in Program MARK and so provide powerful future opportunities for study of this and similar data sets.

I did not estimate the abundance of the humpback whale population in this study, but the patterns of movement described in Chapter 2 suggest that a spatially stratified approach may be productive. Techniques allowing for geographic stratification have recently been applied in the North Pacific and may be well-suited to conditions in the Gulf of Maine (Calambokidis *et al.*, 1997; Straley *et al.*, 2002). Alternatively, methods that model population growth rate directly from mark-recapture data (Pradel, 1996) would also be informative if constructed from GOM-wide survey data to ensure consistent demographic coverage.

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