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GLOBAL REVIEW OF HUMPBACK WHALES
(Megaptera novaeangliae)

Alyson Fleming and Jennifer Jackson

NOAA-TM-NMFS-SWFSC-474

U.S. DEPARTMENT OF COMMERCE
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U.S. DEPARTMENT OF COMMERCE
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National Oceanic and Atmospheric Administration
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National Marine Fisheries Service
Eric C. Schwaab, Assistant Administrator for Fisheries

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Cover Photo:
Aerial photograph of humpback whale mother and calf provided by Wayne Perryman, NOAA Southwest Fisheries Science Center, La Jolla, CA.

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I. INTRODUCTION

This review presents the best available scientific information relevant to assessing the status of the humpback whale (*Megaptera novaeangliae)*. Humpback whale population structure is described by incorporating information on spatial distribution, migratory connections and genetic population differentiation. Data on abundance and trends are presented relative to population structure. Habitat conditions, threats and recovery status are discussed.

In December 1970, the humpback whale was listed as endangered under the Endangered Species Conservation Act of 1969. When the Endangered Species Act (ESA) was passed in 1973, the humpback whale was automatically incorportated onto the ESA's List of Endangered and Threatened Wildlife and Plants with an endangered designation, along with all other previously listed large whale species. A Final Recovery Plan was published for the humpback whale in 1991. All humpback whale populations were listed as one global entity or species under the Act. The listing status of the various populations should reflect current and best available scientific information; hence a review is now being undertaken.

II. OBJECTIVE

The objective of this report is to summarize all relevant information needed for assessing the validity of the current listing, if warranted. This document reflects the best available information on population structure, abundance, health and recovery.

III. BACKGROUND AND LISTING HISTORY

F.R. Notice citation announcing initiation of this review**:**

74 FR 40568; August 12, 2009

Listing History

Original Listing: The humpback whale was listed under the precursor to the Endangered Species Act (ESA), the Endangered Species Conservation Act of 1969, and was provided an "Endangered" designation under the ESA's List of Endangered and Threatened Wildlife and Plants in 1973. The humpback whale remains listed as Endangered under the ESA as one global species.

FR notice: 35 FR 18319
Date listed: December 2, 1970
Entity listed: Humpback whale (*Megaptera novaeangliae)*
Classification: Endangered

Recovery Plan or Outline

Name of plan: Final Recovery Plan for the Humpback Whale (*Megaptera novaeangliae)*
Date issued: November, 1991
Dates of previous revisions: N/A

IV. SPECIES DESCRIPTION AND ZOOGEOGRAPHY

Humpback whales are large, globally distributed, baleen whales with long pectoral flippers, distinct ventral fluke patterning, dark dorsal coloration, a highly varied acoustic call (termed 'song') and a diverse repertoire of behavior. Coloring of the ventral surface varies from white to marbled to fully black. Humpback whale pectoral flippers are typically white in the North Atlantic and black in the North Pacific (Clapham, 2002). Body lengths differ between the sexes with females being approximately 1-1.5m longer than males. The maximum reliably reported body lengths are 17.4 meters for a male and 16.2 meters for a female, both taken in Antarctica (Chittleborough, 1965). The largest individuals recorded at the California whaling stations of Moss Landing and Trinidad were an 18.6m female and a 17.4m male, and though it is unclear how reliable the measurements from these stations are, there is a possibility that individuals of this length existed in unexploited populations (Clapham *et al.*, 1997). Mean lengths from reliable large data sets appear to be 13-15m (Chittleborough, 1965; Mikhalev, 1997). Adult body weights in excess of 40 tons (Ohsumi, 1966) make them one of the largest mammals on earth.

Though numerous subspecies of humpback whales were named historically, they are not widely recognized and *Megaptera novaeangliae (Borowski, 1781)* remains the accepted taxonomic classification. Thorough reviews of known taxonomic listings for humpback whales are presented in Clapham & Mead (1999) and Rice (1998).

The mating system for humpback whales is generally thought to be male-dominance polygyny, also described as a 'floating lek' (Clapham, 1996). In this system, multiple males compete for individual females and exhibit competitive behavior. Humpback 'song' is a long, complex vocalization (Payne and McVay, 1971) produced by males on the winter breeding grounds, and also less commonly, on migration (Cato, 1991; Clapham and Mattila, 1990) and seasonally on feeding grounds (Clark and Clapham, 2004). Behavioral studies suggest that song is used to advertise for females, and/or to establish dominance among males (Darling and Bérubé, 2001; Darling *et al.*, 2006; Tyack, 1981).

V. DIFFERENTIATION/DISTINCTIVENESS OF SOUTHERN AND NORTHERN HEMISPHERE POPULATIONS

Individual humpback whales in the Southern Hemisphere differ from those in the two Northern Hemisphere oceans in the patterning and extent of ventral fluke and lateral pigmentation (Rosenbaum *et al.*, 1995), as well as in the timing and location of reproduction. Observations indicate that mating occurs six months apart in the two hemispheres. Differing estimates of testis weight from the breeding and feeding grounds (and no spermatozoa detected on feeding grounds; Symons and Weston, 1958) indicate that there is seasonal variation in sperm production (Chittleborough, 1965; Omura, 1953), further supporting the asynchrony of seasonal mating between the Northern and Southern Hemisphere populations. Ovulation is also seasonal (Chittleborough, 1957), suggesting that if individual whales travel between the hemispheres outside their usual estrus period, this seasonality may prohibit successful reproduction. However, encounters on common breeding grounds between whales at the very end or start of their respective winter breeding seasons e.g. in Panama and Costa Rica, may result in successful reproduction.

In the southeastern Pacific Ocean some southern-summering humpback whales migrate to Northern Hemisphere breeding grounds in waters off Central and South America (e.g. Acevedo and Smultea, 1995; Flórez-González *et al.*, 1998; Rasmussen *et al.*, 2007; Stone *et al.*, 1990), a region which may be frequented by whales from North Pacific Ocean populations during the winter (Acevedo and Smultea, 1995). It is therefore possible that inter-hemispheric migratory movements and/or mating events take place between populations along the Pacific coast, although there is no genetic, satellite telemetry or sightings evidence for exchange yet detected in this region (Baker and Medrano-González, 2002). A similar pattern occurs in the southeastern Atlantic, where southern-summering humpback whales have been sighted and stranded in Central West African countries as far north as 6°N, including Benin, Ghana and the eastern Ivory Coast (Rosenbaum and Mate, In Review; Van Waerebeek, 2003; Van Waerebeek *et al.*, 2007; Van Waerebeek *et al.*, 2009). The southerly extent of the eastern North Atlantic humpback breeding ground is not well described, although whales found in the Cape Verde Islands (14°N) are geographically distant from the known distribution of Southern Hemisphere humpback whale populations. As in the Pacific, there is no genetic, satellite telemetry or sightings evidence for exchange detected in this region.

Genetically, humpback whales in the three ocean basins cannot be defined as ‘evolutionary significant units’ or ESUs as based on the criteria of Moritz (1994) because mitochondrial DNA is not reciprocally monophyletic among the ocean basins, *i.e.*, the genetic lineages in each northern ocean do not share a recent common ancestor and are nested among the Southern Hemisphere lineages. The global pattern of maternally inherited DNA indicates the occurrence of more than one historical introgression into each of the Northern Hemisphere ocean basins from the Southern Hemisphere, with multiple Northern Hemisphere clades (closely related DNA lineages) nested within the Southern Hemisphere clade (Baker and Medrano-González, 2002; Baker *et al.*, 1993). However gene flow between the Northern and Southern Hemispheres is very limited, estimated at 1-2 females per generation (Baker and Palumbi, 1997). Such limited gene flow strongly suggests both ecological and evolutionary differentiation under a variety of population differentiation criteria (Waples and Gaggiotti, 2006).

VI. NATURAL HISTORY

For the remainder of the document, humpback whale populations occurring in the Northern and Southern Hemispheres will be described separately. However, we have combined these two regions for the purpose of describing reproduction and mortality, as there are many similarities at this most basic level.

A) Reproduction

Ages of humpback whales killed during the whaling period (before the 1950s, peaking between 1750 and 1950) were originally calculated by counting the laminations (light and dark stripes) which accrue in earplugs (waxy accretions which form in the auditory canal) (Chittleborough, 1959b; Chittleborough, 1965). These counts were calibrated by comparison with seasonal cortical growth of the baleen plates. Cortical growth becomes thicker with age, and the evidence of this is visible and can therefore be 'traced', on the surface of the baleen. Baleen-plate age "truthing" provided an earplug age estimate of two laminations accrued per annum for humpback whales (or two 'Growth Layer Groups' sensu Perrin & Myrick, 1980) (Chittleborough, 1959b). However calibration with baleen plates is complicated and potentially inaccurate, as the characteristic sections of baleen are difficult to interpret and rapidly eroded by wear at the tips (Best, 2006; Chittleborough, 1959b; Robins, 1960). More accurate calibration was later provided by comparing the original earplug laminations with counts of ovarian corpora, since these soft bodies (also known as corpora lutea and corpora albicantia) accrue in the ovaries with each ovulation and thereby provide an alternative means of estimating age for females. A review of the original lamination counts and available age calibration evidence from corpora (Best, 2006) concluded that one lamination is accrued annually, rather than two (a single Growth Layer Group). This re-calibration effectively doubles the original estimated time to sexual maturity for eastern Australian humpback whales, suggesting an average age to sexual maturity of 9-11 years. No other estimates of age to sexual maturity have yet been reported from other Southern Hemisphere breeding grounds. In the Northern Hemisphere, sexual maturity has been estimated at 5-11 years of age and appears to vary both within and among populations (Clapham, 1992; Gabriele *et al.*, 2007b; Robbins, 2007).

In the Southern Hemisphere, most information on humpback population characteristics and life history was obtained during the whaling period. Post-partum ovulation is reasonably common (Chittleborough, 1965) and inter-birth intervals of a single year have occasionally been recorded. This may be a consequence of early calf mortality; the associated survival rates for annually born calves are unknown in the Southern Hemisphere. In the Northern Hemisphere, calving intervals were found to be between one and five years, though 2-3 years appears to be most common (Steiger and Calambokidis, 2000; Wiley and Clapham, 1993). Mean calving rates are estimated to be between 0.38 and 0.50 calves per mature female per year (Clapham and Mayo, 1990; Steiger and Calambokidis, 2000; Straley *et al.*, 1994) and reproduction is annually variable (Robbins, 2007). Calving rates were observed to be higher on breeding grounds than feeding grounds (Baker *et al.*, 1987); this likely reflects either sampling bias or neonatal mortality, or both.

Gestation is 11-12 months, and calves are born in sub-tropical waters (Matthews, 1937). Lactation is 10.5-11 months (Chittleborough, 1965), while weaning begins to occur at about age six months and calves attain maternal independence around the end of their first year (Clapham and Mayo, 1990). In the Northern Hemisphere, humpback whales exhibit maternal fidelity to specific feeding regions (Baker *et al.*, 1990; Martin *et al.*, 1984), but this has yet to be confirmed in the Southern Hemisphere.

The sex ratio of adults is roughly 1:1 males:females; surveys of fetal sex ratios from Western Australia and the Antarctic were slightly biased towards males (1.02:1-1.04:1, Chittleborough, 1957) but it is not known if juvenile survival or abortion rates are equivalent between sexes (Chittleborough, 1957). Where it has been studied, sex ratios were found to be at parity across age classes (Gulf of Maine feeding ground and Hawaii breeding ground) (Clapham *et al.*, 1995; Glockner-Ferrari and Ferrari, 1990).

The oldest known humpback whale was documented by Chittleborough (1965); reanalysis of his ear-plug lamination data using an accumulation rate of one Growth Layer Group per year suggests this whale was ~95 years of age when killed. The average generation time for humpback whales (the average age of all reproductively active females at carrying capacity) has been estimated at 21.5 years, based on a compilation of some of the life history parameters reviewed above (Taylor *et al.*, 2007). Estimated annual rates of population increase range from 0-4% to 12.5% for different times and areas throughout the range and in the Northern Hemisphere (Baker *et al.*, 1992; Barlow and Clapham, 1997; Clapham *et al.*, 2003a; Steiger and Calambokidis, 2000); however, it is generally accepted that any rate above 11.8% per year is biologically impossible for this species (Zerbini *et al.*, 2010).

B) Mortality

Annual adult mortality rates between 0.049 and 0.037 have been estimated for the Gulf of Maine and the North Pacific Hawaiian Islands populations (Barlow and Clapham, 1997; Mizroch *et al.*, 2004). In the Southern Hemisphere, estimates of adult survival have been made using photo-identification sightings in Hervey Bay, East Australia (1987-2006) and range between 0.87-1.00 (Chaloupka *et al.*, 1999). Sex-specific survival has been studied on two humpback whale feeding grounds to date, with conflicting results. Adult survival was found to be lower for females than for males in the Gulf of Maine, with both primiparous and parous females exhibiting reduced average annual survival after calving (Robbins, 2007). By contrast, adult female survival was found to be slightly higher than male survival in the Gulf of St. Lawrence (Ramp *et al.*, 2010). The reason for these differences has not yet been determined.

Calf (6 months and older) survival estimated for the Gulf of Maine was low (0.664 (95% CI: 0.517-0.784) and annually variable (Robbins, 2007). Barlow and Clapham (1997) estimated a theoretical calf mortality rate of 0.125 on the Gulf of Maine feeding ground. Using associations of calves with identified mothers (newborn calves are not uniquely identifiable) on North Pacific breeding and feeding grounds, Gabriele (2001) estimated 6-month mortality to be 0.182 (95% confidence intervals (CI) 0.023-0.518). No estimates of neonatal survival (0-6 months) are yet available for Southern Hemisphere humpback whale populations due to the logistical difficulty of surveys and absence of defined feeding areas for most populations. Survival of calves (6-12 months) and juveniles (1-5 years) has not been described in detail for the Southern Hemisphere. A summary of published life history parameters for humpbacks whales is provided in Zerbini *et al.* (2010).

C) Distribution and migratory patterns

1. Northern Hemisphere

In the Northern Hemisphere, humpback whales summer in the biologically productive northern higher latitudes and travel south to sub-tropical and tropical waters in winter to mate and calve. Migratory routes and behavior are likely to be maternally directed (Baker *et al.*, 1990; Martin *et al.*, 1984). Feeding areas are often near or over the continental shelf and associated with cooler temperatures and oceanographic or topographic features that serve to aggregate prey. Discovery tags first helped to elucidate the migratory linkages of humpback whales between their feeding and breeding areas (Dawbin, 1956b; Ivashin, 1983). Initial hypotheses regarding distribution and migration suggested that stocks traveled north-south near coastlines between their two seasonal areas. It is now clear, however, that many humpback whales make pelagic migrations, and some routes are not in simple north-south trajectories.

Feeding areas in the North Pacific Ocean range widely in latitude from California north into the Bering Sea. There are at least four known breeding areas in the North Pacific Ocean (with different subareas) including the western Pacific Ocean and waters off the Hawaiian Islands, Mexico and Central America. Some of these areas have a high degree of internal population structure and may warrant further division.

Primary humpback whale feeding areas in the North Atlantic Ocean range from 42-78°N and include waters around Iceland, Norway and the Barents Sea in the eastern Atlantic Ocean and West Greenland, Newfoundland, Labrador, in the Gulf of St Lawrence and the Gulf of Maine in the western North Atlantic Ocean. Breeding areas occur in the West Indies and (to a much lesser extent) around the Cape Verde Islands.

Recently, a few humpback whales have also been found in the Mediterranean, but little is known about humpback whale use of this region and there is no evidence for a large humpback whale presence there, either currently or in historical times (Frantzis *et al.*, 2004). There are also sporadic sightings of humpback whales in a wide range of places including waters offshore from the southeast US and mid-Atlantic states, in the Gulf of Mexico and in the waters around Ireland. Bermuda is a known mid-ocean stopover point for humpback whales on their northbound migration (Stone *et al.*, 1987).

2. Southern Hemisphere

Migratory movements of Southern Hemisphere humpback whales were originally identified by Kellogg (1987), who described the migrations of six stocks; two for each of the three Southern Hemisphere ocean basins. As the whaling trade developed global momentum in the twentieth century, the International Whaling Commission (formed in 1946) divided the Southern Ocean feeding grounds into six Management Areas, based on regions where the greatest concentrations of baleen whales had been caught (various maps summarized in Mackintosh (1965)). Management Areas (I-VI) were initially considered more representative of fin and blue whale concentrations than of humpback whales, catches of which were more evenly distributed around the southern ocean (Mackintosh, 1965). When humpback whales were later considered as stocks for the purposes of management, the six purported migratory populations were associated with distinct concentrations of humpback whale catches found within Management Areas I-V (populations were named Groups I-V by association with each Area). Area II contained two distinct concentrations of catches, which were associated with the two South Atlantic stocks (Groups IIa and IIb). There was at the time little information regarding humpback concentrations in the central Pacific Area VI (Chittleborough, 1959a; Mackintosh, 1942).

The best assessment of the current winter distribution of humpback whales (May to September) in the Southern Hemisphere is shown in Figures 1-8. As elsewhere in the world, humpback breeding grounds occur in relatively shallow temperate or sub-tropical waters (e.g. coastal or reef systems). Migration towards breeding grounds appears to peak at slightly different times for different reproductive classes, with lactating females traveling north earliest, immature whales preceding mature males and 'resting' (non-pregnant and non-lactating) females, and finally pregnant females migrating last (Chittleborough, 1965; Dawbin, 1966). The staggering of age/sex classes of migrating humpback whales towards higher latitudes has been less well examined, but available evidence suggests that pregnant whales travel south earliest while lactating females migrate last. Some individuals (most likely non-pregnant, non-lactating females) may not always migrate, as winter observations of both sexes of humpback whales on high-latitude feeding grounds have been made (e.g. Matthews, 1937) and sex ratios among some migrating humpback whales are strongly male-biased (e.g. 2.1:1 males to females, Brown *et al.*, 1995; Chittleborough, 1965). However the sex ratio biases may also reflect differences in the availability of the two sexes, given that females have shorter wintering ground residency times than males, on average. A number of migratory 'corridors' for humpback whales are known, characterized by brief residency times and traveling behavior (sustained swimming in a given direction, and little or no activity in when tail flikes are raised above the surface that possibly suggesting a relatively deep dive). Migratory corridors in the Southern Hemisphere include waters off New Zealand, Eden and Point Lookout in Australia, Norfolk Island and the Cook Islands in the South Pacific. In addition, there are many regions where migratory behavior is seen occurring simultaneously with breeding and calving behavior, including the coasts of western South Africa, east South Africa, east Australia and Western Australia. During the austral summer (November to March) humpback whales are distributed throughout the waters of the Southern Ocean, associated with marginal sea ice and regions of Antarctic krill density[1].

D) Feeding

1. *Northern Hemisphere*

Humpback whales are 'gulp' feeders, taking in large, discrete mouthfuls of prey during feeding rather than continuously filtering food, as may be observed in some other large

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[1] Excepting the northern Indian Ocean stock

baleen whales (Ingebrigtsen, 1929). Humpback whales have a diverse diet that appears to vary slightly across feeding aggregation areas. The species is known to feed on both small schooling fish and on euphausiids (krill). Known prey organisms include species representing *Euphausia, Thysanoessa, Meganyctiphanes, Clupea, Scomber, Ammodytes, Sardinops, Engraulis and Mallotus* (Baker, 1985; Clapham *et al.*, 1997; Geraci *et al.*, 1989). Humpback whales also exhibit flexible feeding strategies, sometimes foraging alone and sometimes cooperatively (Clapham, 1993). In the Gulf of Alaska, stable groups of feeding whales have been observed to persist for multiple weeks but do not appear to be genetically related (Perry *et al.*, 1990). This group stability does not seem to be the norm across all feeding areas in the Northern Hemisphere.

Feeding behavior is varied as well and frequently features novel capture methods involving the creation of bubble structures to trap and corral fish; bubble nets, clouds and curtains are often observed when humpback whales are feeding on schooling fish (Hain *et al.*, 1982). Lobtailing and repeated underwater 'looping' movements have also been observed or recorded during surface feeding events, and it may be that certain feeding behaviors are spread through the population by cultural transmission (Friedlaender *et al.*, 2009; Weinrich *et al.*, 1992). On Stellwagen Bank, repeated side rolls were recorded when whales were near the bottom, which likely serves to startle prey out of the substrate for better foraging access (Friedlaender *et al.*, 2009). In many locations, feeding in the water column can vary with time of day, with whales bottom feeding at night and surface feeding during the early daylight hours (Friedlaender *et al.*, 2009).

2. Southern Hemisphere

In the Southern Hemisphere, only one style of foraging ('lunge' feeding) has been reported. When lunge feeding, whales advance on prey with their mouths wide open, then close their mouths around the prey and allow water to pass out through the baleen plates. Southern Hemisphere humpback whales (excluding those in the northern Indian Ocean[2]) forage in the Antarctic circumpolar current, feeding almost exclusively on Antarctic krill (*Euphausia superba*) (Kawamura, 1994; Mackintosh, 1965; Matthews, 1937)[3]. Analyses of stomach contents during the whaling period suggest that occasional feeding on non-euphausiid species in the Antarctic is incidental rather than deliberate (Mackintosh, 1965).

During the austral winter, humpback whales subsist on stored fat and usually do not feed; stomachs examined in sub-tropical waters and on migratory routes during the whaling era were nearly always found to be empty (Chittleborough, 1965). Whether this is because humpback whales rarely encounter prey patches of sufficient size or density to make feeding worthwhile, or whether all energy is devoted to the processes of breeding and calving has not been determined (see Baraff, 1991); however, the substantially lower biological productivity of most sub-tropical waters suggests the former. Infrequent sightings of feeding activity and stomach content data suggest that some individuals may feed opportunistically during the southward migration towards Antarctic waters (e.g.

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[2] This stock is non-migratory

[3] An alternative euphausiid food source, *Thysanoessa macrura* may also be foraged where it is abundant in Areas VI and I, (Nemoto, 1959), but no direct evidence of this has been presented for humpbacks

crustacean *Munida gregaria* in NZ and southern South America (Matthews, 1932), euphausiid *Nyctiphanes australis* in Foveaux Strait (Dawbin, 1956a), euphausiids *Euphausia recurva*, *Euphausia diomedeae* and *Thysanoessa gregaria* in South Africa (from Donkergat whaling station in 1962 and 1963, reviewed in Kawamura (1980))[4].

Antarctic krill tend to be most highly concentrated around the marginal sea ice zone, where they feed on sea ice algae. In turn, Southern Hemisphere humpback distribution is linked with regions of marginal sea ice (Friedlaender *et al.*, 2006) and zones of euphausiid density (Murase *et al.*, 2002), with prey foraging mainly concentrated in the upper 100m of the water column (Dolphin, 1987; Friedlaender *et al.*, 2006). Little is presently known regarding humpback prey interactions in Antarctic waters. However the accessible coastal waters of the western Antarctic Peninsula have allowed detailed studies of prey-predator interactions among baleen whales and krill. A positive relationship of humpback relative abundance with abundance of krill >30mm in length suggests that humpback whales mostly forage for krill age class 2+ (Friedlaender *et al.*, 2008). There is also evidence for a positive relationship between prey density and humpback abundance (Friedlaender *et al.*, 2006).

VII. THREATS AND POTENTIALLY ADVERSE EFFECTS FROM HUMAN ACTIVITIES

The following section identifies and describes global factors believed to have some adverse affects on humpback whales, as well as management measures that are currently in place to mitigate these impacts. Modern whaling caused substantial declines in all humpback whale populations in the mid 20th century, but since the 1966 ban on commercial humpback whaling, whaling is no longer a significant factor impeding recovery. Instead, humpback whale recovery is potentially impacted by a variety of other factors including proximity to dense areas of human habitation, shipping traffic, oil and gas exploration, and fishing activities. Various human activities may give rise to effects from water pollution, increased noise levels, entrapment or entanglement in fishing gear, habitat degradation, ship strikes and whale watching and subsistence hunting. The changing oceanic environment may slow recovery by reducing reproductive output, survival and habitat availability for humpback whales. Threats specific to particular regions are detailed in the sections pertaining to those regions.

A) Anthropogenic Impacts

1) Ship Strikes

Ship strikes (defined here as collisions between any part of a water craft and a live cetacean) often result in life-threatening trauma or death for the cetacean. Impact is often initiated by forceful contact with the bow or propeller of the vessel. Ship strikes on humpback whales are typically identified by evidence of massive blunt trauma (fractures of heavy bones and/or hemorrhaging) in stranded whales, propeller wounds (deep slashes or cuts into the blubber) and fluke/fin amputations on stranded or live whales (e.g. Wiley

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[4] Other incidental reports suggest occasional feeding on clupeoids and stromateoids.

and Asmutis, 1995). The most frequently reported strikes involving all large whale species result from vessels over 80m in length, travelling at 14 knots or faster (Jensen, 2003; Laist *et al.*, 2001).

Humpback whales are the second-most commonly reported victims of vessel strikes (following fin whales). At present, there are >143 recorded ship strikes involving humpback whales worldwide (Van Waerebeek and Leaper, 2008); however the reported number is likely not a full representation of the actual number (particularly in the Southern Hemisphere) as many likely go undetected or unreported (Van Waerebeek *et al.*, 2006). Ship strike injuries were identified for 8% (10 of 123) of dead stranded humpback whales between 1975-1996 along the US mid-Atlantic and southeast states (south of the Gulf of Maine) (Wiley and Asmutis, 1995). When cause of death could be determined, ship strikes made up 4% of observed humpback whale deaths in 2001-2005 (Nelson *et al.*, 2007) and 2003-2007 (Glass *et al.*, 2009) along the US east coast, Canadian Maritimes and Gulf of Mexico region. Again, the true rate may be higher since not all strike injuries are detected or reported. Among strandings along the mid- and southeast US during 1975-1996 for which body length data were available, all 25 were estimated to be of immature whales based on length at death (<11m, Wiley and Asmutis, 1995), suggesting that young whales may be disproportionately affected. However, those waters are thought to be used preferentially by young animals (Barco *et al.*, 2002; Swingle *et al.*, 1993). It should be noted that ship strikes do not always produce outward injuries and may therefore be underestimated for strandings that are not examined for internal injuries.

Examination of 130 records of large whale strandings in Washington State found nineteen with evidence of ship strikes. Only one of these strandings was of a humpback whale despite high abundances of feeding humpback whales in the shipping lanes of this area (Douglas *et al.*, 2008). It was concluded that the dramatic inter-species differences in observed ship strike rates were a function of the species' vulnerability to a strike and their likelihood of being caught on the bow of a ship and being brought in to a port (Douglas *et al.*, 2008).

Whale strikes have been formally recognized as an environmental problem since 1998, when National Marine Fisheries Service and the United States Coast Guard established Mandatory Ship Reporting systems. The systems require ships to report their approach to US ports in designated areas; the ships then receive a return message with information on right whales in the area. Since then many studies have been carried out by the US, Canada and other nations to engender a better understanding of the causes and frequency of ship strike events (e.g., Jensen, 2003; Silber *et al.*, 2009). Reporting of ship strikes is highly variable internationally, with reports required from vessels in the domestic waters of Australia, USA and New Zealand but not in other countries, such as Madagascar, Mozambique, Oman, Colombia and most South Pacific island nations. Mitigation measures to reduce ship strikes have been considered by the International Maritime Organization Marine Environment Protection Committee (IWC, 2010). General whale strike mitigation measures currently in place for some vessels and regions include using dedicated observers (Weinrich and Pekarik, 2007), speed reduction in areas of critical habitat, and shifting of shipping lanes away from areas of whale concentration to accommodate humpback whales and other species (IMO, 2007). Passive acoustic monitoring in areas of high shipping traffic also has promise, as this method is relatively inexpensive, although detection is limited to vocalizing whales and specific source locations can be hard to determine (Silber *et al.*, 2009).

To address the current deficit in monitoring and reporting of ship strikes, a centralized international database on ship strikes was formed in 2007 and is being compiled and curated by the International Whaling Commission Scientific Committee Ship Strikes Working Group (IWC, 2007b). There are 131 reports of humpback strikes included in this database to date (Leaper pers. comm.). It is hoped that the international database will improve the degree of reporting of such incidents, although it must be noted that reporting is not mandatory in many places. Vessel traffic has increased rapidly since the 1960s (Laist *et al.*, 2001), and ship strikes could shortly constitute a major threat to whales congregating or migrating through areas of high traffic (see Sections X and XI). Apart from ship strikes, disturbance of breeding, calving, feeding and resting behavior may reduce the biological fitness of the population, although the degree of this impact is at present poorly understood.

Among ship strike incidents, reports of humpback collisions with sailing vessels have also been increasing rapidly over the last five decades (Ritter, 2009). In a survey of reported cetacean collisions worldwide, Ritter (2009) noted that sailing vessel speeds in the range of 5-10 knots and vessels with monohulls were common to many of the collision reports and that the majority of collisions were with humpback whales.

2) Anthropogenic Sound

Anthropogenic sound has increased in all oceans over the last 50 years and is thought to have doubled each decade in some areas of the ocean over the last 30 or so years (Croll *et al.*, 2001; Weilgart, 2007). Low-frequency sound comprises a significant portion of this and stems from a variety of sources including shipping, research, naval activities and oil and gas exploration. Understanding the specific impacts of these sounds on mysticetes, and humpback whales specifically, is difficult. However, it is clear that the geographic scope of potential impacts is vast, as low-frequency sounds, especially, can travel great distances under water. Low-frequency active sonar (LFA), used by the United States Navy to detect submarines, may result in a 2.4-million-square-mile area of ensonification within which received levels of 120 decibels (dB) and above can be heard (Johnson and Tyack, 2003); although the effects on biological systems are not known. Seismic surveys (loud pulsed sounds are used to detect oil and gas deposits under the sea floor) can raise noise levels two orders of magnitude over background noise levels within a 186,000-square-mile area surrounding the source (IWC, 2005a).

It does not appear that humpback whales are often involved in strandings related to noise events. There is one record of two whales found dead with extensive damage to the temporal bones near the site of a 5,000kg explosion which likely produced shock waves that were responsible for the injuries (Weilgart, 2007). Other detrimental effects of anthropogenic noise include masking and temporary threshold shifts (TTS). Masking results from noise interfering with cetacean social communication, which may range greatly in intensity and frequency. Some adjustment in acoustic behavior is thought to occur in response to masking; humpback whale songs were found to lengthen during LFA sonar activities (Miller *et al.*, 2000). This altered song length persisted two hrs after the sonar activities stopped (Fristrup *et al.*, 2003). TTS is a temporary loss in hearing capability. Hearing loss can also be permanent if the sound is intense enough, but there is great variability across individuals and other factors making it difficult to determine a standardized threshold.

Excessive noise exposure may be damaging during early individual development, may cause stress hormone fluctuations, and/or may cause whales to leave an area or change their behavior within it (Weilgart, 2007). Some responses are subtle and may occur after the exposure. Humpback whales exposed to underwater explosions and drilling associated with construction activities did not appear to change their behavior in reaction to the surveys but did appear to have reduced orientation abilities. Higher rates of fatal entanglement in fishing gear were observed in the area, though the cause for this elevated entanglement rate was unclear (Todd, 1996). Some studies have found little reaction to noise and indicate potential tolerances to anthropogenic sound over short time and space scales (Croll *et al.*, 2001). In one study, blue and fin whales did not appear to avoid LFA sonar, nor did it appear to disrupt foraging (Croll *et al.*, 2001).

There is likely an important distinction between immediate reactions to noise and long-term effects of noise exposure to populations. The cumulative and synergistic effects may be more harmful than studies to date have been able to assess. Though some have argued that habituation to sound may occur, this can easily be confused with hearing loss or individual differences in tolerance levels (Bejder *et al.*, 2006). Regulations regarding marine mammal sound exposure that are currently in place vary depending on the sound source strength and the species of marine mammal(s) present (Southall *et al.*, 2007).

3) Pollution

The ocean is a repository for a range of halogenated organic pollutants[5] which can persist in the environment for long periods. Air-borne pollutants are particularly concentrated in areas of industrialization, and in some high latitude regions, where they are carried atmospherically from industrial areas and then condense back into the ocean (Aguilar *et al.*, 2002). While many pollutants are now either banned or subject to regulated use in some countries (e.g. DDTs and PCBs), their legacy persists for many years in the marine food chain, bio-accumulating in the highest concentrations in top predators. Use of these chemicals is still unregulated in many parts of world, and they can be transported long distances via oceanographic processes and atmospheric dispersal (Aguilar *et al.*, 2002).

Humpback whales can accumulate lipophilic compounds (e.g., halogenated hydrocarbons) and pesticides (e.g. DDT) in their blubber, as a result either of feeding on contaminated prey (bioaccumulation) or inhalation in areas of high contaminant

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[5] These include dichloro-diphenyl-trichloroethane (DDT), hexachlorocyclohexane (HCH) and chlordane (CH) insecticides, polychlorinated biphenyl (PCB) coolants and lubricants, and polybrominated diphenyl ether (PBDE) flame retardants.

concentrations (e.g. regions of atmospheric deposition) (Barrie *et al.*, 1992; Wania and Mackay, 1993). Some contaminants (e.g., DDT) are passed on maternally to young during gestation and lactation (e.g., in fin whales, Aguilar and Borrell, 1994).

The range and concentration of organic contaminants accumulated by humpback whales biopsy-sampled on Northern Hemisphere feeding grounds has been described by Elfes *et al*. (2010). Across the feeding areas, concentrations were high in some areas (southern California and northern Gulf of Maine), potentially reflecting proximity to industrialized areas in the former case and prey choice in the latter (Elfes *et al.*, 2010). There were also higher levels of polychlorinated biphenyls, polybrominated diphenyl ethers and chlordanes in the North Atlantic Ocean (Gulf of Maine and Bay of Fundy) than the North Pacific (California, southeastern Alaska, Aleutian Islands). However the highest levels of DDT were found in whales feeding off southern California, a highly urbanized region of the coast with substantial discharges (Elfes *et al.*, 2010). This same study found a linear increase in PCB, DDT and chlordane concentration with age of the whales sampled. PBDEs were introduced to industrial applications more recently than PCBs, DDT and chlordanes, which may explain the absence of a relationship between concentration and age for this compound. On average, concentrations of these contaminants in humpback whales were low relative to levels found in odontocetes (O'Shea and Brownell, 1994). At present little information on levels of contamination is available from humpback whales on Southern Hemisphere feeding grounds.

The health effects of different doses of contaminants are currently unknown for humpback whales (Krahn *et al.*, 2004). There is evidence of detrimental health effects from these compounds in other mammals, namely disease susceptibility, neurotoxicity, reproductive and immune system impairment (DeSwart *et al.*, 1996; Eriksson *et al.*, 1998; Reijnders, 1986). Contaminant levels have been proposed as a causative factor in lower reproductive rates found among humpback whales off southern California (Steiger and Calambokidis, 2000), but at present the threshold level for negative effects, and transfer rates to calves, are unknown for humpback whales. For humpback young of the year biopsy-sampled in the Gulf of St. Lawrence, Metcalfe *et al*. (2004) found PCB levels similar to that of their mothers and other adult females, indicating that bioaccumulation can be rapid and that transplacental and lactational partitioning did little to reduce contaminant loads.

There is very little known about the effects of oil or petroleum on cetaceans and especially on mysticetes. Oil can be inhaled at the surface, can coat skin, eyes and baleen, and can contaminate prey (Pomilla *et al.*, 2004). Polycyclic aromatic hydrocarbons (PAHs) are components of crude oil which are not easily degraded and are insoluble in water, making them quite detrimental in the marine environment (Pomilla *et al.*, 2004). PAHs have been associated with proliferative lesions and alteration to the immune and reproductive systems (Martineau *et al.*, 2002). Expression of the CYP1A1 gene has been identified in cetaceans in response to exposure to PAHs and halogenated aromatic hydrocarbons (HAHs) and has been used as a biomarker of contamination exposure (Teramitsu *et al.*, 2000). Angell *et al.* (2004) found significant variability of CYP1A1 expression between humpback whale populations across regions in the western North

Atlantic Ocean. Additionally, a comparison of CYP1A1 expression in humpback whales and odontocetes in the western North Atlantic did not find significantly higher levels in the odontocetes sampled as would have been expected based on other studies of HAHs. Though this finding could signify relatively comparable levels of contaminants in humpback whales and the sampled odontocete species, it may also be due to physiological differences in CYP1A1 response (Angell *et al.*, 2004).

Pollution from untreated industrial and domestic wastewater has been implicated as a causal factor for algal blooms, some of which are detrimental to marine organisms. Toxins produced by different algae can be concentrated as they move up the food chain, particularly during algal blooms. Naturally occurring toxin poisoning can be the cause of whale stranding events and is particularly implicated when unusual mortality events occur (unusually large numbers of whales stranding in close proximity and in a relatively short time frame, exhibiting similar or unusual pathological or clinical states or an abnormal physical condition). The best documented unusual mortality event attributable to disease occurred in 1987-1988 in the North Atlantic, when at least 14 mackerel-feeding humpback whales died of saxitoxin poisoning (a neurotoxin produced by some dinoglagellate and cyanobacteria species) in Cape Cod, Massachusetts (Geraci *et al.*, 1989). Three unusual mortality events have since been reported, all on the US East Coast. In the Gulf of Maine in 2003, 16 humpback whale carcasses were found and saxitoxin and domoic acid (produced by certain species of diatoms, a different type of algae) were detected in a portion of the few individuals that could be sampled (Gulland, 2006). Regional-level stranding networks and sampling protocols in many countries (USA, Canada, Bahamas, Oceania, Australia) can provide the means for monitoring trends in humpback whale mortality events and their causes, but there is still a great need for better diagnostic testing of marine mammal tissue samples from these stranding events to determine the cause of death (Gulland, 2006).

4) Tourism and Research Activities

Whale-watch tourism is a global industry with major economic value for many coastal communities (O'Connor *et al.*, 2009). It has been expanding rapidly since the 1980s (estimated 3.7% global increase in whale watchers per year between 1998-2008, O'Connor *et al.*, 2009), with great variation in the extent of regulation and intensity of the activity among regions (Hoyt, 2000). Whale watching operations have been documented in 119 countries worldwide as of 2008, including on many humpback whale feeding grounds, breeding grounds and migratory corridors (O'Connor *et al.*, 2009).

A meta-analysis of published literature concerning the effects of whale-watch boats on cetaceans found the most common reported response of humpback whales was increased swimming speed during exposure; there was little evidence of significant effects on inter-breath intervals and blow rates (Weinrich *et al.*, 2008). Passive acoustic monitoring and localization of humpback whale song in the presence of whale-watch boats also found that whales moved away from the boat in the majority of cases, (68.4% of the time when boats were less than 2.5 miles distant, Sousa-Lima and Clark, 2009). Analyses using passive acoustic monitoring have also found a significant negative effect of boat presence on humpback whale song activity; *i.e.*, boats were the only significant (non-zero) negative interaction term in a multivariate model exploring the interaction of humpback whale singers with a number of other environmental factors such as light, moon and time of day (Sousa-Lima and Clark, 2008).

Only one study has attempted to assess the population-level effects of whalewatching on humpback whales, as the relevant parameters are very difficult to measure. Weinrich and Corbelli (2009) reported that calving rate and calf survival to age two did not seem to be negatively affected by whale watching on a subset of the Gulf of Maine feeding ground (Stellwagen Bank). Some of the negative effects of boat exposure may potentially be cumulative over a season or years due to acoustic masking (see '*Ship Strikes*' section). Additionally, in areas of heavy ship traffic, isolating the impacts of whale watching on biological parameters is difficult and may be inconclusive (Weinrich and Corbelli, 2009) and difficult to determine at either the individual or population level.

Efforts to manage whale watching operations have included limiting the number of whale watching vessels, limiting vessel approach distances to whales, specifying the manner of operating around whales and establishing limits to the period of exposure of the whales. In some areas whale watching industries operate under regulations, while other operate under guidelines or are still unregulated (e.g. New Caledonia, Réunion in northern Indian Ocean), and this industry is still growing rapidly in many areas (over 10% per year in Oceania, Asia, South America, Central America and the Caribbean). Other potential impacts from whale watching also include exposure to anthropogenic noise and the possibility of ship strikes (discussed in the '*Ship Strikes*' and '*Anthropogenic Sound*' sections). The ACCOBAMS (Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contigous Atlantic Area) has published a thorough review of whale watching guidelines in the Atlantic Ocean, the Mediterranean and Black Seas (Carlson, 2009).

Whale-watch boats in some areas carry naturalists affiliated with research groups; they collect data. Data from whalewatching vessels has resulted in contributions to the scientific literature, especially in creating multi-year datasets that allow the tracking of some biological parameters over time. Not all whale watch operations collect data, and coverage varies tremendously by area with the most whale watch-associated data collected in the Gulf of Maine (Robbins, 2000). Though there is the potential for negative impact or interaction of whale watch operations with humpback whales, some whale watch operations have provided valuable insight into the biology and management of observed populations (Robbins, 2000).

5) Fishery Interactions

Entanglement in fishing gear is a documented source of injury and mortality to cetaceans, including humpback whales. Of the nations reporting to the International Whaling Commission between 2003-2008, 64.7% (n=11) noted humpback whale by-catch in their waters (Mattila and Rowles, 2010). Whales have been documented carrying gear by fishery observer programs, opportunistic reports and stranding networks. Some countries (e.g., US, Canada, Australia, South Africa) have well-developed reporting and response networks which facilitate the collection of information on entanglement frequency and impacts. However, such programs do not guarantee that entanglements are detected; fewer than 10% of humpback whale entanglements involving Gulf of Maine humpback whales are reported, despite a strong outreach and response network (Robbins and Mattila, 2004) . Furthermore, opportunistic reports that are not screened by experts do not necessarily yield accurate information about events, including gear type, configuration and original site of entanglement (Robbins *et al.*, 2007b). The likelihood of receiving reports likely varies world-wide due to differences in observer awareness, reporting mechanisms and legal implications (Mattila and Rowles, 2010).

A study of gear removed from whales off the US East Coast showed that 89% involved pots/traps (a slatted or meshed trap placed on the sea floor) or gillnets (Johnson *et al.*, 2005). However, a wide range of gear types were represented, and every part of the gear was found to be capable of entanglement (Johnson *et al.*, 2005). The authors of that study concluded that any line in the water column poses a potential risk of entanglement to humpback whales. This is further supported by the wide range of entangling gear reported in the US North Pacific (Lyman, 2009; Neilson, 2006), Newfoundland (Lien, 1992) and member nations of the International Whaling Commission (Mattila and Rowles, 2010).

More than half of the humpback whale entanglements assessed offshore of the US East Coast involved entanglements around the tail (Johnson *et al.*, 2005). The mouth and flippers are also known attachment sites, but their frequency is more difficult to assess. Scar-based studies have been developed to systematically study the frequency of non-lethal entanglement involving the tail, using techniques that have been ground-truthed from documented entanglement events (Robbins and Mattila, 2001; Robbins and Mattila, 2004). These techniques have been used in the Gulf of Maine (e.g., Robbins *et al.*, 2009; Robbins and Mattila, 2001; Robbins and Mattila, 2004), southeastern Alaska (Neilson *et al.*, 2009) and more broadly across the North Pacific Ocean (Robbins, 2009a; Robbins *et al.*, 2007a). All populations studied in this manner to date have detected individuals with entanglement-related injuries. Annual research in the Gulf of Maine since 1997 has shown that a high percentage of individuals exhibit entanglement injuries and that new injuries are acquired at an average annual rate of 12% (Robbins *et al.*, 2009). A two-year study at southeastern Alaska confirmed frequencies of entanglement injuries that were comparable to that in the Gulf of Maine (Neilson *et al.*, 2009). Research undertaken across the North Pacific as part of the SPLASH project (see the section on the North Pacific for more detail) further suggests that entanglement is pervasive, but that interaction rates may be highest among coastal populations (Robbins et al. 2007; (Robbins, 2009a).

Both eye-witnessed reports and scar-based studies suggest that independent juveniles are significantly more likely to become entangled than adults (Robbins, 2009a). Calves exhibit a lower entanglement frequency, likely due to having less time in which to have encountered gear (Neilson *et al.*, 2009). Sex differences in entanglement frequency have been observed in some locations and time intervals (Neilson *et al.*, 2009; Robbins and Mattila, 2001), but these effects have not persisted in longer studies (Robbins and Mattila, 2004). Entanglement may result in only minor injury or may potentially significantly effect individual health, reproduction or survival. In one study, females with entanglement injuries produced fewer calves than females with no evidence of entanglement; such impacts on reproduction are still under investigation (Robbins and Mattila, 2001). Mark-recapture studies of the fate of entangled whales in the Gulf of Maine suggest that juveniles are less likely to survive than adults (Robbins *et al.*, 2008b). Observed entanglement deaths and serious injuries in that region are known to exceed what is considered sustainable for the population (Glass et al. 2009). However, most deaths likely go unobserved, and preliminary studies suggest that up to 3-4% of the Gulf of Maine population may die each year as a result of entanglements (Robbins *et al.*, 2009).

6) Scientific Whaling and Other Commercial Hunts

An international moratorium on the whaling of all large whale species was established in 1982 by the International Whaling Commission; it took effect in 1986 and affected all member (signatory) nations (paragraph 10e, IWC, 2009). Since the whaling moratorium was put into effect, some nations have continued to hunt whales under Article VIII of the International Convention for the Regulation of Whaling, which allows the killing of whales for scientific research purposes. Three nations originally acquired special permits to carry out scientific whaling: Iceland, Norway and Japan. At present only Japan now pursues scientific whaling, under the programs JARPAII and JARPNII (‘Japanese Whale Research Program under Special Permit in the Antarctic’ and ‘North Pacific’ respectively), while Iceland and Norway hunt whales commercially under objection to the Moratorium (see *Potential Threats: Commercial Whaling*). Scientific whaling is presently unregulated, and no quotas are enforced for this activity (Clapham *et al.*, 2003b). Currently, no humpback whales have been declared as the target of scientific whaling catches, although a take of 50 whales from the Antarctic region has been proposed (Nishiwaki *et al.*, 2007). This proposal has been held in abeyance while the IWC conducts meetings on the “Future of the IWC”, and it is not known if this plan for scientific whaling will be resumed after meetings are completed. However genetic monitoring surveys of Japanese market whale products (1993-2009) have detected tissue from 17 different humpback whales, which suggests that at least this many may have been killed through entanglement or hunting (Steel *et al.*, 2009). In principle, and according to the 1946 Convention, humpback whales could be hunted at any time under the auspices of scientific whaling, with the population impact depending on the magnitude and location of the take.

7) Subsistence Hunting

Current subsistence hunting in the North Atlantic is conducted on the island of Bequia in St Vincent and the Grenadines in the Lesser Antilles (Reeves, 2002). The practice of whaling was not originally part of the local culture but was introduced and influenced by Yankee whaling expertise in the 1870s, with additional expertise imported from Bermuda and Germany (Reeves, 2002). In 1986, St Vincent and the Grenadines asked for a humpback quota from the IWC based on their history of artisanal whaling in the community and the small number of whales taken (Reeves, 2002). Through the late 1980s, it was thought that whaling at Bequia would die out naturally in the near future as there was only a single, elderly harpooner left (Reeves, 2002). However, in 1996, a new whaler and new boat began hunting in Bequia, and Bequia currently retains an IWC quota of up to four whales per season (Reeves, 2002).

A small hunt, not regulated by the IWC, is also thought to exist in the Gulf of Guinea at the island of Pagalu (Aguilar, 1985; Reeves, 2002). No information exists on the fishery past 1975, but as of 1970, whales were still being taken in the area. This practice does not have a clear heritage but it is thought to have been fostered or introduced by the United States in the 18th and 19th centuries (Aguilar, 1985). This hunt employs small boats and primarily targets humpback whale calves. Estimated annual catch is thought to be three or fewer whales.

It does not appear that Tonga had any whale hunt before the introduction of Europeans in the 19th century (Reeves, 2002). Tonga was used as a provisioning station for whaling vessels from the Northern Hemisphere while they operated in the South Pacific. Tongans then began conducting shore-based whaling in the late 1880s or early 1900s, and eventually a taste for whale meat developed, increasing demand and prompting new boats and whalers to enter the growing industry (Reeves, 2002). Catch rates (whales landed) were estimated at 10-20 whales/year for the 1950s and 1960s and at least 3-8 whales/year for the mid 1970s (Reeves, 2002). In 1979 the Tonga Whaling Act was passed, prohibiting the catch of whales on a temporary basis pending the state of the population being assessed by the International Whaling Commission (Reeves, 2002). No whaling has been carried out in Tonga since this time.

Greenland began hunting humpbacks before 1780 (Reeves, 2002). As the take of bowheads decreased from 1750 to 1850, humpbacks became a more frequent target (Reeves, 2002). Only local whalers took humpbacks until 1920, when modern whaling Danish catcher boats were introduced and became important for supplying meat to Greenland and oil to Copenhagen (Reeves, 2002). The subsistence versus commercial nature of Greenland’s hunt has been a point of debate (Reeves, 2002). Though there has not been a take of humpback whales in Greenland waters for approximately two decades, Greenland put in a request to the International Whaling Commission in 2010 for a small quota. Greenland was granted an annual strike limit of 9 whales for the years 2010-2012. An unused quota may be carried forward as long as no more than 2 strikes are added to any annual quota.

B) Non-anthropogenic impacts

1) Parasites

Direct monitoring of species biochemistry and pathology, as used to determine the state of health in humans and domestic animals (e.g. hematology, serum biochemistry, immune function markers), is very limited for humpback whales as for most marine mammals, and there is little published on humpback disease as a result. Humpback whales carry a crustacean ectoparasite (the cyamid *Cyamus boopis*). While the whale is the main source of nutrition for this parasite (Schell *et al.*, 2000), there is little evidence that it contributes to whale mortality. Humpback whales can also carry the giant nematode *Crassicauda boopis* (Bayliss, 1920), which is known to cause a serious inflammatory response (leading to vascular occlusion and kidney failure) in a few balaenopterid species (Lambertsen, 1992).

2) Predation

The most common predator of humpback whales is the killer whale (*Orcinus orca*, Jefferson *et al.*, 1991), although predation by large sharks may also be significant (attacks are mostly undocumented). Rarely, attacks by false killer whales (*Pseudorca crassidens*) have also been reported or inferred.

Predation by killer whales on humpback calves has been inferred by the presence of distinctive parallel 'rake' marks from killer whale teeth across the flukes (Shevchenko, 1975). While killer whale attacks of humpback whales are rarely observed in the field (Ford and Reeves, 2008), the proportion of photo-identified whales bearing rake scars is between zero and 40%, with the greater proportion of whales showing mild scarring (1-3 rake marks) (Mehta *et al.*, 2007; Steiger *et al.*, 2008). This suggests that attacks by killer whales on humpback whales vary in frequency across regions. It also suggests either that (i) most killer whale attacks result in mild scarring, or (ii) that those resulting in severe scarring (4 or more rakes, parts of fluke missing) are more often fatal. Most observations of humpback whales under attack from killer whales reported vigorous defensive behavior and tight grouping where more than one humpback whale was present (Ford and Reeves, 2008).

Photo-identification data indicate that rake marks are often acquired very early in life, though attacks on adults also occur (Mehta *et al.*, 2007; Steiger *et al.*, 2008). Killer whale predation may be a factor influencing survival during the first year of life (Mehta *et al.*, 2007). There has been some debate as to whether killer whale predation (especially on calves) is a motivating factor for the migratory behavior of humpback whales (Clapham, 2001; Corkeron and Connor, 1999). How significantly motivating this factor is also depends on the importance of humpback whales in the diet of killer whales, another debated topic that remains inconclusive in the published literature (Kuker and Barrett-Lennard, 2010; Springer *et al.*, 2003; Wade *et al.*, 2007). No analyses of killer whale stomach contents have revealed remains of humpback whales (Shevchenko, 1975), suggesting that humpback whales comprise a small part of the diet. However these analyses took place during the height of the whaling period, when humpback whales were at a low density and may therefore have been less available for predation.

There is also evidence of shark predation on calves and entangled whales (Mazzuca *et al.*, 1998). Shark bite marks on stranded whales may often represent post-mortem feeding rather than predation *i.e.*, scavenging on carcasses (Long and Jones, 1996).

C) Potential Threats

1) Climate change

There are no known adverse effects to humpback whales from global climate change, although several possible scenarios have been hypothesized and are described here. Rapid

20th century increases in global atmospheric carbon dioxide levels (Solomon *et al.*, 2007) have a number of potential downstream effects, some of which may affect the persistence of humpback whales. Among these, the most significant projected impact is on abundance and distribution of prey.

The density of the Antarctic krill, *Euphausia superba*, near the Antarctic Peninsula shows evidence of substantial decline since the 1970s due to a reduction in winter sea ice and available summer food (Atkinson *et al.*, 2004). These krill are the principal prey for Southern Hemisphere humpback whales, so the effect of decline could be substantial, possibly driving an increase in calving intervals, lowering calf survival or an increase in foraging on alternative prey sources. This effect is likely amplified in Southern Hemisphere regions where feeding areas occur far to the north of the ice shelf *e.g.* South Georgia, South Sandwich Islands, the Magellan Straits, Balleny Islands, since Antarctic krill are recruited at the sea ice edge and disperse northwards over time (Brierley *et al.*, 1999; Ward *et al.*, 1990). Feeding regions with greater geographic distance from krill recruitment sites may therefore be subject to greater fluctuations in seasonal krill abundance. Longer migratory distances between feeding and breeding grounds due to the retreat of ice may also drive changes in seasonal distribution as well as additional prey competition from encroaching warm-water species (Moore and Huntingdon, 2008). However sea ice retreat elsewhere (e.g., the Bering Sea, Overpeck *et al.*, 2005) potentially creates additional habitat for humpbacks, or at least may allow some degree of range expansion towards the poles (Learmouth *et al.*, 2006). If prey abundance and distribution and habitat availability have shifted significantly since the start of the 20th century (prior to modern whaling), this may affect the recovery of humpback whales.

Ocean acidification is the process whereby increasing atmospheric carbon dioxide is absorbed by the ocean and reacts with dissolved carbonates to form carbonic acid, lowering pH and lowering the oceanic load of both carbonates and aragonites (Orr *et al.*, 2005). Carbonates and aragonites are essential components of the ecosystem, as they provide the material for producing calcareous skeletons in nearly all marine fauna. Under predicted levels of oceanic carbon dioxide uptake in the 20th century, under-saturation of carbonate will occur by 2050 in the Southern Ocean (Orr *et al.*, 2005). Saturation levels are affected by water temperature; carbonates are most readily dissolved in warm tropical water and least saturated at the poles (Doney *et al.*, 2009). Studies of the effects of reduced-pH seawater (*i.e.*, water undersaturated with carbonates) on skeletal development in pteropods, echinoderms, corals and notothenoids have all noted a decrease in muscle mass and suggest that there is a greater metabolic cost to growing shells as seawater pH lowers (Doney *et al.*, 2009; Kurihara, 2008). An eight-year study along the coast of the state of Washington, U.S., found a significant decline in pH over time, strongly correlated with population dynamics of calcareous organisms (Wootton *et al.*, 2008). Calcaerous organisms were found to perform more poorly than non-calcareous organisms during low-pH years (Wootton *et al.*, 2008). Studies of Antarctic krill development also indicate a decrease in hatching success under pH conditions ~7.4-7.7 (Kurihara, 2008). It must be noted that all studies of direct effects have been carried out under short-term experimental conditions, and that the ecosystem-level effects of acidification over longer time scales are therefore poorly understood (Doney *et al.*, 2009). However if acidification does adversely influence the development and growth of krill and other planktonic life as suggested by these experiments, then over the coming decades ocean acidification may deplete primary prey resources substantially for humpback whales; and if so, the occurrence and rate may differ in various locations where the rates of acidification differ.

Arctic sea ice is disappearing rapidly, with an annual decrease in summer ice of 7.4% per decade (IPCC, 2007) and some projections indicating a complete loss of late summer sea ice by the end of the current century (Overpeck *et al.*, 2005). Other potential impacts from climate change include increased human incursion into Arctic waters for the purposes of oil and gas exploration, fishing and shipping (Alter *et al.*, 2010). Alter *et al*. (2010) identified seven potential negative impacts of climate change on humpback whales. These include increased threats from ship strikes, bycatch, acoustic disturbance, prey depletion and habitat degradation at high latitudes, habitat degradation in sub-tropical waters as the density of coastal communities increases in response to terrestrial warming and impacts from coastal wind, tide and wave energy developments. Coastal habitat degradation in humpback breeding and calving habitat may also occur as a result of rising sea levels, since flooding of coastal land will bring an increase in the marine influx of sewage and pollutants (Simmonds and Elliott, 2009).

Sub-decadal climate variations driven by El Niño and the North Atlantic Decadal Oscillation also provide a suggestive insight into cetacean responses to climate change over longer timescales (Simmonds and Isaac, 2007). Among the baleen whales, gray whale calf production was found to be positively correlated with the length of time that optimal feeding habitat was free of seasonal ice cover the previous year (Perryman *et al.*, 2002). Studies of calving rates in southern right whales off the coast of Argentina found a strong negative relationship between calving success and anomalously high sea surface temperatures in the previous year (Leaper *et al.*, 2006). It is not known whether humpback whales are similarly influenced by temperature anomalies.

2) Commercial Whaling

Iceland and Norway currently hunt a number of whale species commercially under objection to the IWC moratorium, although humpback whales have not been hunted by either nation in recent years. At present there is an international moratorium on commercial whaling, which will remain in place unless a 75% majority of IWC signatory members vote to lift the moratorium. Following this, under current IWC management procedures, humpback whale stocks considered to be over 54% recovered relative to their pristine (pre-whaling) levels (based on a detailed “comprehensive assessment” of their population status) could be subject to commercial whaling, with a quota determined by the *Revised Management Procedure*. This procedure implements a quasi-Bayesian *Catch Limit Algorithm* to calculate allowable catches for each stock (Cooke, 1992). The effects of these catches on population abundance would be simulated via a series of *Implementation Simulation Trials* prior to agreement of quotas for commercial hunting. Since whaling is carried out under objection by Iceland and Norway, they are not presently subject to this management scheme for allocating quotas for any species.

VIII. REGULATORY BODIES WITH CONSERVATION MANAGEMENT IMPLICATIONS FOR HUMPBACK WHALES

A) International

There are a number of international organizations with conservation management implications for humpback whales. The reader may want to refer to the Marine Mammal Commission's Compendium of International Treaties and Agreements pertaining to marine resources, wildlife and the environment for texts of the treaties (Weiskel *et al.*, 2000).

Antarctic Treaty

The Antarctic Treaty promotes cooperation among countries with interests in the Antarctic. The Protocol on Environmental Protection to the Antarctic Treaty came into force in 1998 and prohibits any commercial activities relating to Antarctic mineral resources. The Protocol has six Annexes, among which Annex II (Conservation of Antarctic Flora and Fauna) is co-incidentally of relevance to humpback whales, restricting 'harmful interference' with any native wildlife. However any targeted hunting of whales in Antarctic waters defers to the International Convention for the Regulation of Whaling, which is upheld by the International Whaling Commission (Article 7, Annex II, see '*International Whaling Commission'* in this Section). Annexes I-IV cover the prevention of marine pollution, waste disposal, assessment of environmental impacts and management of Antarctic Specially Protected or Specially Managed Areas. The combined force of the Protocol acts to minimize habitat degradation and water pollution in humpback feeding areas.

Convention on the Conservation of Migratory Species of Wild Animals (CMS)

The CMS is an intergovernmental treaty within the UN Environment Programme that aims to conserve migratory species throughout their range. There are currently 113 governments party to this convention. Where migratory species are listed as Endangered (Appendix I) or in need of concerted coordination among countries (Appendix II), the Convention works to facilitate the creation of regional Agreements (legally binding treaties) or Memoranda of Understanding among parties within the range of the species. Non-range states may also be parties to the Agreements or MOUs. Humpback whales are currently listed in Appendix I (Convention on the Conservation of Migratory Species of Wild Animals, 2009), categorized as in danger of extinction throughout all or a significant proportion of their range. This listing requires range states to protect humpback whales where they occur, conserve or restore habitats, mitigate obstacles to migration and control other endangering factors.

The International Maritime Organization (IMO)

The IMO is a collection of international conventions, which develop and support the framework for shipping and associated issues of safety, environmental concerns, legal matters, technical co-operation, maritime security and shipping efficiency. There are 169 member states and three associate members in the IMO. The MARPOL convention (International Convention for the Prevention of Pollution from Ships) and the International Conventions on (1) Oil Pollution Preparedness, Response and Co-operation, and (2) Prevention of Marine Pollution by Dumping of Wastes and Other Matter, guide IMO policy pertaining to threats to the marine environment and therefore to marine mammals by proxy.

Issues pertaining to pollution are overseen by the Marine Environment Protection Committee. This committee has the power to designate Particularly Sensitive Sea Areas (PSSA) and 'Areas To Be Avoided' by regular shipping. These are regions considered significant for ecological, economic or scientific reasons and which are thought vulnerable to international maritime activities. PSSA regions include the Great Barrier Reef (Australia), the Galapágos Islands (Ecuador), and the Papahānaumokuākea Marine National Monument in the Northwestern Hawai'ian Islands, all regions of biological significance for humpback whales. The IMO can endorse measures to alter shipping routes to protect PSSAs and Areas To Be Avoided. Areas To Be Avoided have been established in both U.S. and Canadian waters to reduce the threat of ship strikes to whales.

There are also Special areas designated under MARPOL Annexes I, II and V (concerning oil, noxious liquid substances and garbage respectively) where for a given set of oceanographical and ecological conditions and existing sea traffic, there is a need for special additional guidelines for the prevention of the above mentioned sea pollution from shipping traffic. Special Areas covered under these Annexes (with co-incidental relevance for humpback whales) include the Antarctic, Mediterranean, North West European Waters, the Oman area of the Arabian Sea, Caribbean Sea and southern South African waters. The Antarctic is subject to protection from pollution under all three Annexes. The IMO is currently in the process of introducing amendments to MARPOL Annex I which will prohibit the carriage of heavy oils in the Antarctic, except in search and rescue circumstances (IMO, 2009).

The IMO can also issue recommendations regarding ship noise levels and measures for avoiding ship strikes with cetaceans. Voluntary guidelines have been issued for ship quieting technologies (IMO, 2009) and for minimizing ship strikes with cetaceans (IMO, 2008).

The International Union for the Conservation of Nature (IUCN)

The IUCN is an international environmental organization and scientific body which supports the development of laws, policies and best-practice guidelines regarding environmental conservation and sustainable development. The policy of the IUCN is determined by the World Congress of delegates to the IUCN, which are composed of members from the above organizations. Members are able to attend Regional and National Committees and are in return required to support and facilitate the objectives and activities of the IUCN. IUCN's Species Survival Commission is a group of over 7500 volunteers worldwide who form over 100 specialist groups and task forces. Humpback whale status under the IUCN is reviewed by the Cetacean Specialist Group.

The IUCN Red List provides a standardized, objective and explicit series of criteria for determining threat status of species, subspecies and subpopulations. Specialist groups can initiate and update reviews for species, which are categorized as Data Deficient, Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern and Not Evaluated, according to specific scientific criteria applied to each threat category determination. The Red List is thus considered an authoritative index of changes to current biodiversity and is currently the most comprehensive inventory of conservation status for flora and fauna worldwide. The goal of Red List status is to inform governments and provide conservation priorities for natural resource planners by drawing attention to species, subspecies and populations in the greatest need of conservation action and providing a baseline for future conservation measures. The Red List has been used as a biodiversity indicator and authoritative reference for national and international policy and agreements pertiaining to species and ecosystem level conservation, such as the Convention on Biological Diversity (CBD) and the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES).

At present, humpback whales are listed globally as 'Least Concern' under the IUCN criteria for threat status. Small discrete breeding populations in the western North Pacific and west coast of Africa were noted as potentially being subject to local threats to persistence (Irwin, 1992). The 'subpopulations' of humpback whales breeding in Oceania and the northern Indian Ocean are currently considered 'Endangered'. These listing statuses were driven by (1) a median estimated decline of >70% for the Oceania sub-population relative to levels in 1940 (Childerhouse *et al.*, 2008) and (2) the low abundance of humpback whales in the northern Indian Ocean (<100 individuals, Minton *et al.*, 2008a). A proposal has been submitted to IUCN to consider threatened 'subpopulation' status for humpback whales in the western North Pacific; that proposal is currently under review.

The International Whaling Commission

The International Whaling Commission (IWC) is the organization that implements the International Convention for the Regulation of Whaling. Currently the IWC oversees the regulation of the commercial whaling industry for all whale species considered to be at >54% relative to pre-exploitation abundance based on a detailed 'Comprehensive Assessment' of the species catch history and abundance (see Section VII: '*Commercial Whaling*'). Species considered to be at <54% are subject to protection from whaling. Since the moratorium on commercial whaling was declared in 1982, there has been no commercial whaling of humpback whales.

Recent Comprehensive Assessments of some IWC Southern Hemisphere humpback 'stocks' (or discrete breeding/calving grounds; for a more detailed description see '*Section XII: IWC Stocks and definitions*' and Appendix 2) provide estimates of recovery that include levels over 54%. These stocks, 'C' (Western Indian Ocean breeding/calving ground), 'D' (West Australia) and 'G' (Southeastern Pacific), would possibly therefore be subject to regulated whaling were the moratorium to be lifted. The Comprehensive Assessment estimate of recovery for 'A' (Southwestern Atlantic, primarily Brazil) was at 27-34% of pre-exploitation abundance when it was conducted in 2006 leaving this population under protection. Comprehensive Assessments of 'E' (East Australia), 'F'

(Oceania), 'X' (Northern Indian Ocean, primarily Oman) and 'B' (Southeastern Atlantic) have not yet been completed.

The IWC also conducted a Comprehensive Assessment of North Atlantic humpback whales in 2001 and 2002 (IWC, 2002a, 2003a). The results of the assessment were inconclusive and the sub-committee was unable to provide estimates of recovery or advice on the population level in relation to the carrying capacity of the environment. The assessment did conclude that populations were increasing in a number of areas and that the appropriate management unit was the feeding sub-stock (IWC, 2002a, 2003a).

The IWC has also established a series of sanctuaries, which are areas where commercial whaling is in theory prohibited. A 75% IWC voting majority is required to establish sanctuaries. The Indian Ocean sanctuary was established in 1979 and has since been reviewed and renewed three times by the IWC (in 1989, 1992 and 2002). The sanctuary extends south to 55°S and encompasses 20-130°E longitude between Africa and Australia. The Southern Ocean sanctuary was established in 1994 and has since been reviewed and renewed once by the IWC (in 2004). The sanctuary circles the Southern Hemisphere, extending between 40°S and 60°S in all regions except for the Indian Ocean, where the northern boundary meets the southern boundary of the Indian Ocean sanctuary at 55°S. These sanctuaries are periodically reviewed by the IWC.

'Scientific permit' or "special permit" whaling is the practice whereby IWC member nations issue permits to hunt whale species under Article VIII of the International Convention for the Regulation of Whaling. This permit allows the killing of whales for scientific research purposes. Scientific permits override regulations pertaining to the whaling moratorium and to the Southern Ocean and Indian Ocean sanctuaries and are not regulated by quotas. Under Article VIII, whale products from whales taken under scientific permit must be utilized (*i.e.*, sold as various commercial products) after scientific data have been collected. Japan is currently the only nation undertaking scientific permit whaling, although Iceland has also been involved in this activity in the recent past. All permits are subject to periodic review by the IWC, which considers whether the permit has clear aims and reliable methology and whether the collection of data is essential to the management of whale species and other important research questions. However the issuance of each permit is decided by the member nation, rather than the IWC, so these reviews do not necessarily affect the renewal of permits or numbers of whales killed. At present, no humpbacks are taken under scientific permit whaling (although see Section VII: '*Scientific Whaling*').

The North Atlantic Marine Mammal Commission (NAMMCO)

NAMMCO (formed in 1992) is an international body concerned with coordinating the management of hunting and scientific research on marine mammals in the North Atlantic. Decisions are made by the Council, which coordinates recommendations for scientific research, provides whaling management advice and also advises on marine mammal hunting methods. Observers from NAMMCO oversee the whaling and sealing activities of four member nations: the Faroe Islands, Greenland, Iceland and Norway. Hunting of humpback whales has not yet occurred under the authority of NAMMCO, although prior to the whaling moratorium and formation of NAMMCO, these countries did hunt humpback whales. NAMMCO does not currently have the jurisdiction to provide quotas for humpback whales, although there have been recent proposals to change this for large whale species in general (e.g. request from Greenland, refused by the IWC, to take annual quota of 10 humpback whales, NAMMCO, 2008).

B) Domestic

National Oceanic and Atmospheric Administration (NOAA)

Within NOAA exist both the National Marine Fisheries Service and the Office of National Marine Sanctuaries, both of which have management implications for humpback whales.

The Office of National Marine Sanctuaries establishes and administers protected marine areas within US waters. Some of these sanctuaries are important habitats for humpback whales and were, in large part, established because of public interest in this and other large whale species. These relevant sanctuaries include the Hawaiian Islands Humpback Whale National Marine Sanctuary, Stellwagen Bank, Gulf of the Farrallones, Channel Islands, Monterey Bay, Cordell Bank, and the Olympic Coast National Marine Sanctuaries. Fishing is largely unregulated within the sanctuaries, but the dumping of waste material and oil and gas exploration have been prohibited. The Sanctuaries program's authorizing legislation is the National Marine Sanctuary Act.

The Office of Protected Resources (OPR) within the National Marine Fisheries Service is mandated by the Endangered Species Act (ESA) and the Marine Mammal Protection Act (MMPA) to manage and help conserve marine mammal populations within US territorial waters. Organization of management exists on both national and regional levels and includes both scientific and policy branches that coordinate regionally in order to design and implement management measures. The most relevant pieces of legislation for humpback whales are certainly the ESA and the MMPA, but other acts and conventions often have overlapping geographic or legislative goals and mandates, such as the Magnuson-Stevens Fishery Conservation and Management Act, the Coastal Zone Management Act, and the Convention on International Trade in Endangered Species.

The ESA was enacted in 1973 and its goal is to prevent the extinction of endangered species. The MMPA was enacted in 1972 and with certain exceptions it prohibits the take of any marine mammals in US waters or by US citizens on US-flagged vessels. The goal of the MMPA is to maintain marine mammals as functioning elements of their ecosystem. The MMPA also established the Marine Mammal Commission, which provides recommendations to other federal agencies with regard to their marine mammal programs and with regard to Federal actions that may affect marine mammal populations. It is worth noting that these two Acts are some of the more inclusive and sweeping pieces of legislation in US environmental policy.

IX. STATUS OF NORTH ATLANTIC POPULATIONS

In 1992, a large scale international research collaboration called the Year of the North Atlantic Humpback Whale (YONAH) was initiated to study North Atlantic humpback whales on their principal West Indies breeding grounds and selected feeding grounds (Smith *et al.*, 1999). Sampling included two years of photographic identification and biopsy sampling for genetic analysis. Results from YONAH helped to describe the population structure of North Atlantic humpback whales by providing detailed information on movements between breeding and feeding areas. The YONAH project also produced the first basin-wide population estimate (see 'Abundance' section). A subsequent project, MONAH (More North Atlantic Humpbacks) was conducted from 2003 to 2005 to provide a second estimate of abundance from which growth rates can be calculated. Results from this project are expected within the next year.

In 2001 and 2002, the IWC Scientific Committee conducted a Comprehensive Assessment of North Atlantic humpback whales (IWC, 2002a, 2003a). The Committee reviewed existing knowledge of this population and, through examination of whaling records and recent sighting, photographic identification and genetic information, attempted to assess the current status of humpack whales in the North Atlantic (relative to estimated pre-exploitation levels). Much of the information summarized in this section was drawn from that extensive review, but updated as appropriate with newly available information.

A) Distribution and population structure

Feeding Grounds

Principal modern feeding grounds of North Atlantic humpback whales include the Gulf of Maine, eastern Canada (including the Gulf of St Lawrence, Newfoundland and Labrador), West Greenland, Iceland and waters off northern Norway (including Jan Mayen and Bear Island) (Stevick *et al.*, 2006d). Humpback whales are also known to feed in waters around Bermuda, especially during the late winter/early spring, presumably as a stop-over during the northbound migration (Stone *et al.*, 1987). Sightings have been made less frequently in other mid- to high-latitude North Atlantic areas, such as off the US mid-Atlantic states, the Scotian Shelf (Canada), portions of western Europe (especially Ireland) and the Mediterranean Sea. Historic whaling data suggest that humpbacks also fed in summer months in the north-central North Atlantic to the west of the Mid-Atlantic Ridge. The historical density of animals in this area is unclear from the data, but the summer dates of observations suggest it is (or was) unlikely to be just a migratory corridor (Reeves *et al.*, 2004a).

Feeding ground population structure has been a significant focus of regional and ocean-basin-wide studies (Larsen, 1996; Palsbøll *et al.*, 1995; Stevick *et al.*, 2003a). Strong maternally directed fidelity to feeding grounds has been documented through photo-identification of individual whales over periods of years to decades (Clapham *et al.*, 1993; Clapham and Mayo, 1987; Katona and Beard, 1990). There have been few records of exchange between feeding grounds (Katona and Beard, 1990). Exchange that has been documented shows a negative correlation with distance between feeding areas, with neighboring feeding grounds being the most frequent sites for exchange (Stevick *et al.*, 2006d). In its Comprehensive Assessment of North Atlantic humpback whales, the Scientific Committee of the International Whaling Commission concluded that “feeding substocks” were an appropriate management unit in the North Atlantic, but it additionally recognized smaller reproductively (i.e. genetically) distinct management units within larger feeding substocks. (IWC, 2002a).

Primary Feeding Areas

Gulf of Maine

The Gulf of Maine is the southern-most primary feeding aggregation in the North Atlantic. The whales aggregate at a variety of shallow banks, ledges and slopes from the waters off Nantucket to southern Nova Scotia (CeTAP, 1982). Individuals exhibit preferences for specific Gulf of Maine sites but also undertake movements that span the feeding ground (Robbins, 2007). Population distribution also varies within and between years, presumably in relation to prey availability (Payne *et al.*, 1990; Weinrich *et al.*, 1997). Sand lance, *Ammodytes* spp., is thought to be the preferred prey in the southern Gulf of Maine (Overholtz and Nicolas, 1979; Payne *et al.*, 1986), while Atlantic herring, *Clupea harengus,* is thought to be preferred in the north (Paquet *et al.*, 1997; Weinrich *et al.*, 1997). Females and juveniles are more frequently encountered in the southwestern Gulf of Maine, possibly reflecting a preference for sand lance (Robbins, 2007).

A high (>70%) annual resighting rate of individual whales has been documented in the Gulf of Maine (Clapham *et al.*, 1993), and relatively little exchange has been documented with other primary feeding grounds (Katona and Beard, 1990; Stevick *et al.*, 2006d). However, approximately one-quarter of individuals identified on the Scotian Shelf had a prior Gulf of Maine sighting history (Clapham *et al.*, 2003a). Gulf of Maine whales have also been documented at the Gulf of St. Lawrence, Newfoundland, Laborador and West Greenland (Katona and Beard, 1990; Stevick *et al.*, 2006d). Some of these may simply pass through the Gulf of Maine on migration. However, periods of high rates of exchange with eastern Canada have been linked to periods of low prey availability in the Gulf of Maine (Stevick *et al.*, 2006d).

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

The North Atlantic humpback whale population was previously considered a single stock for U.S. management purposes, but the Gulf of Maine was later reclassified as a separate feeding stock (Waring *et al.*, 2000). This decision was based on evidence of strong site fidelity, limited population exchange and significant differences in mtDNA haplotype frequencies relative to other primary feeding populations (Palsbøll *et al.*, 2001).

Scotian Shelf

The Scotian Shelf lies between the Gulf of Maine and the Gulf of St. Lawrence and is less well studied than either area. A photo-identification study undertaken on the Scotian Shelf in 1998-1999 identified 52 individuals. The absence of inter-year matches on the Scotian Shelf over a two-year sampling period suggests the population of whales feeding on the Scotian Shelf is larger than was previously thought (Clapham *et al.*, 2003a). As noted above, 25% of identified individuals had a prior sighting history in the Gulf of Maine (Clapham *et al.*, 2003a). No matches were made to any other feeding areas (Clapham *et al.*, 2003a).

Eastern Canada

Humpback whales are widely distributed in the coastal waters off eastern Canada. The main concentration extends from central Labrador to the Southeast Shoal of the Grand Banks, including southern Labrador, the Strait of Belle Isle, the eastern and southeastern coasts of Newfoundland and several offshore banks (Kingsley and Reeves, 1998; Whitehead, 1983). Humpback whales also occur in the Gulf of St Lawrence, especially between the mainland of Quebec and Anticosti Island (Gauthier and Sears, 1999). Recent photo-identification studies suggest that the Gulf of St. Lawrence, Newfoundland and Labrador comprise a single population based on levels of exchange (Stevick *et al.*, 2006d). However, genetic analyses indicate small but significant differences in mitochondrial DNA frequencies between Labrador/Newfoundland and the Gulf of St. Lawrence (Palsbøll *et al.*, 2001), as well as fewer than expected genetic recaptures between those areas (Palsbøll *et al.*, 1997). In Newfoundland, capelin (*Mallotus spp.*) is the dominant prey source of humpback whales though records indicate that haddock (*Melanogrammus spp.*), euphausids (*Euphausia spp., Thysanoessa spp., Nematoscelis spp.*), mackerel (*Scomber spp.*), sand lance (*Ammodytes spp.*) and squid (decapodiformes) are also prey bases when they reach significant densities (Stevick *et al.*, 2006d). Feeding in the Gulf of St Lawrence is dominated by herring, capelin, sand lance and krill.

West Greenland

Humpback whales are abundant around Greenland in summer. Their main prey source appears to be small fish, such as sand lance, and krill (Perkins *et al.*, 1982). Numerous steep-sided shallow banks separated from the shore by a deep channel and abutting the deep Davis Strait drive cold, nutrient-rich water to the surface, creating high productivity and plentiful prey aggregations (Larsen and Hammond, 2004). Three main areas of humpback concentrations that appear to be consistent across years include the area off Nuuk, the area around 63°30’N and the area off Frederikshab (Larsen and Hammond, 2004). Photographic resightings of 169 individuals indicated that while they clearly fed in multiple areas, there was a tendency to return to the same area in multiple years. However, no consistent preference was detected among the 15 animals with the highest annual capture rates (≥4 years).

Recent aerial surveys suggest substantially larger population sizes (see following section on abundance) and an apparent range expansion since the YONAH project (Heide-Jorgensen *et al.*, 2008). Many individuals may actually be outside of the main surveyed areas, so the full extent of their distribution in this area is unknown. The West Greenland feeding ground may extend past the continental shelf farther west into deeper water (>200m) (Heide-Jorgensen *et al.*, 2008). Humpback whales have been reported from areas far north off West Greenland (e.g., 71°N) (Heide-Jorgensen *et al.*, 2008).

Iceland

Humpback whales around Iceland feed primarily on capelin and herring (Stevick *et al.*, 2006d). The oceanography around Iceland creates unpredictable prey distributions that can vary substantially from year to year (Stevick *et al.*, 2006d). Irregular prey patterns are consistent with lower site-specific fidelity of humpback whales observed in Iceland waters (Stevick *et al.*, 2006d). Humpback whales appear to be divided between eastern and western Iceland without much interchange between them (Stevick *et al.*, 2006d). This split in distribution may be related to the distribution of prey that develops through the summer season, with whales to the west of Iceland following the Icelandic capelin stock north along the Polar Front into the Greenland Sea, while the humpback whales to the east move into the Barents Sea (Stevick *et al.*, 2006d). Photo-identification studies detected little evidence of difference between Iceland and Norway populations based on identification exchange; genetic evidence for population structure is discussed in a following section (Stevick *et al.*, 2006d).

Barents & Norwegian Seas

Sighting survey data showed that humpback whales are widely distributed in the Barents and Norwegian Seas, with aggregations around Bear Island and Hopen Island (Øien, 2001). There was a shift in distribution observed from the Norwegian Sea in the late 1980s to Bear Island in the mid-1990s. This may have been linked to changing abundance and distribution of capelin populations, a major humpback prey source (Øien, 2001).

Humpback whales have been detected acoustically in the waters off northwestern Norway in the early fall, towards the coast of Iceland as fall progressed and then moving through the southern part of the Norwegian Sea in a counter-clockwise direction (Charif *et al.*, 2001). Detections were heard throughout the winter in the southern part of the Norwegian Sea and at rates comparable to those recorded in the Caribbean breeding grounds. This agrees with historical data and the hypothesis of Ingebrigtsen (1929) who proposed that humpbacks traveled in summer months from an area east of Iceland north to Jan Mayen and Spitsbergen to reach the Barents Sea (Charif *et al.*, 2001). Here, they were thought to stay for the fall and early winter months before making a migration west towards the Norwegian Sea near the northern coast of Norway. Whaling data from the northeastern Atlantic show catch records of females with late-term fetuses; this suggests the presence of a nearby calving (and perhaps mating) ground different from the West Indies or Cape Verde Islands (Ingebrigtsen, 1929). Survey work over the past twenty years indicates that feeding whales are observed between Norway and the Faroes (Charif *et al.*, 2001). Humpback abundance and distribution off eastern Iceland is not well known, but sightings and acoustic detections in the area support a southwesterly movement away from the Barents and Norwegian Seas in the winter (Charif *et al.*, 2001).

Breeding Grounds

Nuclear genetic evidence supports the existence of at least two breeding regions in the North Atlantic, indicating that the North Atlantic humpback population is not panmictic (Larsen, 1996). Whales from the Gulf of Maine, the Gulf of St Lawrence, Newfoundland, Labrador and West Greenland primarily migrate to the West Indies for breeding. Some individuals from the central and eastern North Atlantic also migrate to the West Indies, but a significant portion are thought to breed in another, as yet unidentified, location. The Cape Verde Islands are a known wintering area for humpback whales, and a historical whaling ground (Reeves *et al.*, 2002). However, recent observations indicate that the number of whales wintering there is low relative to the abundance of humpbacks in the eastern North Atlantic; consequently, the Cape Verdes are not likely to represent the major "second" breeding area (Wenzel *et al.*, 2010).

When examining the distribution of humpback whales throughout breeding areas in the North Atlantic, it is useful to explore what is known about their historical distributions in these areas as well. Humpback whale breeding areas were a common destination for whaling ships. Through a review of whaling ship logbooks, information has been garnered on the relative densities, distribution and timing of occurrence of whales around the North Atlantic breeding areas (Reeves *et al.*, 2002; Reeves *et al.*, 2001; Smith and Reeves, 2003). However, the number of whales recorded as being caught in each area can only be interpreted as an approximation of relative abundance since whaling effort can't be precisely quantified from the logbook data (Reeves *et al.*, 2001).

West Indies Breeding Area

The West Indies breeding range extends along the Atlantic margins of the Antilles, from Cuba to northern Venezuela (Balcomb and Nichols, 1982; Whitehead and Moore, 1982; Winn *et al.*, 1975). Available photo-ID and molecular genetic matching suggest that animals found across this range constitute a single breeding population). However, historical distributions of humpback whales in the West Indies differ from present day patterns (Reeves *et al.*, 2001). In the 19th century, whales were hunted in the eastern and southeastern Caribbean but few were recorded off the islands of the Greater Antilles (Reeves *et al.*, 2001). Most of the modern studies in the region since the 1970s have focused on large breeding populations at the Greater Antilles, especially at Silver and Navidad Banks off the northern Dominican Republic coast. Currently, far fewer humpback whales are observed in the Lesser Antilles, though there has been only limited research effort in these areas (Swartz and Burks, 2000). The absence of a large number of whales from the southern chain of islands is considered to be a result of the intensity of whaling in this region (Reeves *et al.*, 2001). However, it is not clear why humpback whales have not recolonized these waters since whaling ceased. Several theories have been put forth by Reeves *et al.* (2001). These include (1) that recent surveys have not covered the more southerly islands late enough in the season to observe the main arrival of individuals, (2) that a small aboriginal hunt at Bequia of 0-6 animals/year may be inhibiting the population's recovery, (3) that historical records do not necessarily reflect the complete distribution during that time, (4) that the fewer numbers of individuals found in the more southern islands are descendents of a distinct population in the region that was reduced dramatically due to whaling, or that (5) the distribution of humpbacks wintering in the West Indies has changed since the early 1900s. Reeves *et al.* (2001) proposed that a change in the distribution of humpbacks within this breeding region was most likely. They suggested that each oceanic breeding area has one focal point and that following heavy depletions in the southern islands, the point shifted farther north (Reeves *et al.*, 2001). However, a recent review of historical records from Hispaniola has strongly suggested that humpbacks were always abundant in the northern West Indies around the Dominican Republic and that rather than a shift occurring after whaling, the lack of records from this region reflects an inability of 19th century whalers to obtain licenses to hunt there (Bonnelly di Calventi and Clapham pers. comm.).

Historically, humpbacks were most abundant in the Windward Islands from February to May (Reeves *et al.*, 2001). Current observations in the more northern islands do not show such a late season presence of whales in the breeding ground (Reeves *et al.*, 2001). Humpbacks appear to range quite broadly across this breeding area, frequently crossing deep-water areas (Reeves *et al.*, 2001). It appears that the more southerly islands including Barbados and the Grenadines as well as the Trinidad-Venezuela coasts still support the same whale behaviors that they did historically (Reeves *et al.*, 2001). Mating and calving has been observed to still occur in much of the more southern islands where whales were historically found in greater numbers than they are today.

There is currently no evidence that Southern Hemisphere humpback whales use the West Indies for breeding, although data are limited with which to address this question. Occurrence of Southern Hemisphere humpback whales in this location is also unlikely given the six-month difference in breeding cycles between the populations in two hemispheres.

Cape Verde Islands

Relatively little survey effort has been dedicated to the Cape Verde Islands region (Wenzel *et al.*, 2010). It is known from historical records to have been a 19th century whaling ground of some importance (Reeves *et al.*, 2002). Whaling vessels leaving from New England to hunt in the North Atlantic would often visit the region. An examination of logbooks showed that approximately 1,105 humpbacks were recorded as either caught, struck or sighted in this region from 1826 to 1902 (Reeves *et al.*, 2002). An overview of logbook data describing encounter rates of whales, indicates that humpback density in the Cape Verde Islands was similar to that found in the southeastern Caribbean at the same time (Reeves *et al.*, 2002). Peak months of whale presence historically appear to be similar to those of the West Indies, from February to April (Reeves *et al.*, 2002).

Previously, the West Indies and Cape Verde Island groups were thought to be part of one large population based on shared patterns in song (Reeves *et al.*, 2002). However, both males and females occupy the Cape Verde Islands at the same time that the West Indies are occupied by humpback whales and given the distance between them it is unlikely that humpback whales occurring in the two areas intermix into one breeding stock. Additionally, there is little evidence that whales move between these two regions.

It has been suggested that the Cape Verde Island whales more likely belong to an eastern North Atlantic population that migrates from European waters (Reeves *et al.*, 2002). A small number of individuals have been matched through photographic resightings between the Cape Verde Islands and waters west of Iceland, around Bear Island, Norway and waters off the Azores (Wenzel *et al.*, 2010). Mothers, calves, singers and competitive groups were all observed in this area (Hazevoet and Wenzel, 2000). Resighting rates of individuals between years was quite high (22% of the 88 individuals identified), but resightings within a season were rare, apparently due to relatively extensive movements of individuals (Wenzel *et al.*, 2010). Only four matches have been made between the Cape Verde Islands and the North Atlantic Humpback Whale Catalog (NAHWC), which primarily has photographs taken in the western North Atlantic but has recently received more eastern North Atlantic photographs. All 4 matches made between the Cape Verde Islands and the NAHWC were to eastern North Atlantic feeding areas. The location of these 4 matches and the overall low match rate with the NAHWC suggests that most humpback whales in the Cape Verde Islands utilize feeding areas in the eastern North Atlantic where there has been less scientific effort and therefore fewer fluke photographs taken (Wenzel *et al.*, 2010).

The high resighting rate of humpback whales around the Cape Verde Islands and the small number of identified whales suggests low population size (Wenzel *et al.*, 2010). Why the Cape Verde population remains small is not entirely clear. Whaling in the Cape Verde Islands and within higher latitude feeding areas off Europe likely contributed to a major population decline (Reeves *et al.*, 2002). A decline in right whale (*Eubalaena glacialis*) abundance in the presumed calving ground of Cintra Bay off Western Sahara may have prompted whaling ships to exploit other areas and to shift operations to other whale species, including whales at the Cape Verde Islands (Reeves *et al.*, 2002). Since research effort in the area has been limited compared to the West Indies breeding area, it is difficult to determine if the lack of many photographic matches and small observed breeding population is a function of survey effort or an indication that many humpback whales from the northeast Atlantic winter at another, yet unknown, breeding area.

Other Areas

Mid-Atlantic States

Sightings of humpback whales have increased in the coastal waters from New Jersey to North Carolina starting in the 1990s (Barco *et al.*, 2002). Whales from at least three feeding aggregations visit this area, which may serve as a supplemental feeding ground for some animals in winter months (Barco *et al.*, 2002). As noted above, nearly half of the individuals that could be identified were confirmed to have a Gulf of Maine sighting history. Five humpback whales were successfully matched to feeding areas in eastern Canada, including Newfoundland and the Gulf of St Lawrence (Barco *et al.*, 2002). It is likely that these results underestimate the presence of Canadian humpback whales due to lower photo-identification research effort off Canada than the Gulf of Maine during the time of this study. As summarized by Barco et al. (2002), the population using this area is thought to be comprised primarily of juveniles. It is not known how many individuals use this area, although observed densities appear to be low. Distribution and residency times are also poorly understood for this region, and it remains unclear whether sighted individuals also visit the West Indies breeding ground.

Western Europe

Ireland

There were six catches of humpback whales in Irish waters recorded between 1908 and 1914 (Rogan, 2001). More recently, survey efforts have yielded low but possibly increasing sighting rates for humpbacks. Seventy humpbacks were killed between 1903 and 1929 off Scotland (Rogan, 2001). This limited sighting and catch record makes it difficult to assess whether this area was ever a significant habitat for humpback whales, or whether a formerly abundant local population was heavily depleted by unrecorded whaling at an earlier time (Rogan, 2001). In light of the current knowledge regarding historical whaling in the North Atlantic, the latter seems unlikely.

Mediterranean Sea

There were only two humpback whale sightings known from the Mediterranean until 1989 (Aguilar, 1989). Between 1990 and 2004, six new sightings and three entanglements were observed (Frantzis *et al.*, 2004). It is unclear why this apparent increase in sightings has occurred, why these animals were there and where they came from. It is unknown if the Mediterranean is serving as a feeding ground or if the individuals observed were lost or exploring (Frantzis *et al.*, 2004). Most sightings were during the Northern Hemisphere spring to fall (March to October) with the exception of one sighting in both January and February. No matches were found between any of the humpback whales sighted in the Mediterranean and existing catalogs (Frantzis *et al.*, 2004).

Migration

Though understanding of population structure has been improved immensely over the past two decades, details of migratory destinations and routes remain largely deduced from regional observations at each endpoint of the migration. Photographic matching of individuals from breeding to feeding grounds has been the most widely used tool to investigate migration. Microsatellite-based genetic tagging has also been used to match individuals between the two seasonal habitats. Though photographic identification and genotype data have been immensely helpful in elucidating the connections between habitats and the destinations of individuals and populations, there exists relatively scant information on the migratory routes of the individuals, the specific timing of migrations and the speed of travel (Reeves *et al.*, 2004a). Historical whaling records show the presence of humpback whales in offshore pelagic environments that may have been sites of migration (Reeves *et al.*, 2004b). Detections of singing humpback whales on open ocean bottom-mounted hydrophones in both the North Pacific and North Atlantic Oceans suggest that migratory routes are often not in coastal waters (Charif *et al.*, 2001; Norris *et* *al.*, 1999). This technique has been especially helpful in covering regions not often surveyed.

Results from YONAH show that all primary feeding grounds are represented in the West Indies winter population (Stevick *et al.*, 2003a). Genetic matches have also linked humpback whales from the western, central and eastern North Atlantic feeding areas to the West Indies (Bérubé *et al.*, 2004; Palsbøll *et al.*, 1997). The abundance of humpback whales seen from each feeding area was proportional to the population sizes sampled in each feeding ground (Stevick *et al.*, 2003b).

Timing of arrival was also variable by feeding ground origin, with humpback whales from the Gulf of Maine and eastern Canada arriving earlier in the season than whales from Greenland, Iceland and Norway. Additionally, evidence of sex segregation was observed, with males arriving earlier in the winter from all known feeding grounds (Stevick *et al.*, 2003a). Sighting dates in the West Indies were found to be similar from one year to the next for individual females (but not males) during the YONAH project (Mattila *et al.*, 2001).

Age composition was found to differ between the West Indies population and the Gulf of Maine population, with the West Indies population being significantly older (Robbins, 2007). Two- and three-year olds were particularly underrepresented in the West Indies population (Robbins, 2007). Sporadic sightings in the Gulf of Maine between January and March (the peak of the breeding season) were found to include a combination of late migratory departures, early arrivals and a few over-wintering individuals (especially juveniles, Robbins, 2007). Sightings of humpback whales off the mid-Atlantic coast in the winter may be indicative of over-wintering behavior by young whales of this age class (Barco *et al.*, 2002). However, it is unknown how long these animals stay off the mid-Atlantic coast.

Humpback whales were consistently acoustically detected between November and March heading southwest off the northern British Isles (Charif *et al.*, 2001). However, there were no acoustic detections of returning animals at the end of the winter as might have been expected. No verified acoustic detections occurred in the summer or early fall, but the occurrence of singing during this period is thought to be lower than during the winter months, and the areas occupied by the whales feeding during these months would likely be in shallower areas on the shelf outside the study's acoustic range (Charif *et al.*, 2001). It was concluded that the waters of the British Isles represent a migratory pathway for humpback whales, with some individuals likely originating from Norwegian waters. The destination of these migrating whales remains unknown, but it has been suggested that, if these humpback whales proceeded along their observed southwesterly course, the West Indies is a more probable destination than a more eastern breeding area (Charif *et al.*, 2001).

Genetic Differentiation

Genetic differentiation is caused by restrictions in gene flow between regions, which in turn is driven by limited movements of individuals (or population connectivity) between those regions. Restrictions to gene flow imply that different regions are semi-independent in their population growth rates, exploitation history and recovery status, and may also exhibit different reproductive parameters. Levels of maternal (mitochondrial) genetic differentiation in North Atlantic humpback whales support the existence of two mitochondrial DNA (mtDNA) clades, or groupings based on evolutionary relatedness – a Common North Atlantic clade and a Western North Atlantic clade (Baker and Medrano-González, 2002; Larsen, 1996; Palsbøll *et al.*, 1995). Individuals from the western North Atlantic, central North Atlantic and northeastern North Atlantic feeding regions are found in both clades.

The Norway and Bear Island (northeastern North Atlantic) feeding aggregation is significantly different from those in Iceland and Jan Mayen (central North Atlantic) in mtDNA haplotype composition (Larsen, 1996). The degree of differentiation between the northeastern North Atlantic and the central North Atlantic (K_{ST} =0.047) is comparable to that between the western North Atlantic (Gulf of Maine, Gulf of St Lawrence, Newfoundland and West Greenland) and the central North Atlantic (K_{ST} =0.040) (Larsen, 1996; Palsbøll *et al.*, 1995).

Nuclear genetic analysis supports a distinction between the northeastern North Atlantic and the West Indies population and suggests the existence of two breeding areas (Palsbøll *et al.*, 2001). However, if the Cape Verde Islands is the only other breeding area besides the West Indies, the number of whales observed in the breeding areas is significantly lower than the number of whales observed on the feeding grounds. Analyses to date can not distinguish between the possibilities of 2, 3, 4…or more populations, and sample sizes from the northeastern North Atlantic feeding grounds remain small.

Mitochondrial DNA analysis of western North Atlantic feeding areas indicated that feeding areas did not differ significantly (Palsbøll *et al.*, 1995). Gulf of Maine samples showed three distinct maternal lineages, each with a different haplotype (Palsbøll *et al.*, 1995). It has been hypothesized that the haplotype homogeneity of western North Atlantic feeding areas is a result of the relatively recent availability of these feeding grounds, which occurred after the last glaciations 10,000 years ago (Palsbøll *et al.*, 1995).

Nuclear DNA is less varied in humpback whales across the North Atlantic, though the western and central (Iceland and Jan Mayen) feeding grounds differ significantly from each other as well as from the West Indies breeding grounds (Larsen, 1996; Stevick *et al.*, 2003a).

B) Abundance

Feeding Area Abundance Estimates

Gulf of Maine

Abundance estimates using mark-recapture methods derived from the YONAH data set estimated 652 (CV=0.29) individuals within the Gulf of Maine from 1992 and 1993 photo-id sampling cruises (Clapham *et al.*, 2001). This mark-recapture-based estimate may be biased by either sampling effort or heterogeneity in whale distribution. There were at least 501 cataloged individuals known to be alive in 1992 because they were seen that year, or both before and after (Clapham *et al.*, 2001). Using the same approach, there were at least 843 individuals alive in 2003, but this total is not directly comparable to the previous estimate because the approach does not account for different levels of effort expended (Robbins, 2009b).

Line-transect surveys were conducted in 1999 in the Gulf of Maine and in the lesser studied Scotian Shelf area (Clapham *et al.*, 2001). Both ship and aerial survey data were utilized. Abundance was estimated at 816 (CV=0.45) humpback whales for the Gulf of Maine alone or 902 (CV=0.41) whales including the Scotian Shelf (Clapham *et al.*, 2003a). Both ship and aerial surveys may be negatively biased since the surveys did not account for the portion of individuals unavailable for sampling that were below the surface during the ship or aircraft's transit through the area. NMFS considers the best current estimate of the Gulf of Maine population to be 847 animals (CV=0.55). This estimate is based on a line-transect sighting survey conducted in August 2006 from the southern edge of Georges Bank to the Gulf of St. Lawrence and assuming 25% exchange between the Gulf of Maine and the Scotian Shelf (Waring *et al.*, 2008).

Canadian Maritimes

YONAH data were again used for an estimate of abundance in Canadian waters. Mark-recapture methods yielded an estimate of 1,807 whales (CV=0.053) (Stevick *et al.*, 2003b). However, survey effort around this region was very variable spatially and this likely resulted in substantial negative bias. A revision of the estimate was made by subdividing the area into three regions within which survey effort was more uniform. This method produced an estimate of 2,509 whales (CV=0.077) and although it is likely less biased, this estimate does not account for movement of whales among the sub-regions and is therefore probably negatively biased still (Stevick *et al.*, 2003b).

West Greenland

Abundance was estimated for West Greenland from 1988 to 1993 using systematic surveys and photo-identification techniques. Abundances ranged from 362 to 615 individuals, but the 1990-1991 estimate was anomalously high resulting from less complete sampling coverage (Larsen and Hammond, 2000). An adjusted mean for the study period, not including 1990-1991, was 385 whales (SE=24). Average abundance of the West Greenland feeding aggregation was estimated at 360 individuals (CV=0.07) for the period 1988-1993 (Larsen and Hammond, 2000) . One concern for estimating abundance in this area was the observation that females with calves may spatially segregate from other classes. With few calf sightings in the surveys, the population may have been underestimated if regions with calves were not being sampled (Larsen and Hammond, 2000). However, there were insufficient data to assess the effect of spatial segregation on abundance estimates.

The most recently available estimate is from aerial line transect surveys and suggests an abundance of 3,039 individuals (CV=0.45) in West Greenland in 2007 (Heide-Jorgensen *et al.*, 2008). The disparity between the photo-identification and line-transect survey abundance estimates is credited to the difference in geographical coverage of the two estimates. The photo-identification estimate was based on a much smaller, concentrated area of whale abundance while the aerial surveys covered a larger area than any previous survey in West Greenland (Heide-Jorgensen *et al.*, 2008).

Iceland

Shipboard line-transect surveys were also conducted in Icelandic waters in 1995 with the purpose of estimating whale abundance. An estimate of 14,600 was produced (95% CI=5,100-41,500) (Pike *et al.*, 2001). The Scientific Committee of the International Whaling Commission considered this estimate unlikely based on earlier estimates from the area and when considering estimates for the whole of the North Atlantic (IWC, 2002a). It was based on relatively few transect lines and did not provide thorough coverage of the sampling area. Furthermore, the two survey ships may have sampled the same large aggregation of animals each once, therefore elevating the estimate (IWC, 2002a). The survey effort and spatial scale was not considered ideal for estimating the abundance of humpback whales. Although the Scientific Committee did not consider this estimate reliable in its Comprehensive Assessment of North Atlantic humpback whales, the results were interpreted to suggest that humpbacks were generally abundant in the Iceland region (IWC, 2002a). An area north of Iceland covered by shipboard surveys in 1996-2001 was found to have an estimated 3,246 (CV=0.512) humpback whales (Øien, 2009). An estimate of 4,928 (CV=0.463) was produced from aerial surveys in 2001 in coastal Icelandic waters (Pike *et al.*, 2009).

Norway

Numerous line-transect surveys were conducted primarily for surveying minke whales in the Norwegian and Barents Seas, but opportunistic sightings of humpback whales provided estimates of abundance including 1,126 humpback whales in 1988, 689 in 1989 and 889 in 1995 (IWC, 2002a; Øien, 2001). These survey areas did not overlap with those surveyed for the Iceland data above. The areas surveyed changed slightly between years, but the survey plan was the same in 1989 and 1995 (IWC, 2002a). These estimates were also likely negatively biased because they did not account for individuals missed when not at the surface. Another study estimated abundance from shipboard surveys to be 1,059 (cv 0.248) in 1995 and 1,450 (cv 0.29) for the period 1996-2001 (Øien, 2009).

Breeding ground/ocean basin estimates

In addition to abundance estimates for feeding areas, population-wide estimates have also been made from breeding areas. In addition, some studies have used data from both feeding and breeding areas to calculate ocean-basin-wide estimates.

Abundance estimates were calculated for the North Atlantic population by pooling feeding area samples and breeding area samples collected during the YONAH project from 1992 to 1993 (Stevick *et al.*, 2003b). These estimates included application of an error rate in addition to sample pooling to collectively improve the estimates. Abundance was estimated at 11,570 (CV=0.069) individuals (Stevick *et al.*, 2003b). Although this figure is larger and more precise than any previous estimate, it is likely also negatively biased estimate for the entire ocean basin (Stevick *et al.*, 2003b).

Another set of estimates was calculated for 1979 to 1993, excluding feeding ground samples from Iceland and Norway in order to represent just the West Indies breeding population (Stevick *et al.*, 2003b). By excluding these areas, the West Indies sample is then considered to be representative of the western North Atlantic feeding areas and therefore unbiased. If, however, whales from a separate breeding area migrate to the northwestern Atlantic to feed, there would be a positive bias in these estimates. Estimates made using this method ranged from 5,930 to 12,580 (CVs 0.070-0.039). The most precise estimate for the West Indies breeding population is 10,752 (CV 0.068). These estimates of the West Indies breeding population are considered to be the most accurate for the North Atlantic (Stevick *et al.*, 2003b).

C) Genetic Diversity

Genetic diversity is an approximator for long-term population size; where high diversity suggests large ancestral populations and low diversity the opposite (Soulé, 1976). Low diversity may also reflect a recent population bottleneck, with the magnitude of diversity loss dependent on the severity and duration of the bottleneck. Inbreeding of small populations can reduce genetic diversity and thereby reduce the reproductive potential or productivity of a population. This effect has not yet been shown for any humpback whale population. Here we summarize available information on genetic diversity.

Genetic analysis has found 25 haplotypes in the western North Atlantic, 12 haplotypes in eastern North Atlantic samples and 19 haplotypes in the Gulf of Maine population (Larsen, 1996; Palsbøll *et al.*, 1995; Rosenbaum *et al.*, 2002). However, it is not clear how many of these haplotypes overlap, as they are all from different studies. At the basin level, humpback whales in the North Atlantic appear to have higher haplotype diversity than humpback whales in the North Pacific Ocean (Baker and Medrano-González, 2002). Haplotype diversity was found to be lowest in populations around Norway and Iceland and highest around the northwestern feeding areas off Greenland, Gulf of St. Lawrence and Gulf of Maine (Baker and Medrano-González, 2002). Observed nucleotide diversity is also higher in the North Atlantic than the North Pacific (Baker and Medrano-González, 2002).

D) Trends

There is no reliable estimate of trend for the entire North Atlantic population. The best available estimate of the average rate of increase for the West Indies breeding population is 3.1% (SE=0.005) for the period 1979-1993 (Stevick *et al.*, 2003b).

The Gulf of Maine feeding population is part of the West Indies population and was estimated to be increasing at a rate of 6.5% for the period 1979-1991 (Barlow and Clapham, 1997). However, using data from 1992 through 2000, the population showed a lower growth rate of 0-4% (Clapham *et al.*, 2003a). Population growth rates were calculated using demographic parameters estimated from photo-identification mark-recapture data, reproductive rates (birth intervals and maturation ages) and non-calf survival rates. Apparent low calf survival between 1992 and 1995 hindered estimation of maturation age, not allowing for a more precise estimate of population growth rate. The authors hypothesized that the apparent decline in growth rate during this later period could have resulted from: 1) a shift in humpback whale distribution to areas less sampled, 2) a reduction in adult female survival, 3) increased interbirth intervals or 4) high mortality of calves (first-year whales) (such as off the mid-Atlantic coast) (Barco *et al.*, 2002; Clapham *et al.*, 2003a). They considered reduced calf survival to be the most likely explanation but noted an apparent improvement in calf survival after 1996. A subsequent study confirmed both low average reproductive rates and calf survival during much of the 1992-2000 period (Robbins, 2007). The average estimated calf survival rate for the period 2000-2005 (0.664, 95% CI: 0.517-0.784) fell between the values assumed by Clapham et al. (2003) of 0.51 to 0.875, and did not include neonatal mortality prior to arrival on the feeding ground (Robbins, 2007). No subsequent growth rate estimates are available.

There are few estimates of population trends for the eastern North Atlantic. During the period 1979-1988, annual sightings of humpback whales at Iceland were estimated to have increased by 14.8% per year ((Sigurjónsson, 1990; Sigurjonsson and Gunnlaugsson, 1990). However, these numbers are at the boundary of what is thought to be the maximum possible rate of increase for humpback whales (Zerbini et al. 2010); it is not clear whether immigration into this feeding area may exist and contribute to this observed high level of increase, or whether the survey method employed was reliable (Smith and Pike, 2009).

E) Habitat or Ecosystem Conditions

Studies of humpback whales in the North Atlantic indicate a substantial degree of heterogeneity and flexibility in the use of habitat. Historical records indicate that the Lesser Antilles in the West Indies was previously an area of high humpback concentration, while the Greater Antilles presently support the great majority of whales on the breeding ground (Swartz *et al.*, 2003; Winn *et al.*, 1975). However, as noted above, it is possible that similar concentrations of whales occurred in the northern West Indies but were not hunted there for logistical or political reasons. Though numbers are lower in the Lesser Antilles today than in the 19th century, this area is probably still used as nursing, mating and calving grounds with the exception of the Gulf of Paria (Swartz *et al.*, 2003). This latter area once hosted numerous whales before exploitation by Yankee whaling (whaling primarily based out of New England ports that peaked between 1815 and the early 1900s) but does not seem to have been reoccupied (Reeves *et al.*, 2001). It has been suggested that this may be due to disturbance from oil and gas activities or frequent shipping traffic (Swartz *et al.*, 2003), but further research is necessary to confirm this.

A number of studies conducted on feeding grounds have examined the link between humpback whales and their habitat. There is historical evidence that humpbacks may have fed west of the Mid-Atlantic Ridge, but it is not known if this remains a feeding habitat today (Reeves *et al.*, 2004a). In the Gulf of St Lawrence, humpback whales were found to associate with thermal fronts that aggregate nutrients and prey (Doniol-Valcroze *et al.*, 2007). Humpbacks were often close to the fronts but not as consistently close as blue whales, which are obligate krill feeders (Doniol-Valcroze *et al.*, 2007). It was found that small fish species are also somewhat removed from thermal fronts, thus at least partially explaining the distribution of humpback whales, which feed on both fish and krill (Doniol-Valcroze *et al.*, 2007).

The geographic and temporal scale of shifts in habitat use are widely variable, from small movements within a single day to seasonal shifts in distribution and density as documented between Stellwagen Bank and Jeffrey's Ledge in the Gulf of Maine (Payne *et al.*, 1990). Humpbacks on Stellwagen Bank were found to switch feeding location in the water column as a function of time of day and light levels as their prey underwent diel vertical migrations (Friedlaender *et al.*, 2009). Whales were found to feed more often over mud and sandy-bottom habitats on Stellwagen Bank than over gravel (Hazen *et al.*, 2009). Tidal state was highly correlated with prey aggregation and therefore also correlated to humpback whale presence (Hazen *et al.*, 2009). Though habitat-prey-predator relationships were visible in many of the foraging and habitat-use studies, these relationships were usually complex and often involved time lags and multi-variable interactions that were difficult to fully describe (Doniol-Valcroze *et al.*, 2007; Friedlaender *et al.*, 2009; Hazen *et al.*, 2009).

In addition to habitat use varying over time, it also appears to vary with age class, gender and/or reproductive state. As noted above, juveniles and mature females (especially those with calves) are more frequently encountered in the southwestern Gulf of Maine than other areas (Robbins, 2007). Sand lance are the predominant prey in that region, and it has been hypothesized that this type of prey may occur in more consistently predicatable locations and be easier to feed on than other prey species (Robbins, 2007). Within the southwestern Gulf of Maine, juveniles and adults were often found in different areas whereby juveniles were generally found feeding in areas where prey densities were lower than in adult feeding areas. Additionally, juveniles more frequently fed lower in the water column while adults were observed feeding at the surface (Weinrich *et al.*, 1997).

F) Threats and Anthropogenic Impacts

The greatest known threats to humpback whales in the North Atlantic are entanglement in fishing gear and ship collisions.

On the US East Coast, humpback whales were the most common species reported entangled, with 75 confirmed reports between 2003 and 2007 (Glass *et al.*, 2009). Of these, 14 entanglements resulted in deaths or serious injuries, averaging 2.8 observed per year (Glass *et al.*, 2009). These estimates exceed the calculated potential biological removal (PBR) of 1.1 whales per year for this population (Glass *et al.*, 2009) (Waring *et al.*, 2008). However, despite well-established entanglement reporting and response networks in this region, scar-based studies suggest that fewer than 10% of entanglements are witnessed and reported (Robbins and Mattila, 2004). Furthermore, cause of death was not determined for the vast majority (86%) of observed deaths in this region during the same period (Glass *et al.*, 2009).

Approximately half of the Gulf of Maine population bear scars indicative of a previous entanglement, and an average of 12% of individuals in the population acquire new injuries annually (Robbins, 2009b). Entanglements rates are higher for juveniles than adults (Robbins, 2009b) and juvenile survival appears to be more significantly impacted by entanglements than adult survival is (Robbins *et al.*, 2008b). Females with evidence of previous entanglement appeared to produce fewer calves than non-scarred females (Robbins and Mattila, 2001). Entanglement mortality estimates based on scar-based studies also suggest a significant contribution to the total human-caused mortality rate in humpback whales occurring in the Gulf of Maine (Robbins *et al.*, 2009). However, details of the impact of entanglement on survival and fecundity remain under investigation (Robbins pers. comm.)

In addition to US records, humpback whale entanglement reports are regularly received by the Canadian Whale Release and Stranding Group off Newfoundland. A total of 988 entangled humpback whales were reported between 1979-2009, with most entanglement events involving box traps, posts, gillnets, ropes and other gear. Of these, 703 individuals were released alive (disentangled), while 103 were confirmed to have died (IWC 2010). From 2000-2007, 67% of humpback whale entanglements occurred offshore from 25nmi to beyond 200nmi from the coast (Ledwell and Huntingdon, 2009).

Entanglement frequency and impacts are less well understood in other areas of the North Atlantic. A review of progress reports submitted by member nations to the International Whaling Commission (2003-2008) revealed humpback whale entanglement reports from Denmark (Greenland), Iceland, Ireland, Italy, Spain and the United Kingdom (Mattila and Rowles, 2010). The Atlantic Large Whale Disentanglement Network has also received reports from the West Indies, Bermuda and the Netherlands (S. Landry/PCCS, pers. comm.). Finally, a relatively high percentage of the few sightings in the Mediterranean involved entangled whales and may warrant particular concern depending on the population identity of these whales (Frantzis *et al.*, 2004).

There were an average of 1.6 confirmed humpback whale ship strike deaths each year between 2003 and 2007 (Glass *et al.*, 2009) along the US east coast, Canadian Maritimes and Gulf of Mexico region (Glass *et al.*, 2009). As in the case of entanglement, observed events exceed the calculated potential biological removal (PBR) of 1.1 whales per year for the Gulf of Maine humpback whale population (Glass *et al.*, 2009; Waring *et al.*, 2008). However, cause of death could not be determined for the vast majority (86%) of observed deaths in this region during the same period; ship strikes do not necessarily produce outward injuries (Glass *et al.*, 2009). Therefore, the contribution of ship strikes to humpback whale mortality estimates may be underestimated.

Ship strike injuries made up 8% (10 of 123) of dead stranded humpback whales between 1975 and 1996 along the US mid-Atlantic and southeastern states (Wiley and Asmutis, 1995). Among strandings along the mid- and southeastern US during 1975-1996 for which body length data were available, all 25 individual whales were estimated to be immature based on length at death (<11m, Wiley and Asmutis, 1995), suggesting that young humpback whales may be disproportionately affected. However, that region is thought to be used preferentially by young animals (Barco *et al.*, 2002; Swingle *et al.*, 1993).

Many humpback whale feeding areas in the North Atlantic are exposed to a high level of ship traffic. In addition to ship strikes, this also raises concerns about noise levels in the marine environment. Stellwagen Bank and other areas in southern New England are areas where the overlap of whales and shipping is especially high. NOAA requires that any activity that may expose whales to received levels of impulse sound levels >160 dB re 1 μPa, or continuous sound levels >120 dB re 1 μPa, must obtain a permit to do so. This does not currently apply to ships in transit. Assessments of the acoustic habitat on Stellwagen Bank have showed that this permitted noise level exists across almost the entirety of the Bank as a result of one transiting tanker, while nearly 800 transits of such vessels were recorded in 2006 (Hatch *et al.*, 2008). Additionally, this same study reported that given background sound levels on the Bank, a right whale call may be detectable by human listening devices at a distance of no more than 0.75 miles (Hatch *et al.*, 2008) suggesting that social communication among other cetacean species may be similarly adversely affected. The implications of these background noise levels for humpback whales are not known and the population-level impacts are even less understood.

Another contribution to ship traffic in humpback whale habitats is whale watching. Weinrich and Corbelli (2009) examined the effect of vessel exposure on calving rates and calf survival on Stellwagen Bank. They found no direct evidence that whale watching was having a negative impact on calving rates or calf survival. While the measures of individual whale watching exposure were believed to be an accurate index of exposure, the authors cautioned that the cumulative time of whale watching vessel exposure was likely to be highly underestimated in the study. Some of the data showed a positive relationship between whale watching and calf survival, though this is almost certainly coincidental and probably driven by the overlap of prime whale habitat and the presence of vessels with scientific observers aboard (Weinrich and Corbelli, 2009).

From 1987 to 1988, 14 humpback deaths were observed as a result of saxitoxin-contaminated mackerel (Geraci *et al.*, 1989). It is likely that more than the observed 14 observed humpback whales were affected by this event but were not observed dead at sea or stranded in nearby coastal areas. Seven juvenile humpback whales stranded along the North Carolina and New Jersey coasts in 1990, but the reason for these strandings is unknown (Waring *et al.*, 2008). In 2003 an Unusual Mortality Event[6] was observed involving 12-15 humpback deaths on Georges Bank (Waring *et al.*, 2008). Low levels of domoic acid were found in sampled tissues, but it is not known if these levels were high enough to be the cause of death. An UME involving at least 21 humpback whales occurred in the Gulf of Maine from July, 2006 until the end of 2007, but its cause remains unknown (Waring *et al.*, 2008).

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[6] Unusual Mortality Events (UMEs) are defined under the MMPA as "a stranding that is unexpected; involves a significant die-off of any marine mammal population; and demands immediate response." For more information see *Federal Register* notice (71 FR 75234), published on December 14, 2006.

G) Recovery from Exploitation

An estimated 29,279 humpback whales were killed by whaling operations of various kinds in the North Atlantic in the period beginning in 1664 (Smith and Reeves, 2003). The vast majority of humpback whales were caught on their shared breeding grounds, which has made it impossible to allocate most takes to specific feeding populations. Coastal small-scale whaling operations and non-mechanized pelagic whaling are estimated to have removed 2,000 humpbacks during the 19th century (Smith and Reeves, 2003). Another 5,000 humpbacks were taken off Iceland and Norway between 1885 and 1910 (Ingebrigtsen, 1929; Sigurjonsson and Gunnlaugsson, 1988). By the early 1900s, the easily accessible coastal species, including humpback whales, had been sufficiently depleted in these locations that whalers switched their focus to other whales. Between 1895 and 1930, at least 1,600 humpbacks were taken in Canadian waters, and small subsistence hunts continued in Greenland until 1985 (Smith and Reeves, 2003; Tønnessen and Johnsen, 1982).

A 300-hundred-year catch history for humpbacks in the North Atlantic makes it difficult to assess how these numbers reflect the size of the standing population at any one time (Reeves and Smith, 2002). Pre-whaling humpback whale abundance based on mtDNA variability has been estimated at 240,000 individuals, but the validity of these estimates are much debated (Roman and Palumbi, 2003). Whalers hunted whales in many areas, both feeding and breeding areas, and the intensity of whaling varied over time (Reeves and Smith, 2002; Smith and Reeves, 2003). Humpbacks were also depleted early on in whaling history when catch records were less accurate. Additionally, these older records are less likely to have survived to the present. (Stevick *et al.*, 2003b). However, it is currently impossible to reconcile the genetic estimates of abundance with a catch history, even allowing for probably unrealistically large gaps in the latter.

As stated previously, the IWC Scientific Committee conducted a Comprehensive Assessment of North Atlantic humpback whales and found the results inconclusive (IWC, 2002a, 2003a). In order to improve the assessment, Punt *et al.* (2006) developed age- and sex-structured population dynamics models to further examine the status of North Atlantic humpback whales, concluding that abundances were increasing but that the extent of such increases was still indeterminable, due to uncertainty surrounding the abundance estimates at the Cape Verde Islands breeding ground. Most recently, areas of inconsisties surrounding population structure, distribution, abundance estimates and trends were identified in order to direct research and enable a more accurate assessment of the status of North Atlantic humpback whales (Smith and Pike, 2009). The major gaps and inconsisties identified include the potential existence of a third breeding area and the mismatch of abundance estimates made at feeding grounds versus breeding grounds. Resolving the question of a third breeding ground was determined to be the most important research priority, despite the challenge of doing so. Improving the basin-wide catch history and the abundance estimate of the Cape Verde Islands breeding group was also highlighted as needed research (Smith and Pike, 2009). Further research is currently underway to address some of these tasks, including the MONAH project which will provide revised estimates of abundance and growth rates for the West Indies breeding population.

X STATUS OF NORTH PACIFIC POPULATIONS

A) Distribution & Population Structure

Humpback whales in the North Pacific undergo seasonal migrations from northern-latitude feeding areas in the summer months to more southern-latitude breeding areas in the winter months. Feeding areas are dispersed across the Pacific Rim from California, USA to Hokaido, Japan. Within these regions, humpback whales have been observed to spend the majority of their time feeding in inland and coastal waters. Much more is known about the humpback whales occurring east of the Aleutian Islands than elsewhere; and the western feeding grounds remain relatively understudied.

Breeding areas in the North Pacific are more geographically separated than the feeding areas and include regions offshore of mainland Central America; mainland, Baja California and the Revillagigedos Islands, Mexico; Hawaii; and Asia including Ogasawara and Okinawa Islands and the Philippines. As observed in the 1991 Humpback Recovery Plan, a major difference between the Atlantic and Pacific humpback populations is their distribution relative to national and international boundaries. About half of the humpback whales in the North Pacific Ocean breed and calve in the US territorial waters off Hawaii, and more than half feed in US territorial waters. In the Atlantic in contrast, relatively few humpback whales feed in US waters and the single predominant breeding and calving area is not in US waters.

As data gathering, particularly using photo-identification and genetic studies techniques, increased from the mid-1990s to the present, distinctions between populations have been refined. An increasing number of relatively distinct groups have been identified, starting with the separation of western and eastern stocks (Darling *et al.*, 1996; Darling and Cerchio, 1993; Darling and McSweeney, 1985). The eastern stock was then genetically recognized as being made up of two separate groups - a central stock that feeds in Alaska and breeds in Hawaii and an “American” stock that feeds in waters off California and breeds offshore of Mexico (Baker *et al.*, 1994). The “American” stock was then subdivided again, making the Mexico offshore breeding stock (with feeding destination then currently unknown), separate from the continental Mexican stock that migrates to the waters off California, Oregon and Washington States (Barlow, 1994; Barlow *et al.*, 1997).

Between 2004 and 2006, a multinational coordinated study called Structure of Populations, Levels of Abundance and Status of Humpbacks (SPLASH) examined humpback whale population structure and abundance in the North Pacific. Field efforts were conducted at all known North Pacific breeding and feeding areas. A total of 18,469 quality fluke identification photographs were taken, producing a total of 7,971 unique individuals cataloged. A total of 6,178 tissue samples were also collected for genetic studies of population structure, with fairly even representation of wintering and feeding areas. With the completion of the project’s field components, greater resolution of migratory connections and interchange between and within regional populations has been possible. It is very clear that a great deal of structural complexity exists within the North Pacific and that it does not contain a single panmictic population.

Feeding Areas

It is difficult to define distinct feeding areas for humpback whales because the species occurs in a nearly continuous arc around the North Pacific basin. However, SPLASH results have further informed observations made from previous studies and allowed the recognition of more robust feeding area definitions resulting from a high degree of feeding site fidelity within an area and relatively low interchange rates with other areas. The interchange that does occur appears to decrease as a function of geographic distance, meaning that individuals seen in multiple feeding grounds were most often previously seen in the adjacent feeding areas. Any interchange that has been observed between feeding areas is discussed in each regional section below.

California and Oregon

The feeding area boundary between the humpback whales feeding off British Columbia and those feeding off the US coast has been debated. Until recently, most studies described California, Oregon and Washington as one feeding group (Calambokidis *et al.*, 1996; Calambokidis *et al.*, 2000b). Now it appears that the distinction is better supported as one group feeding offshore of California and Oregon and another feeding offshore of northern Washington and southern British Columbia (Calambokidis *et al.*, 2008).

Humpback whales occurring off California and Oregon to southern British Columbia were found to have a higher degree of within-region interchange than between these regions and the northern feeding areas (Calambokidis *et al.*, 1996; Calambokidis *et al.*, 2001). Within-region interchange decreases as a function of geographic distance within the waters off California and Oregon (Calambokidis *et al.*, 2001). The inter-year photographic identification match rate of humpback whales within California was found to be 88% (Calambokidis *et al.*, 1996).

Humpback whales are generally seen off the coast of California and Oregon in spring, summer and fall. Most sightings of humpback whales have been in coastal waters, often within 30nmi of the shoreline (Calambokidis and Barlow, 2004). Areas of particularly high concentration of humpback whales were found around the Farralon Islands, north and south of San Francisco Bay and around Point Conception (Calambokidis *et al.*, 2004). However, humpback whales were also detected in waters off California (80-100nmi) during winter and early spring aerial surveys (Forney and Barlow, 1998). Photo-identification of some of these individuals has revealed that most of the whales occurring in these waters are part of the California feeding aggregation. An exception is one whale identified in this area that was also sighted in the Gulf of Alaska, indicating that it may have been in transit off California (Calambokidis, pers. comm.).

The occurrence of humpback whales in coastal waters between Newport, OR and Crescent City, CA was correlated with the position of the alongshore upwelling in both June and August (Tynan *et al.*, 2005). In June, humpback whales were found offshore on the western edge of a strong alongshore coastal jet (current) and upwelling front at Heceta Bank and Cape Blanco (Tynan *et al.*, 2005). Some individuals were found in upwelled waters (e.g., relatively cool, saline waters) with high surface chlorophyll, while most remained in warmer waters with more intermediate salinity values (Tynan *et al.*, 2005). In August, humpback whales were found over Heceta Bank inshore of the jet associated with areas of high chlorophyll and high acoustic backscatter indicating the presence of larger prey such as fish (Tynan *et al.*, 2005). Tynan et al (2005) speculated that increased vertical mixing associated with the bank topography supported greater prey availability and therefore increased feeding opportunities for humpback whales.

British Columbia and Northern Washington

An analysis of historical whaling data from British Columbia whaling stations on Vancouver Island and the Queen Charlotte Islands suggests that a resident subpopulation of humpback whales existed offshore of British Columbia (Gregr *et al.*, 2000). Differences in the timing of historical depletion of this population compared to both the population to the north in southeastern Alaska and the population to the south offshore of California and Oregon suggest that it was a distinct subpopulation (Gregr *et al.*, 2000). British Columbia catches decreased dramatically around 1917 (Gregr *et al.*, 2000). A review of California historical whaling showed depletion between 1919 and 1926, while the western Gulf of Alaska still sustained catches into the 1930s. The decline in catches from all British Columbia whaling stations concurrently implies that the British Columbia population extended northward to latitude 54°N (Gregr *et al.*, 2000).

Individuals in the resident population appear to have followed a structured migration, with immature individuals arriving on the feeding ground first and pregnant females arriving through the season (Gregr *et al.*, 2000). Sex ratios appeared to be even, and records also indicate that some humpback whales foraged through the winter in this location (Gregr *et al.*, 2000). The population was likely small and was depleted quickly over a few seasons. Approximately 200 individuals were taken from around the Strait of Georgia, likely extirpating the population by the early 1900s (Gregr *et al.*, 2000).

In a recent study in waters off northern Washington, humpback whales were found to be the most common large cetacean, concentrated in areas that were likely important feeding grounds (Calambokidis *et al.*, 2004). Sightings were most numerous in an area off the northern Olympic Peninsula between Juan de Fuca canyon and the edge of the continental shelf. Another area east of the Barkley Canyon and north of the Nitnat Canyon off the coast of Washington also supported high densities of whales (Calambokidis *et al.*, 2004). Observations across years showed slight shifts in distribution on small scales.

Despite the high density of humpback whales seen in northern Washington, a relatively small number of individuals appear to regularly use the area as based on photographic identification data (Calambokidis *et al.*, 2004). The proportion of humpback whales seen that had been sighted in previous years in northern Washington decreased each year of the study. Simultaneously, the match rate of individuals in this region to Oregon and California decreased (Calambokidis *et al.*, 2004). The authors believed that the most parsimonious explanation for this was that a shift in distribution of humpback whales from feeding areas farther north into the northern Washington region began in the late 1990s (Calambokidis *et al.*, 2004). It does not appear that there exists a clear demarcation between this feeding region and that of southern British Columbia just to the north, though exchange rates do decrease with increasing distance from each feeding area (Calambokidis *et al.*, 2004).

Recent results from the SPLASH study support the grouping of northern Washington with southern British Columbia feeding areas and their distinction from a northern British Columbia feeding area (Calambokidis *et al.*, 2008). This classification was supported by the presence of only one photographic identification match of a humpback whale across both northern and southern British Columbia (Calambokidis *et al.*, 2008). Though rates of exchange were low between northern and southern British Columbia, the highest exchange rate across feeding areas surveyed by SPLASH occurred between northern British Columbia and southeastern Alaska (Calambokidis *et al.*, 2008). Gregr *et al.* (2000) suggested that the British Columbia feeding area may be increasing in abundance slowly due to immigration from other neighboring feeding areas (e.g., southeastern Alaska).

Southeastern Alaska

Southeastern Alaska supports a large population of humpback whales (Straley *et al.*, 2009). Humpback whales are distributed through all major waterways of the southeastern Alaska coastline, and annual concentrations of humpback whales are consistently seen in Icy Straight, Lynn Canal, Stephens Passage, Chatham Straight and Frederick Sound (Dahlheim *et al.*, 2009). Humpback whales have been observed in Glacier Bay during each year surveyed (Dahlheim *et al.*, 2009).

Abundance and distribution of humpback whales in southeastern Alaska were observed to follow a strong seasonal pattern (Straley *et al.*, 2009). Humpback whales increased in number throughout the spring and were found to congregate in particular areas such as those near Icy Straight, Frederick Sound and Stephens Passage (Dahlheim *et al.*, 2009). As the number of humpback whales increased over the summer months, the distribution of whales was found to spread throughout the region more evenly. Numbers remained high through the fall season (Dahlheim *et al.*, 2009). Mean group size varied significantly across years in this region as well as across seasons, with the smallest groups occurring in the spring and the largest in the fall (Dahlheim *et al.*, 2009).

Humpback whales in southeastern Alaska were found in a variety of habitats across the region, including open-ocean, open-straight environments, near-shore waters, strong tidal current areas, and protected bays and inlets (Dahlheim *et al.*, 2009; Straley *et al.*, 2009). Whales were less often seen in Sumner and Clarence Straight across all 17 years of one study though numbers have been increasing more in recent years in this area (Dahlheim *et al.*, 2009). The west side of Prince of Wales Island was surveyed during three different seasons with whales sighted each time (Dahlheim *et al.*, 2009). Studies of humpback whales in Glacier Bay and Frederick Sound found abundance and distribution to be strongly linked to krill availability (Bryant *et al.*, 1981).

Results from the SPLASH project indicate that southeastern Alaska has a high degree of interchange with northern British Columbia and the northern Gulf of Alaska (Calambokidis *et al.*, 2008).

Northern Gulf of Alaska, Aleutian Islands and Bering Sea Feeding Areas

Feeding areas west of southeastern Alaska are understudied compared to those to the east. However, it is known that whaling resulted in loss of large numbers of humpback whales from the Gulf of Alaska, the Alaska Peninsula and the Aleutian Islands (Zerbini *et al.*, 2006b). Feeding areas west of southeastern Alaska known to be occupied by humpback whales today include the northern Gulf of Alaska, the western Gulf of Alaska, the Bering Sea, the Aleutian Islands and Russian feeding areas of the Commander Islands, the east coast of Kamchatka and the Gulf of Anadyr.

The first photographic identification study of humpback whales west of Prince William Sound recorded only 15 whales and found no matches to whales of Prince William Sound or southeastern Alaska (Baker *et al.*, 1986). Further research on the movements of humpback whales between neighboring feeding areas in the northern Gulf of Alaska supported the existence of a distinct feeding aggregation around Kodiak Island (Waite *et al.*, 1999). Low rates of exchange were found between the waters around Kodiak Island and the area of Prince William Sound (Waite *et al.*, 1999). Only 3-6% of Kodiak Island humpback whales were estimated to also visit Prince William Sound (Waite *et al.*, 1999). Additionally, only 2-3% of the Kodiak Island humpback whales were estimated to visit southeastern Alaska (Waite *et al.*, 1999). As of 1999, 127 individual humpback whales were identified around Kodiak Island (Waite *et al.*, 1999). This relatively large local population, and the low exchange rate, indicate that the Kodiak Island feeding aggregation is likely to be discrete. However, the degree of site fidelity to this area is unclear, as re-sights of whales across years has been relatively low (Waite *et al.*, 1999). The reason for this is yet unexplained.

Twenty two humpback whales were identified in the Shumagin Islands during surveys from 1992-1994, with no matches to any of the other feeding areas that were presently known along Alaska or California (Brueggeman, 1989). One study suggested that the humpback whales around the Shumagin Islands may be a separate feeding aggregation given high densities of individuals seen in the area during aerial and ship surveys (Brueggeman, 1989). Mitochondrial DNA analysis recently found that humpback whales around the Shumagin Islands had different haplotype frequencies from those in southeastern Alaska, Prince William Sound and California (Witteveen *et al.*, 2004).

In 1992 and 1993, surveys found very few humpback whales along the Alaska Peninsula West of the Shumagin Islands (Waite *et al.*, 1999). One whale identified offshore of the Shumagin Islands was re-sighted in Prince William Sound (Waite *et al.*, 1999). However, it is unknown if individuals ever stay offshore for the entire feeding season or if offshore areas are largely inhabited by individuals in transit (Waite *et al.*, 1999).

Results from surveys of the central-eastern Bering Sea and the southeastern Bering Sea in 1999 and 2000 indicated humpback whales were less abundant than other cetacean species in the area (Moore *et al.*, 2002). Humpback whales were most often found on the Middle Shelf at 50-100m water depths (Moore *et al.*, 2002). Sightings were almost strictly concentrated in the southeastern Bering Sea with one exception of a large aggregation (17 animals) mixed with killer whales and arctic cod in the Central-eastern

Bering Sea (Moore *et al.*, 2002). Small amounts of survey trackline south of the Peninsula and just north of Unimak Pass also revealed the presence of humpback whales (Moore *et al.*, 2002). Results from this study suggested that baleen whales may be re-occupying highly productive oceanographic frontal zones where they were previously abundant during commercial whaling harvests (Moore *et al.*, 2002).

Line-transect surveys were also conducted in 2001, 2002 and 2003 from the Central Aleutian Islands to the Kenai Peninsula (Zerbini *et al.*, 2006b). Humpback whales were found to be coastally distributed from the Kenai Peninsula out to Umnak Island, but none were seen west of Umnak Island on those surveys (Zerbini *et al.*, 2006b). Interestingly, humpback whale distribution between Unalaska and the Shumagin Islands (Eastern Aleutians) was similar across the study years, while aggregations of whales around Kodiak Island showed shifts in distribution across years (Zerbini *et al.*, 2006b). Humpback whales were seen in waters southwest of Kodiak Island, in Marmot Bay and in the Kupreanof Strait in all three years, but areas of high density varied across years, including the Barren Islands, Afognak Island and waters north and west of Kodiak Island (Zerbini *et al.*, 2006b). An examination of small-scale distributions observed during these 2001-2003 studies as well as past surveys of the area indicate that humpback whales were frequently found in former whaling grounds such as Port Hobron and Akutan. However, Zerbini *et al*. (2006b) caution that this alone does not necessarily indicate a recovery to pre-whaling levels.

Most humpback whales showed a high degree of site fidelity to these feeding areas. Of the few within-season interchanges between feeding areas that were observed, the northern Gulf of Alaska was found to have a relatively high rate of interchange with southeastern Alaska and the western Gulf of Alaska (Alaska Peninsula area) (Calambokidis *et al.*, 2008). Additionally, the Eastern Aleutians and the southern Bering Sea also had relatively high rates of within-season interchange (Calambokidis *et al.*, 2008). Between seasons, interchange was observed between the northern and western Gulf of Alaska at an intermediate rate (Calambokidis *et al.*, 2008).

Russia Mainland and Commander Islands feeding areas

As part of the SPLASH project, surveys were conducted around the Commander Islands and along the Kamchatka Peninsula north into the Bering Sea. Humpback whales were found in three main regions; the Commander Islands, one area off the east side of Kamchatka and in the Gulf of Anadyr at the northern end of the Bering Sea (Calambokidis *et al.*, 2008).

Breeding Areas

Humpback whale breeding and calving occurs in three broad regions in the North Pacific: the eastern North Pacific, the Hawaiian Islands and the western North Pacific. Some degree of interchange exists within each of these breeding areas (e.g., between Mainland Mexico and Baja California Mexico). However, the degree of interchange within each breeding area varies substantially between regions. Results from the SPLASH study suggest that Hawaii is one breeding region, rather than multiple breeding regions, given the amount of exchange between islands. However, the western and eastern North Pacific breeding areas showed a higher degree of structure and isolation of sub-areas within each region.

Movement between these three broad breeding regions also exists, though frequency of exchange is thought to be low. The SPLASH study found that two whales were known to have moved between the western North Pacific breeding region and Hawaii, and that 17 moved between the eastern North Pacific breeding region and Hawaii (Calambokidis *et al.,* 2008). Calambokidis *et al.* (2001) found four transits of three individual whales between Japan and Hawaii as well as six transits of five individual whales between Mexico and Hawaii (three from the Islas Revillagigedos and two from Baja California). Sightings of the same whale on different breeding grounds were always in different years. Salden *et al*. (1999) documented the movement of three humpback whales between Japan and Hawaii, two of which were observed in both locations over a 10-12 year period.

A significant male bias has often been observed on breeding areas. Biopsy sampling from the SPLASH project found a male to female ratio of greater than 2 to 1 on breeding areas overall (Baker *et al.*, 2008). Of the animals for which sex was known offshore of California, males were more than twice as likely to be sighted on a breeding ground than females identified from California (Calambokidis *et al.*, 2000b).

Hawaii

A high degree of interchange between waters off each of the principal islands has been observed for humpback whales in Hawaii. Transits between the islands of Kauai and Hawaii were observed to be relatively common, with approximately even numbers of whales moving northwest or southeast (Cerchio *et al.*, 1998). Males are found to move between islands more frequently than females, but overall it appears that whales are more likely to be found around the same island within seasons. Observations suggest that though transits may be made between islands relatively quickly, observations of individual whales between islands appear to be more common between seasons (Cerchio *et al.*, 1998). Additionally, animals may move as a group or loose aggregation within a winter season, causing fluxes in local abundances. These patterns in distribution and movement may also differ across subgroups. This low island-specific fidelity further suggests that Hawaii be treated as a single breeding region. The amount of interchange between islands does not show a simple relationship with geographic distance (Calambokidis *et al.*, 2008).

Although the main Hawaiian Islands are a well studied habitat of humpback whales, it is interesting to note that historical whaling records indicate that humpbacks may not have used the main Hawaiian Islands as breeding habitat as recently as 200 years ago (Herman, 1979). The Northwest Hawaiian Islands have been surveyed to a much lesser degree than the main Hawaiian Islands. A pilot study carried out in 2007 surveyed likely humpback habitat identified by habitat modeling and found whales occupying expected habitat types similar to those they inhabit in the main Hawaiian Islands and other breeding areas (Johnston *et al.*, 2007). Though numbers of sightings were relatively low, behavior, vocalizations and group composition were indicative of breeding activity. Previously posed as a migratory route, observations from this study and a telemetry study suggest that the Northwest Hawaiian Islands are used by humpback whales as a breeding ground (Johnston *et al.*, 2007). It is difficult to determine whether these observations indicate a range expansion, or a recent scientific discovery of an established breeding habitat. From 1980 to 1990, numbers of animals around Kauai and Niihau Islands were observed to increase, and one suggested reason for this is a range expansion as population densities increased in the four-islands region (Mobley *et al.*, 1999). Findings from the SPLASH project suggest that there is a yet undiscovered breeding ground in the North Pacific. Though the Northwest Hawaiian Islands may be another breeding area for some of the more westerly feeding humpback whales, more research is needed to confirm this.

The majority of humpback whales in Hawaii were found in shallow water of 100 fathoms. However, acoustic detections indicated that 50% of singers detected are located in deeper water (Frankel *et al.*, 1995). The density of singers was higher in shallower water since the total area was smaller, but the relatively even split in abundance suggested that these different habitats have different functional roles for singers (Frankel *et al.*, 1995).

In addition to singers displaying different water depth distributions from the rest of the population, habitat selection and therefore distribution also varied for females at different reproductive stages. One study found mothers with calves were more frequently observed in waters on the west side of Maui than on the northwest side of Hawaii (Craig and Herman, 2000). Calves represented a more significant part of the population offshore of Maui (Craig and Herman, 2000). Mothers and calves were distributed in shallow water more often than non-calf groups (Smultea, 1994). These distributional differences may also vary over time, as dates of arrival into breeding areas are thought to be later for females with calves than for females without calves or for males (Craig and Herman, 2000). Differences in distribution and density for different sectors of the population have important implications in abundance estimation, since regional and temporal aggregations must be considered before assuming that sampled densities are representative of the pattern observed through the entire population.

Males showed evidence of a higher rate of return to Hawaiian breeding grounds and were present in higher numbers than females (Craig and Herman, 1997). It was found that individual males were resighted for a greater number of years than females and that more males were seen in consecutive years than females (Craig and Herman, 1997). From these data, and in light of evidence of even sex ratios in the population as a whole, Craig and Herman (Craig and Herman) concluded that individual males likely complete the migration to breeding grounds more often than individual females. Divergence from parity has been observed on humpback breeding grounds, and during migration in other regions, from historical whaling catch data or more recent biopsy data (Brown and Corkeron, 1995; Chittleborough, 1965; Dawbin, 1966; Mackintosh, 1942).

Western North Pacific

Of the three breeding regions, the western North Pacific breeding region remains the least studied. Historically, humpback whales were caught in the winter around Taiwan, Hainan, the Ogasawara, Mariana, Marshall and Ryukyu Islands (Darling and Mori, 1993b). Currently, there are few records of humpback whales offshore of Taiwan and Saipan. A humpback whale sighted offshore of Saipan in 1991 made the front page of the local newspaper, indicating the rarity of such an occurrence at that time (Darling and Mori, 1993b). Recently, humpback whales have also been observed in Okinawa and Ogasawara, at a more northerly location than the other Western North Pacific breeding area. This may be the northern remnant of a larger pre-whaling distribution across the region. Additionally, humpback whales have been observed in the Philippines, significantly south of these areas.

Darling and Mori (1993a) suggested the same stock of whales occupied both Ogasawara and Okinawa, but with small sample sizes it was unclear if individual whales used both areas in one breeding season. Greater sampling effort at these regions in recent years revealed that Ogasawara and Okinawa were distinct from one another, with a small degree of interchange both within and between years (Calambokidis *et al.*, 2008). Ten humpback whales from Okinawa were sighted in Ogasawara and five whales from both Okinawa and Ogasawara were observed in the Philippines (Calambokidis *et al.*, 2008). Less data were available from the Philippines but this area also appears to be distinct from Okinawa and Ogasawara (Calambokidis *et al.*, 2008; Witteveen *et al.*, 2009). Isotopic analysis showed that the Philippines shared a similar $d^{13}C$ signature with Okinawa but not Ogasawara, implying that humpback whales from the Philippines and Okinawa may have had more overlap in feeding destinations (Witteveen *et al.*, 2009).

Multiple studies have found low rates of interchange between the Hawaiian breeding area and the western North Pacific breeding area (Calambokidis *et al.*, 2008; Calambokidis *et al.*, 2001; Darling and Cerchio, 1993; Salden *et al.*, 1999). All matches of individually identified whales to date have been from two different breeding seasons with at least one feeding season in between. Some individual whales have been observed to alternate between Hawaii and Asia multiple times across years, displaying a high degree of plasticity in movement, while other individuals display very high site fidelity (Salden *et al.*, 1999).

Eastern North Pacific

The breeding region in the eastern North Pacific includes mainland Mexico, the Baja California Peninsula, Mexico, the Revillagigedos Islands, Mexico and Central America. A variable degree of interchange occurs between these four regions.

Humpback whales have been observed along the mainland coast of Mexico from Mazatlan to Oaxaca including the waters around Isla Isabel, Isla Tres Marias and Bahia de Banderas (Urban-R and Aguayo L, 1987). The seasonal distribution of humpback whales in this area is November to June, which is similar to that of the Revillagigedos Islands but different than the Baja California Peninsula where individuals appeared to arrive in September and remained in the area until April or May (Urban-R and Aguayo L, 1987). The distribution of humpback whales offshore of Baja California is centered at the southern end of the peninsula and extended from the western side of the peninsula beginning near Bahia Magdalena to the eastern side as far north along the peninsula as Bahia de La Paz (Urban *et al.*, 2000; Urban-R and Aguayo L, 1987). Humpback whales have been observed in the Revillagigedo Archipelago at Isla Socorro, Isla Clarion and Isla Benedicto, but the majority of surveys have been focused around Isla Socorro. Humpback whales in the three Mexican Pacific areas occupied waters less than 200m in depth (Urban-R and Aguayo L, 1987).

The highest rate of interchange of humpback whales within the Mexican Pacific breeding area has been observed between Baja California and the mainland (Calambokidis *et al.*, 2008). Migratory destinations for humpback whales from Baja California Sur and the mainland showed a similar composition (mainly California-Oregon, British Columbia and northern Gulf of Alaska) while the main migratory destinations for humpback whales from the Revillagigedos Islands differed, traveling to known summering areas in northern Gulf of Alaska, western Gulf of Alaska, Bering and southeastern Alaska. Based on this interchange and migratory destination information, the Baja and Mainland populations have previously been grouped together as the coastal population separate from the Revillagigedos Islands population (Urban *et al.*, 2000; Urban-R and Aguayo L, 1987). Recent results from the SPLASH study indicate that Baja California and the Mainland were not significantly different genetically, nor were Baja California and the Revillagigedos Islands. However, the Revillagigedos Islands and the Mainland were significantly differentiated (at $p<0.05$ but not at $p<0.01$) (Baker *et al.*, 2008). Baja California may be both a breeding destination for some whales and a migration route for whales destined for other breeding destinations in the eastern North Pacific.

Another breeding area for humpback whales exists offshore of Central America along the western coasts of Costa Rica, Panama, Guatemala, El Salvador, Honduras, and Nicaragua (Calambokidis *et al.*, 2008; Rasmussen *et al.*, 2002). Observations of humpback whales have been made offshore of northern and southern Costa Rica from Isla Ballena south to Drake's Bay (Rasmussen *et al.*, 2002). Survey effort in Golfo Dulce, Costa Rica has not yielded many sightings (Rasmussen *et al.*, 2002). Frequencies of sightings of humpback whales appear to fluctuate over the course of the winter season, with whale sightings peaking at slightly different times in each area (Rasmussen *et al.*, 2002). Observations of humpback whales have also been made off the coast of Panama but to a lesser degree. A small number of individual humpback whales have been sighted in both Panama and Costa Rica (Rasmussen *et al.*, 2002).

Migration

Much research effort has been focused on the population structure of humpback whales in the North Pacific. Strong fidelity to both feeding and breeding sites has been observed, but movements between feeding and breeding areas are complex and varied. An overall pattern of migration has recently emerged. Asia and Mexico/Central America were found to be the dominant breeding areas for humpback whales that migrate to feeding areas in lower latitudes and more coastal areas on each side of the Pacific, such as California and Russia. The Revillagigedo Archipelago and Hawaiian Islands were the primary winter migratory destination for humpback whales that feed in the more central and higher latitude areas (Calambokidis *et al.*, 2008). However, there were exceptions to this pattern, and it seems that complex population structure and strong site fidelity coexist with lesser known, but potentially high, levels of plasticity in the movements of humpback whales (Calambokidis *et al.*, 2008). Additionally, the SPLASH data suggested that there is a yet undiscovered breeding area in the North Pacific, as humpback whales from the Aleutian Islands and the Bering Sea were not well represented in the samples from any breeding area (Calambokidis *et al.*, 2008).

Individuals from numerous breeding areas are found in the same feeding area. When considered by breeding region, migrations have been documented from Central America to northern Washington-southern British Columbia and California-Oregon; Mexico to every feeding ground; Hawaii to every feeding ground and Japan to every feeding ground except California-Oregon and southeastern Alaska. Many of these connections were based on observations of only a few individuals, and as a result it is unknown how common some of these patterns may be. Taking into account the subdivisions within the breeding regions, a higher degree of feeding area specificity is apparent.

Eastern Pacific

Humpback whales from Central America were found to migrate, almost exclusively (~86% of all matches made between Central America and a feeding ground), to the California-Oregon feeding area with a few matches to northern Washington-southern British Columbia (Calambokidis *et al.*, 2000a; Calambokidis *et al.*, 2008). Rasmussen *et al.* (2002) speculated that this high match rate to only one feeding ground may be a result of geographic distance since Central America is the farthest breeding area south and to reduce travel, humpback whales may be apt to utilize the most southern feeding area as well. These whales were then typically found offshore of southern California when on the feeding ground (Calambokidis *et al.*, 2000a).

Mainland Mexico had a much more varied migratory composition than Central America (Urban *et al.*, 2000). The most frequent connection was still to the California-Oregon feeding area, followed by the northern Washington-southern British Columbia feeding area. A significant number of individuals also migrated to the northern Gulf of Alaska. Other areas included the Bering Sea and southeastern Alaska and, to a lesser extent, the western Gulf of Alaska and northern British Columbia (Calambokidis *et al.*, 2008). When on the California-Oregon feeding ground, these whales were typically found in more northerly waters (Calambokidis *et al.*, 2000a).

Humpback whales from the Revillagigedos Islands migrated to a variety of feeding destinations (Urban *et al.*, 2000). The greatest numbers of connections were to the northern Gulf of Alaska, then the western Gulf of Alaska, the Bering Sea, southeastern Alaska and northern British Columbia all in relatively equal frequency (Calambokidis *et al.*, 2008). A few matches were made to northern Washington and southern British Columbia, Russia and California-Oregon (Calambokidis *et al.*, 2000a). It is notable that there are few matches from the Revillagigedos Islands to California-Oregon, while California-Oregon was the most common destination for animals migrating from mainland Mexico.

Humpback whales migrating from waters off Baja California most frequently traveled to either the California-Oregon feeding area or the northern Gulf of Alaska (Calambokidis *et al.*, 2008; Urban *et al.*, 2000). Other migratory destinations included the western Gulf of Alaska, the Bering Sea and the northern Washington-southern British Columbia feeding areas. The Aleutians, southeastern Alaska and northern British Columbia were all also observed destinations of a few humpback whales from the Baja California breeding area. When observed in the California-Oregon feeding area, the humpback whales from the Baja California breeding area had an intermediate distribution between those from Central America and the Mexican mainland (Calambokidis *et al.*, 2000a). Baja California appears to function partly as a late-season mixing area for whales coming from the Mainland and the Revillagigedos (Calambokidis *et al.*, 2008; Urban *et al.*, 2000).

Central Pacific

Humpback whales breeding in Hawaii have been observed to migrate to every feeding ground in the North Pacific with the majority of individuals migrating to southeastern Alaska (Calambokidis *et al.*, 2008). The neighboring feeding regions of northern British Columbia and the northern Gulf of Alaska were also very common migratory destinations for humpback whales that wintered in Hawaii. The Bering Sea was also a common destination. Among those individuals from the Bering Sea that matched to any breeding area, the vast majority of whales were from Hawaii.

Western Pacific

The western North Pacific breeding grounds are found in fewer feeding locations than the other breeding regions. However it is worth noting that this area has not had the same degree of survey effort as the other regions.

The Russian feeding areas are the least studied humpback whale feeding area in the North Pacific. Individuals on the eastern side of the Kamchatka Peninsula have been observed to migrate to all three known Asian breeding grounds, but matches of known individual whales have not been made with Hawaiian or Mexican area breeding grounds. However, individuals from the Commander Islands and the Gulf of Anadyr have been linked to Hawaii and Mexico more often than to Asian breeding areas. These results suggest that the Commander Islands and Gulf of Anadyr may be more accurately grouped with the Aleutian Island and Bering Sea feeding areas respectively (Calambokidis *et al.*, 2008).

Humpback whales from the Philippines have only been observed to migrate to the Russian feeding grounds, but low sample sizes in the Philippines may have limited to chance of detecting other migratory matches (Calambokidis *et al.*, 2008). Okinawa appeared tightly linked to Russian feeding areas, though some whales also migrated to the Aleutians and the Bering Sea (Calambokidis *et al.*, 2008; Nishiwaki, 1966). Whales occurring in the Ogasawara area appear to be the most varied with respect to migratory destination and that region may be somewhat analogous to the Baja California area in acting as a migratory stop-over point for animals from multiple areas. Individuals migrated to Russia, the Bering Sea and the western and northern Gulf of Alaska (Calambokidis *et al.*, 2008). One individual was previously matched between Ogasawara and southern British Columbia. It was first observed off Japan in April 1990 and March

1991, and then again five months after the March observation in British Columbia in August 1991. It was then resighted offshore of Japan in 1993, having returned to the Ogasawara breeding area (Darling *et al.*, 1996).

Genetic Differentiation

A high degree of genetic differentiation exists between most humpback whale breeding and feeding area aggregations within the North Pacific basin (see North Pacific 'Genetic Differentiation' for an introduction to genetic differentiation). Analysis of Molecular Variance (AMOVA) of mtDNA haplotypes showed significant differences among 8 feeding areas (overall $F_{ST} = 0.179$, $p<0.001$) and among 6 breeding areas (overall $F_{ST} = 0.106$, $p<0.001$) (Baker *et al.*, 2008). Sample sizes in a few regions were too small for comparison, but where these were adequate, pair-wise F_{ST} comparisons revealed that nearly all feeding aggregations were significantly distinct from one another, with a few exceptions (Baker *et al.*, 2008). The Bering Sea and the Eastern Aleutian Islands were not significantly different from each other or from the Western or Northern Gulf of Alaska (Baker *et al.*, 2008). Northern British Columbia and southeastern Alaska were also not significantly different from one another (Baker *et al.*, 2008). Though most pair-wise comparisons were significant, there was considerable variation in F_{ST} values, with some regions showing markedly high levels of differentiation. California-Oregon, southeastern Alaska and Russia were particuarly distinct from one another ($F_{ST}=0.478$, $p<0.001$) (Baker *et al.*, 2008).

Breeding ground comparisons, for which there were adequate sample sizes, showed that all areas were distinct from one another with the exception of Baja California, Mexico which did not differ significantly from the Revillagigedos Islands or mainland Mexico regions (Baker *et al.*, 2008).

Comparisons between most breeding and feeding areas also showed significant genetic differences, even for areas with strong migratory connections. Okinawa differed from every feeding ground, while southeastern Alaska differed from every breeding ground (Baker *et al.*, 2008). Some known migratory pathways were supported by the genetic comparisons, though not consistently by region. Humpback whales sampled in the California-Oregon feeding area did not differ significantly from those sampled in the Central America breeding area, though they did differ from those sampled in the mainland Mexico breeding area (Baker *et al.*, 2008). Additionally, the genetic composition of humpback whales sampled in the Western Gulf of Alaska was not significantly different from the genetic composition of whales sampled off the Revillagigedos Islands or Baja, Mexico but was different from the genetic composition of humpback whales sampled off mainland Mexico (Baker *et al.*, 2008).

Nuclear DNA analysis is not yet completed for the SPLASH project. Previous nuclear DNA work has supported the distinction of the California feeding stock from the southeastern Alaska feeding stock (Baker *et al.*, 1998).

B) Abundance

Regional Estimates

Breeding Areas

The size of whale populations frequenting each breeding area was most recently estimated at 10,000 individuals in Hawaii; 6,000-7,000 animals in the Mexican areas with Baja California being the largest at 5,000 and 750 individuals in both the mainland Mexico and the Revillagigedos Islands breeding aggregations; 1,000 for the western Pacific areas; and 500 for Central America (Calambokidis *et al.*, 2008).

Feeding Areas

The population of whales occurring in the California-Oregon area was estimated to be between 1,400 and 1,700 animals in 2004-2006 (Calambokidis *et al.*, 2008). Mark-recapture studies showed increasing abundance from 1991-1997, a decrease in 1999-2001 and an increase in 2002-2003 (Barlow, 1995; Calambokidis *et al.*, 2004; Calambokidis *et al.*, 1993). Line-transect surveys estimated an abundance of 1,769 humpback whales in 2005 (Barlow and Forney, 2007). The most recent mark-recapture study of the California-Oregon population provided a population estimate of 2,043, the largest to date for this area (Calambokidis, 2009). Though this population has been increasing overall since 1991, the population size estimates have varied substantially. The potential for immigration from other populations has been considered and ruled out.

The southern British Columbia/northern Washington population appears to be the smallest feeding aggregation in the North Pacific with estimates from SPLASH data of less than 500 animals (Calambokidis *et al.*, 2008). Conversely, the northern British Columbia population was grouped with the southeastern Alaska population for abundance estimates, yielding the largest of the feeding populations in the North Pacific with estimates from SPLASH data placing it around 3,000-5,000 animals (Calambokidis *et al.*, 2008). Additionally, abundance has been estimated for the Shumagin Islands separately at 410 individuals in 2002 and for the more northern part of southeastern Alaska at 961 individuals (Straley *et al.*, 2009; Witteveen *et al.*, 2004). The most recent estimates of abundance for the feeding areas west of southeastern Alaska are 6,000-14,000 for the Aleutians and Bering Sea areas combined, and 3,000-5,000 for the western and northern Gulf of Alaska combined (Calambokidis *et al.*, 2008). At a finer geographical scale, humpback whales were also estimated to number approximately 2,644 between the Kenai Peninsula and Unimak Island and 102 in the southeastern Bering Sea (Moore *et al.*, 2002; Zerbini *et al.*, 2006b).

Basin-wide

The most current estimate of abundance for the entire North Pacific basin, resulting from the SPLASH project, is 18,302 individuals (Calambokidis *et al.*, 2008) This is significantly larger than any previous estimates for the basin and is greater than some of the published estimates of pre-whaling abundances (Rice, 1978). This estimate has been corrected for some known biases, and although other biases may be influencing this estimate, they are likely to be negative, making this estimate a conservative one (Calambokidis *et al.*, 2008). Barlow *et al.* **(**submitted**)** used the SPLASH data to make a new estimate of humpback whale abundance in the North Pacific by correcting for some of the known biases, such as those caused by not sampling calves and by births and deaths between sampling periods. This new estimate (21,808 CV=0.04) is higher than previous estimates but may still be an underestimate of actual humpback whale abundance due to biases that could not be corrected with available data.

C) Genetic Diversity

A total of 28 mitochondrial haplotypes were found in the North Pacific population from sampling during the SPLASH project (Baker *et al.*, 2008). Haplotype diversity was calculated for each feeding and breeding area in the SPLASH data set. Of the feeding regions, the more central areas (southeastern Alaska, northern British Columbia and northern Gulf of Alaska) had the lowest haplotype diversity, while the eastern and western feeding areas had higher diversity (Baker *et al.*, 2008). For the breeding grounds, Ogasawara, all three Mexican areas and Central America displayed high haplotype diversity, while Hawaii, Okinawa and the Philippines had slightly lower diversity (Baker *et al.*, 2008).

Nucleotide diversity in humpback whales in the North Pacific basin is lower than that found among humpback whales sampled in the Atlantic Ocean (Baker and Medrano-González, 2002). Within the basin, the California feeding area and Mexican breeding areas had the highest levels of nucleotide diversity while Alaska had the lowest (Baker and Medrano-González, 2002).

D) Trends

Trends in abundance have been calculated for some regions of the North Pacific as well as for the North Pacific overall. The only other mark-recapture study to examine North Pacific abundance on a basin scale was the NPAC study based on photographic identifications of individual whales from 1990-1993 from 3 wintering regions (Hawaii, Mexico, Japan) and feeding areas from California to the Aleutian Islands (Calambokidis *et al.*, 1997). Comparing the NPAC best estimate of 6,010 to the SPLASH results gives an estimate of 4.9% annual increase over the 13-year time span. If the SPLASH results are compared to the basin-wide estimate made in 1966 by Johnson and Wolman (1984) of approximately 1,200 individuals, a 6.8% annual increase is found for the 39-year time span (Calambokidis *et al.*, 2008).

Other growth rates have been calculated on more regional scales including ~8% per year for the U.S. West Coast from 1991-2008 and 6.6% per year for the Alaskan Peninsula and Aleutian Islands from 2001-2003 (Calambokidis, 2009; Zerbini *et al.*, 2006b). Between 1991 and 2007, a 10.6% annual increase in population size was calculated for southeastern Alaska (Dahlheim *et al.*, 2009).

Using regional estimates from the NPAC study (1990-1993) and the SPLASH study (2004-2006), trends were calculated for Hawaii and Asia. The humpback whale population found in waters off Hawaii showed an annual growth rate of 5.5-6.0%, and an annual growth rate of 6.7% was observed in the western Pacific population (Calambokidis *et al.*, 2008). The western Pacific estimate is less robust, however, as sampling effort was significantly greater in the SPLASH study, which may bias the western Pacific estimate upwards (Calambokidis *et al.*, 2008).

E) Habitat or Ecosystem Conditions

Humpback whales utilize a wide variety of habitats in the North Pacific while in feeding and breeding areas and during migrations. Though there are a few exceptions, most whales on breeding areas have been found in water depths of less than 200m (Chittleborough, 1953; Oviedo and Solis, 2008; Winn *et al.*, 1975). The lower temperature limit for suitable humpback whale breeding habitat is estimated at 21.1°C (Rasmussen *et al.*, 2007). Some studies have found humpback whale distribution to be correlated with group composition (e.g., females with calves, solo animals, singers etc.,) such as those discussed in the Hawaii distribution section above (Craig and Herman, 2000; Frankel *et al.*, 1995; Smultea, 1994). However, in Costa Rica, distinct habitat use patterns by different group types were absent and all individuals were found to co-occur in the same two locations: the east coast of Cano Island and the west coast of Osa Peninsula from Drake Bay to Punta Salsipuedes (Oviedo and Solis, 2008). In both these areas, the water is less than 100m in depth and the slope angle is 10% or less. Cano Island and Osa Peninsula serve as both a breeding area and nursery site (Oviedo and Solis, 2008).

In feeding areas in the Pacific, there are variable patterns of habitat use from coastal areas to areas quite distant from shore with varying oceanographic characteristics. In southeastern Alaska, habitat use has been observed to change throughout the season, with Glacier Bay and Icy Strait having greater densities of humpback whales in June and July with a prey base of euphausiids, while Frederick Sound and Stephens Passage showed greater numbers of whales in August and September with a prey base of fish (Baker *et al.*, 1992). Some individuals were observed to remain in these localized habitats throughout the season, suggesting that for some individual whales, habitat specificity is quite high. This demonstrates that humpback whale prey-choice may vary within a season or across geographic area. There is some evidence suggesting that these prey choice shifts may also exist on longer than seasonal time scales as larger-scale changes in the oceanographic environment (e.g. Pacific Decadal Oscillation or El Nino Southern Oscillation) cause fluctuations in prey availability (Calambokidis, pers. comm. 2009).

In the southeastern Bering Sea, humpbacks were regularly associated with the Inner Front, a front found around the 50m depth contour and characterized by high mixing rates and nutrient-supplying cold belts (seasonal summer bands of cold surface water found towards the shoreward edge of the front) resulting in high productivity (Kachel *et al.*, 2002). A dramatic shift in the relative abundance of fish species was observed in the Gulf of Alaska in the late 1970s when the abundance of shrimp and small fish declined drastically and was replaced by pollock and flatfish (Anderson and Piatt, 1999). An estimate of prey requirements for humpbacks feeding around Kodiak Island is 2.37×10^6 kg of pollock which is equal to nearly 22% of the 2002 commercial Pollock catch and may actually be as high as 30% (Witteveen *et al.*, 2004). Whether this adaptation to a pollock-dominated prey base has had any impact on humpbacks in the area is unclear. In the California current, humpbacks are observed to shift their foraging habitat as local oceanography changes through the summer, feeding offshore in the early part of the summer and moving coastward in August (Tynan *et al.*, 2005; Yen *et al.*, 2004). Areas of high humpback density vary among years as well, likely as a consequence of oceanography and resulting prey field differences (Calambokidis *et al.*, 1991).

F) Threats and anthropogenic impacts

Specific information on threats is not available for all areas and habitats in the North Pacific occupied by humpback whales throughout their life cycle. Significantly more data, observations, and reporting are available from US waters in relation to human-related threats than from other regions in the North Pacific. Though the information is low in some areas, it is clear that threats are present. Examination of SPLASH photographs found over 20% of individuals showed signs of entanglement scarring in all known feeding areas in the North Pacific with some areas having greater than 50% scarring rates. The paucity of information on threats and their corresponding magnitudes on the high seas and in the waters of other nations should be considered when examining population abundances, structure and trends.

US West Coast

Ship strikes have been reported along the Canadian coastline and from Washington down through southern California. Compared to the US east coast, the number of ship strikes involving humpbacks appears to be lower on the west coast overall but is twice as high as reported collision occurrences in Hawaii and Alaska. Data from the NMFS stranding network database for the US Northwest shows a total of 17 records involving humpback whales. Three of the records reported fishery interaction, two reported boat interaction and five records were inconclusive as to whether human interaction was involved. The IWC ship strike database also listed two humpbacks struck offshore of California, but no further information was available regarding the fate of the whale or severity of the incident. Douglas *et al.* (2008) summarized ship strike information off the Washington coast and the Strait of Juan de Fuca between 1980-2006 and found only one record of ship-struck humpback, located on the Pacific coast north of Gray's Harbor, Washington, one from 1980-2006 on the "outer" coast north of Grays Harbor. The whale was believed to be sexually immature, which is consistent with trends towards a greater percentage of immature humpback whales being involved in collisions as seen in other regions. The low rate of ship strikes off the Washington coast despite the high levels of ship traffic in the area was hypothesized to be caused by underreporting of such events and the smaller concentrations of humpbacks in this area compared to locations like Hawaii and Alaska (Douglas *et al.*, 2008). Between 2002 and 2006, there were seven injuries and one death resulting from ship strikes reported for unidentified whales in the California-Oregon-Washington stock as defined by NMFS (Carretta *et al.*, 2008).

Levels of persistent organic pollutants are known to be relatively high in marine mammals, though typically lower in mysticetes as compared to odontocetes due to their different trophic levels. Southern California humpbacks were found to have the highest levels of DDT, PCBs, and PBDEs of all North Pacific humpbacks sampled on their feeding grounds (Elfes *et al.*, 2010). The DDT levels detected were greater than those found in the typically more contaminated Gulf of Maine humpbacks due to the historic dumping of DDT off Palos Verdes Peninsula (Elfes *et al.*, 2010). The population level impact of contaminants is still difficult to determine, though Elfes (2010) suggests the levels found in humpbacks are unlikely to have a significant impact on their persistence as a population.

Of all feeding areas assessed, California had the highest incidence of rake marks attributed to killer whale attacks (20%) (Steiger *et al.*, 2008). Most of the attacks are thought to occur on breeding/calving grounds when the whales are calves, and this high percentage observed in California likely results from a high rate of killer whale attacks in Mexican breeding areas (Steiger *et al.*, 2008). Though this percentage is high, it does not appear to be preventing population recovery (Steiger *et al.*, 2008).

Between 2002 and 2006, 12 humpback whales were reported seriously injured in commercial fisheries offshore of California and one was reported dead (Carretta *et al.*, 2008). The fishing gear involved included gillnet, pot and trap gear (Carretta *et al.*, 2008).

Hawaii

Collisions of humpback whales and ships appear to be increasing in Hawaiian waters over the past three decades, with two collisions reported from 1975-1984, six from 1985-1994 and 13 from 1995-2003 (Lammers *et al.*, 2003). Collisions are not evenly distributed geographically. The highest level of reported collisions was from Maui, while Kauai had the lowest (Lammers *et al.*, 2003). Slightly differing from other areas with reported ship strikes, collisions in Hawaii often involve medium sized boats between 31 and 60 ft long (Lammers *et al.*, 2003). Travel speeds were up to 10-30 knots. 61-100ft boats were the second most commonly involved size class, while boats less than 31ft and greater than 100ft comprised less than 16% of reported incidents (Lammers *et al.*, 2003). Whale watch vessels are often involved in reported ship strikes in Hawaii, but as noted by Jensen and Silber (2003), the number of passengers, size of the vessel and mandated regulations make some types of vessel (naval, federal or tourist) more likely to report incidents. Of mariners surveyed in Hawaii, nearly half estimated that less than a quarter of collisions are reported (Lammers *et al.*, 2003). Lammers *et al*. (2007) found that over half the humpback whales in collisions in Hawaii were calves. Data from the IWC Ship Strike database show a total of 44 incidents, most without any details and nine reported as causing injury (compiled from Jensen, 2003; Laist *et al.*, 2001; Lammers *et al.*, 2003). Some evidence exists that humpback whales may avoid areas with high levels of pleasure-craft traffic around Maui (Glockner-Ferrari and Ferrari, 1990).

Seventeen percent of humpback whales in Hawaii were found to have killer whale rake marks, a value close to the average for the entire North Pacific (Steiger *et al.*, 2008). This is not thought to pose a major conservation threat.

Based on SPLASH data, Robbins *et al*. (2007a) found entanglement scarring on 31.6% of the Hawaiian humpback population.

A substantial amount of research has focused on characterizing the acoustic environment of marine mammals and the potentially deleterious effects that increased noise levels in the ocean may have. Though no longer active, the Acoustic Thermometry of Ocean Climate (ATOC) projectors offshore of California and Hawaii were observed to have relatively subtle but significant effects on humpback whales. In Kauai, humpback whales were observed to increase their time and distance traveled between breaths during active sound projection (Frankel and Clark, 2000). Humpback whales also altered their distribution to be at a greater angle and distance away from the sound source, though not always consistently (Frankel and Clark, 2002). The ramifications of these short-term behavioral changes are not yet understood but have implications in an increasingly noisier marine environment. Noise levels from whale watching vessels were monitored, and though some vessels produce noise levels greater than the background noise of signing whales, it was concluded that this was unlikely to have a significant impact on the humpback whales in the area (Au and Green, 2000).

Alaska

Available evidence suggests that ship strikes are also increasing in Alaska (Gabriele *et al.*, 2007a). From 1978-2006, 62 collisions were reported in Alaskan waters, involving a wide range of vessel types and large whale species (Gabriele *et al.*, 2007a). The most commonly reported vessel type was small private boats less than 15m in length. However, this trend may be influenced by reporting and not accurately reflect the true frequency of vessel type involved. Of the 62 collisions, 49 had unknown outcomes and 11 collisions resulted in death of the whale. 46 of the 62 reported collisions involved humpback whales (Gabriele *et al.*, 2007a). Ship strikes were calculated to account for 1.8 fishery-related deaths per year (Angliss, 2008).

A recent assessment found that 78% of whales in northern southeastern Alaska had been non-lethally entangled in fishing gear (Neilson *et al.*, 2009). Between 2003 and 2004, 8% of whales in the Glacier Bay and Icy Strait area acquired new entanglement related scars (Neilson *et al.*, 2009). Calves were found to have lower scarring rates but are thought to have more lethal encounters with entanglement. The results of the study also show that males may have a higher rate of entanglement than females, but it is not known why this difference exists or if it is real and will persist over time (Neilson *et al.*, 2009).

Between 2001 and 2005, 53 incidents of humpback whale entanglement were reported in northern and southeastern Alaska, making the US fishery-related minimum mortality and serious injury rate 3.2 humpbacks for the Central Pacific stock (Angliss, 2008). For western Alaska, one humpback whale death was observed from 2000-2004 through observer coverage of the Bering Sea sablefish pot fishery. In 1997, a humpback was reported by a US Coast Guard vessel as dead and floating entangled in unidentifiable gear (Angliss, 2008). These reports are likely much lower than the actual level of entanglement or stranding, as there are very few reports received from west of Kodiak. The US fishery-related minimum mortality is 0.2 humpbacks for the Western Pacific stock (Angliss, 2008).

Western Pacific

Information on entanglements and ship strikes is rare for western Pacific breeding grounds though some information exists on bycatch. Brownell *et al*. (2000) found 6 records of bycatch and two records of strandings in Japanese and Korean fisheries data between 1995 and 1999. Additionally, humpback whale meat has been identified in markets, though it is unknown if this came from bycatch or not (Baker *et al.*, 2006b; Brownell *et al.*, 2000). In 2004 another humpback whale was reported as stranded and detected in a Korean market (Baker *et al.*, 2006b). Though it is clear that some incidental fisheries mortality occurs and is the source of some whale meat in Asian markets, the magnitude of these catches remains unknown. IWC National Progress Reports from Japan show an average of 1 bycaught and 1 stranded humpback whale per year between 1993 and 2003. Nearly all of the bycatch events involved trap nets.

Marine pollution in Asian waters appears to be quite high compared to other areas. A large-scale study of contaminants in cetaceans around the North Pacific and the coastal waters of India found DDT levels to be high in humpback whales from the Japan Sea, coastal waters of Hong Kong and India (Minh *et al.*, 2000). Though levels in mysticetes or humpback whales specifically from this area are not well known, these high contaminant levels in the same region indicate significant marine pollution.

G) Recovery from Exploitation

An estimated 28,000 humpback whales were removed from the North Pacific in the 20th century before the species was placed under international protection (Rice, 1978). Remaining population sizes may have been as low as 1,000 to 1,400 humpbacks (Gambell, 1976; Johnson and Wolman, 1984). The number of individuals removed is likely an underestimate because of under-reporting by Soviet whaling (Yablokov, 1994). Russian whaling continued in the North Pacific until 1980 (Zemsky *et al.*, 1995).

The California-Oregon population likely remains well below pre-exploitation size despite observed positive population trends over the past decades. The Bay City, WA shore station took 1,331 humpback whales from 1911 to 1919 (Clapham *et al.*, 1997). Shore stations at Moss Landing and Trinidad in California took 1,871 humpback whales between 1919 and 1926 (Clapham *et al.*, 1997). When combined with records from factory ships operating off Alaska and the shore station at Bay City, WA, 5,084 humpback whales were taken from 1919 to 1926 (Clapham *et al.*, 1997). From 1956 to 1965, a further 841 humpback whales were killed by California shore whaling stations, likely depleting this population again while numbers were still low from the earlier 1900s whaling (Clapham *et al.*, 1997). British Columbia coastal whaling stations took 5,638 humpback whales between 1908 and 1967 (Gregr, 2000). Humpbacks offshore of Kodiak Island, Alaska are estimated to have reached a low of 27 individuals in 1938 from a pre-exploitation population of 343 individuals, while their current population is estimated at 157 individuals (Witteveen *et al.*, 2004).

Nishiwaki (1959) estimated that 1,200-1,400 humpback whales migrate past the Ryukyu Islands (Darling and Mori, 1993b). In the Ryukyu Islands, 815 humpback whales were killed between 1954 and 1961, and whaling ceased in 1961 because of a shortage of whales (Darling and Mori, 1993b). Offshore of Ogasawara, 600 humpback whales were killed between 1910 and 1948 while 440 were killed offshore of Taiwan during the same period. Both of these operations closed in 1940s due to depleted stocks (Darling and Mori, 1993b).

For stocks that have calculated trends in the North Pacific, most seem to be increasing. Though there is no comprehensive assessment of the impact of whaling and the number of individuals removed, it appears clear that in most regional feeding and breeding areas, numbers remain lower than pre-exploitation abundances. Additionally, some geographic areas where humpback whales used to be observed do not appear to have been re-colonized (Gregr *et al.*, 2000).

XI STATUS OF THE NORTHERN INDIAN OCEAN POPULATION

A) Distribution and Population Structure

The distribution of humpback whales in the Arabian Sea is known from whaling records (Mikhalev, 1997; Wray and Martin, 1980), observations from merchant vessels (Brown, 1957; Slijper *et al.*, 1964) and winter surveys off the coast of Oman (Minton *et al.*, In press). Oman forms the west coast of the Arabian Sea between 16.5-26.5°N. Sightings and survey data suggest that humpback whales are most concentrated in the shallow near-shore areas off the coast, particularly in the Gulf of Masirah and Kuria Muria Bay regions (Minton, 2004), while sightings and strandings suggest a population range including the northern Gulf of Aden, the Balochistan coast of Pakistan (Gore, pers. comm.), western India and Sri Lanka, with occasional sightings on the Sistan and Baluchistan coasts of Iran and also Iraq (Figure 5, Al Robaae, 1974; Braulik *et al.*, 2010). Illegal Soviet catches along the coasts of Oman, Pakistan and India during November and December in 1966 included >50% of whales (*n*=238) with full stomachs, and a fetal-length distribution similar to that seen in the Northern Hemisphere at the same time of year (Mikhalev, 1997), while singing (an activity associated with mating) was recorded from this region during January-March (the Northern Hemisphere breeding season Whitehead, 1985a). Recent surveys in Oman have confirmed the presence of humpback whales year-round in this region (Baldwin, 2000; Minton *et al.*, In press), following a reproductive cycle similar to that of seasonally migratory breeding populations in the Northern Hemisphere.

Most distribution information is available from the western Arabian Sea, and at present little is known regarding humpback distribution to the east (Reeves *et al.*, 1991). Photo-identification data collected from the coast of Oman suggests a high degree of winter residency in this region, with multiple individuals re-sighted between the Gulf of Masirah and Dhofar (Oman; Minton *et al.*, In press). Despite three years of boat-based surveys in February and October, no humpback whales were seen or detected acoustically in the southern Gulf of Oman (Muscat region), although occasional opportunistic/incidental sightings have been made in the Gulf of Oman (Figure 5).

Migratory connections

Photo-identification re-sights suggest humpback whales may move seasonally between the Dhofar region (Kuria Muria Islands) in winter and the Gulf of Masirah to the north in summer, with similar re-sighting rates between and within regions (Minton *et al.,* In press). During the February/March Dhofar surveys, singing was detected, suggesting breeding activity, and most whales encountered were male, consistent with reports from other humpback breeding grounds (see *Western Indian Ocean*). This is consistent with a January-April breeding season previously proposed from whaling data (Mikhalev, 1997; Mikhalev, 2000). During the Gulf of Masirah October/November surveys, equal sex ratios were encountered and no singing was detected. Feeding has been observed in both regions and seasons, though more commonly in the Gulf of Masirah. Whaling data indicate that feeding occurs along the coasts of Oman, Pakistan and India, where monsoon-driven upwelling regions may produce primary productivity sufficient for feeding (Mikhalev, 1997). However dedicated summer (May to September) surveys have not yet been carried out due to the Southwest monsoon which creates dense fog and heavy swells not suitable for small-boat surveys.

Population Structure (between breeding regions)

Genetic samples (nuclear microsatellites and mitochondrial control region) and fluke pigmentation markings indicate that this breeding population is significantly differentiated from other Indian Ocean Southern Hemisphere breeding grounds (Pomilla pers comm., Rosenbaum *et al.*, 2009). Nuclear genetic analysis suggests that this population is the most strongly and significantly differentiated in all comparisons among other Indian Ocean and South Atlantic breeding populations (pair-wise FST range between Oman and other Indian Ocean breeding populations 0.38-0.48, Pomilla *et al.*, 2006). Levels of mitochondrial differentiation between Oman and other Indian Ocean breeding grounds are around ten times higher than among the other breeding grounds (pair-wise FST range between Oman and other Indian Ocean breeding populations 0.11-0.15, Rosenbaum *et al.*, 2009).

Despite extensive comparisons of photo-identification catalogs and genotyped individuals between Oman and the other Indian Ocean catalogs and genetic datasets, no matches have been detected between regions (Minton *et al.*, 2010; Pomilla *et al.*, 2006). Humpback whales from this region carry fewer and smaller barnacles than other Southern Hemisphere whales and do not exhibit the white oval scars indicative of cookie cutter shark bites, a feature very commonly seen on other Southern Hemisphere humpback whales (Mikhalev, 1997). Connections with the Northern Hemisphere are highly unlikely, as there is no northward passage through the Arabian Sea, the Indian Ocean population shares no mitochondrial haplotypes in common with the North Pacific and song patterns are very different (Rosenbaum *et al.*, 2009; Whitehead, 1985a), suggesting that whales from these populations have no recent biological connectivity.

B) Abundance

Mark-recapture studies using three different pairings of tail fluke photographs collected in Oman in two main research areas over a period of four and a half years (2000-2004) yielded a population estimate of 82 individuals (95% CI 60-111). However, sample sizes are small, and there are various sources of possible negative bias, including insufficient spatial and temporal coverage of the population's suspected range (Minton *et al.,* In press).

Cow-calf pairs were very rarely observed in surveys off the coast of Oman, composing only 7% of encounters in Dhofar, and not encountered at all after 2001. Whaling catches off Oman, Pakistan and northwest India also included low numbers of lactating females (3.5% of mature females) relative to pregnant females (46% of mature females); catches occurred during the winter calving season, so many calves may be expected to have weaned by this time. However a low proportion of immature whales (12.4% of all females) was also found, even though catches were indiscriminate with respect to sex and condition (Mikhalev, 1997). This suggests one or more of the following possibilities; (1) calf mortality in this population is high, (2) the whales have reproductive 'boom and bust' cycles which respond to high annual variation in productivity, (3) the main calving and nursery area may be outside the whaling and survey regions. Given the small estimate of abundance provided by the recent survey, the first two possibilities seem most likely.

C) Genetic Diversity

For an introduction to genetic diversity, see 'Genetic Diversity' in the 'Status of North Atlantic Populations' section. Nuclear and mitochondrial genetic diversity of humpback whales from Oman (up to 47 individuals sampled) is the lowest among all Southern Hemisphere breeding grounds (Pomilla, pers comm.,12 Olavarría *et al.*, 2007; Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009). Mitochondrial analysis revealed only eight distinct maternal lineages (haplotypes), half of which are private to Oman (not detected on other breeding grounds, Pomilla *et al.*, 2006). Nuclear observed heterozygosity is 0.71 (SD 0.02), mitochondrial haplotype diversity is 0.69 (SD 0.050) and mitochondrial nucleotide diversity is 0.02 (SD 0.01) (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009).

D) Trends

No trends in abundance are available from this region.

E) Habitat or Ecosystem Conditions

Climatic and oceanographic conditions in the Gulf of Oman and Arabian Sea are strongly influenced by Indian northeast and southwest monsoon systems, to the extent that the Arabian Sea ocean basin completely reverses surface water circulation semi-annually (Burkill, 1999; Kindle and Arnone, 2001). Winter upwellings are driven by the Indian northeast monsoons and create regions of high productivity and extensive algal growth, particularly along the Gulf of Oman coast (Brock and McClain, 1992). In the summer, the southwest monsoons generate an offshore jet stream of wind, which creates strong cold-water upwellings, high productivity and plankton blooms off the Arabian Sea coast of Oman (and to a much smaller extent western Pakistan, Ryther *et al.*, 1966) and low coastal sea-surface temperatures during July and August (Sheppard *et al.*, 1992; Wilson, 2000). The high levels of phytoplankton are associated with a pronounced oxygen minimum layer (caused by decomposing phytoplankton) located at about 1000m depth. As a result of this minimum layer, there is little diel vertical migration of zooplankton (Hitchcock *et al.*, 2002) and the dominant consumers in the ecosystem are mesopelagic copepod-feeders, rather than the clupeids more commonly found in other global upwelling zones.

There is considerable inter-annual variation in the monsoon-driven upwellings, the causes of which are complex but may include El Niño effects (Brock and McClain, 1992). Zooplankton concentrations seem less seasonally influenced than phytoplankton, with no significant differences in biomass observed between seasons (Roman *et al.*, 2000). While primary productivity in the Arabian Sea is of similar magnitude to that found in polar regions where humpback whales feed, the variation in productivity is more pronounced as a result of these oceanographic effects, so climatic effects such as global warming and El Niño events may therefore have a more rapid influence on humpback feeding success in this region.

Shallow protected areas (preferred nursery habitat for humpback whales in other regions) are uncommon in Omani waters, which may explain the limited observations of cow-calf pairs in the surveyed areas (Minton *et al.*, In press). It has been hypothesized that the Gulf of Masirah, which is characterized by shallow, protected waters close to shore and high primary productivity, is good humpback nursery habitat, though logistic challenges have limited winter surveys in this region (Minton *et al.*, In press). Presently one breeding habitat has been identified in Kuria Muria Bay in Dhofar, also a protected, shallow coastal habitat (Minton *et al.*, In press).

F) Threats and Anthropogenic Impacts

The effect of pollutants on cetaceans is a major concern in the region, as the Arabian Sea is a center of intense human activity with poor sea circulation, so pollutants can persist for long periods. Since the 1970s, the coastal and marine infrastructure in Oman has developed at a rapid rate, with over 80% of the population now living within 13 miles from the coast, and expanding development of oil and gas resources and fishing fleets (Minton, 2004). Major ports and harbors, coastal resorts and industrial plants have been constructed, bringing polluting outflow pipes and increased vessel traffic, with greater noise disturbance, reduced water quality and increased ship strike risks in the coastal breeding areas critical for humpback calving. The coast of Oman now ranks as one of the most highly used tanker shipping routes in the world (Kaluza *et al.*, 2010). A high-speed ferry network is also now under development and includes areas considered critical for this population, including Kuria Muria Bay, the Kuria Muria Islands and Masirah Island (Baldwin, pers comm.). Poisonous algal blooms and biotoxins have been implicated in some mass fish, turtle, and possibly cetacean, mortality events on the Oman coast, although no events have yet been known to include humpback whales. Coastal run-off from industrial activities is likely to be increasing rapidly, while regular oil spills in shipping lanes from tankers also contribute to pollution along the coast as oil is advected to coastal areas (e.g. Shriadah, 1999).

Of 23 individual whales for which caudal peduncle photographs were examined for evidence of entanglement or other sources of scarring, 70% had scarring consistent with encounters with fishing gear, although only 39% of these were considered conclusive (Minton *et al.*, In press). A subgroup of individuals represented by the highest quality photographs also revealed 33% with scars likely to have been caused by entanglement. These estimates are likely to be conservative, as entanglement can involve other body parts, and scars can heal and be difficult to detect photographically. This implies that at least 33% of whales had been entangled in fishing gear at some stage.

All ten live entanglement incidents documented between 1990 and 2006 for large baleen whales involved humpback whales entangled with bottom set gillnets, often with weights still attached and anchoring the whales to the ocean floor (Oman Cetacean Database; pers comm. Minton, 2004). The majority of entangled whales (70%) for which length information was documented were juveniles (<10m length). In a survey of 782 beach-cast cetaceans on the beaches of Oman between 1999 and 2003, only one humpback whale was identified among 29 baleen whales, which may reflect their low population abundance in the region or a high degree of self-rescue during entanglement (see '*Entanglement*') (Minton, 2004). However many specimens were too degraded to identify, and stranded humpback whales may have gone undetected. Three verified humpback entanglements and strandings have also been reported from Karachi and Pasni in Pakistan, including one entanglement in a trawl net (Gore, pers. comm.).

There is high fishing pressure in areas off Oman where humpback whales are sighted (Minton, 2004), although the majority of fishery activity is considered artisanal and traditional rather than commercial. Fishing using traps with float lines is frequently deployed around the Dhofar region, while gillnetting from dhows is ubiquitous in the both the Gulf of Masirah and Dhofar regions (Minton, 2004). Levels of fishery bycatch are currently unknown. Humpback whales in Oman also share their prey (*Sardinella spp.*) with tuna and other commercial pelagic fish targeted by the gillnet fisheries.

Seismic surveys have frequently been conducted as part of offshore oil exploration off the coast of the Arabian Sea. This activity brings risks of ship strikes and severe noise disturbance (see *Threats: Anthropogenic Sound*).

Liver damage was detected in 68.5% of necropsied whales during whaling in 1966, with degeneration of peripheral liver sections, cone shaped growths up to 20cm in diameter and blocked bile ducts (Mikhalev, 1997). While this pathology was consistent with infection by trematode parasites, none were identified during necropsy, and the causes of this liver damage remain unknown.

Evidence that this population has undergone a recent genetic bottleneck (see '*Recovery from Exploitation*') and is currently at low abundance (Minton *et al.,* In press) suggests that there may be an additional risk of impacts from increased inbreeding (which may reduce genetic fitness and increase susceptibility to disease) and a reduction in the benefits of sociality and demographic stochasticity (Courchamp *et al.*, 1999), *i.e.* loss of maternal traditions regarding seasonal habitat use and reduced population resilience to fluctuations in calving and survival rates. At low densities, populations are more likely to suffer from the 'Allee' effect, where inbreeding and the heightened difficulty of finding mates reduces the population growth rate in proportion with reducing density.

G) Recovery from Exploitation

In 1966, illegal Soviet whaling killed 238 humpback whales off the coasts of Oman, Pakistan and India over the course of one month (Mikhalev, 1997). Although the estimated abundance of Omani humpback whales is <100 whales (Minton *et al.*, In press; Minton *et al.*, 2008a), there is preliminary genetic evidence from microsatellite data for a recent bottleneck in the population, and mitochondrial data also suggest a decline in diversity (Pomilla pers comm.,[7]).

It is also notable that lengths from catches reported by Mikhalev (1997) were greater in the Arabian Sea than for Southern Hemisphere catches during the same period. Additional observations of high pregnancy rates in the 1960's coupled with low calving rates indicate a small, unexploited population, possibly at equilibrium at the time of whaling. However since available estimates of abundance are very small, and the number of observed cow-calf pairs is unusually low for a humpback breeding ground (Mikhalev, 1997; Minton *et al.*, In press), this population may be unusually vulnerable to the threats of fisheries, coastal development and pollution laid out above. This is of particular concern in light of the numerous lines of evidence suggesting that this population is both spatially, genetically, and demographically isolated from other humpback whale breeding populations in both hemispheres (Mikhalev, 1997; Minton *et al.*, 2010; Minton *et al.*, In press; Minton *et al.*, 2008b; Rosenbaum *et al.*, 2009).

XI STATUS OF SOUTHERN HEMISPHERE POPULATIONS

A) Summary of current IWC stock definitions and divisions

IWC humpback stocks (A-G and X) have traditionally been defined based on wintering grounds known for humpback whales at low latitudes in the Southern Hemisphere. The stocks define breeding grounds in the southwestern Atlantic (A), southeastern Atlantic (B), southwestern Indian Ocean (C), southeastern Indian Ocean (D), southwestern Pacific (E), Oceania (E and F), southeastern Pacific (G) and northern Indian Ocean (X) respectively. These designations have been subdivided in order to reflect improved understanding of substructure within some of these regions: Gabon (B1) and west South Africa (B2) in the southeastern Atlantic; Mozambique (C1), the Comoros Archipelago (C2), Madagascar (C3) and the Mascarene Islands (C4) in the southwestern Indian Ocean, and east Australia (E1), New Caledonia (E2), Tonga (E3), the Cook Islands (F1) and French Polynesia (F2) in the southwestern Pacific and Oceania (illustrated in Appendix 2).

All available population assessments to date have therefore been carried out using these stock definitions. Nearly all information relevant to population assessments of Southern Hemisphere humpback whales has been summarized by breeding ground, or stock, so this is why it is presented in this way in the following Section. One of the major challenges in considering whale populations by breeding ground is estimating how many catches were made from each of these populations during the whaling period, since the mixing of breeding populations at high latitudes is still poorly understood, yet this is where the majority of catches were made. The current stock boundaries agreed by the IWC are

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[7] Pomilla C, Collins T, Minton G, *et al.* (In prep) Genetic distinctiveness and decline of a small population of humpback whales (*Megaptera novaeangliae*) in the Arabian Sea.

shown in Appendix 2 (IWC, In Press) and determine the way that catches from the Antarctic feeding grounds are allocated to their respective stocks in these assessments. These boundaries have changed many times in the last ten years as information pertaining to migratory connections has become available (see IWC, In Press for a summary), so longitudes of all catch allocations are given in the text where population assessments are summarized.

B) Population summary of Antarctic feeding grounds

Compiled estimates of summer encounter rates from Japanese Scouting Vessel (JSV) and IWC International Decade of Cetacean Research (IDCR) surveys between 1976 and 1988 (mainly conducted south of 60°S) found higher encounter rates in the regions 0-60°E, 80-120°E, 150-160°E, 120-180°W and 40-80°W relative to the intervening longitudes; these higher rates were consistent throughout the season and across the years surveyed. The highest encounter rates were obtained in the vicinity of the Western Antarctic Peninsula (Kasamatsu *et al.*, 1996). Feeding grounds north of 60°S have also been described in the southeastern Pacific (Magellan Straits), southwestern Atlantic (South Sandwich Islands and offshore of South Georgia, see Section Xi, Xviii).

Winter ice extent in the Antarctic depends on processes which are strongly modulated by atmospheric circulation (Harangozo, 2004), with the highest levels of productivity generally found close to the coast and transported offshore by currents, winds and gyres (Nicol *et al.*, 2008). Antarctic regions which experience the greatest extent of winter sea ice retreat are likely to be a good source of Antarctic krill, since krill are strongly associated with the ice extent and abundance of associated sea ice algae (Atkinson *et al.*, 2004). However the relationship between sea ice and primary productivity is not simple, as productivity levels also correlate strongly with the rate of sea ice retreat, with faster spring/summer retreat bringing higher levels of productivity in some regions, e.g., Prydz Bay, the Ross Sea and the eastern Weddell Sea and Antarctic Peninsula (Nicol *et al.*, 2006). Other factors, including proximity to fronts, localized upwelling, ocean circulation and bathymetry and coastline morphology (Bathman *et al.*, 1997; Moore and Abbott, 2000; Strutton *et al.*, 2000) can all influence levels of summer productivity.

Estimates of humpback whale abundance south of 60°S have been made from three circumpolar surveys of the Antarctic spanning 1978/97-1983/84, 1985/86-1990/91 and 1991/92-2003/04. Strata covered 64.3, 79.5 and 99.7% respectively of open ocean south of 60°S, while survey design and regions covered differed between surveys and so are not directly comparable over time. Using standard distance sampling methods described in Branch and Butterworth (2001), abundance from the surveys was calculated as 7,100 (CV=0.36), 10,200 (CV=0.3) and 41,500 (CV=0.11), respectively (Branch, In Press). These estimates are negatively biased, as there was no upward correction for whales missed on the track-line. Furthermore, feeding grounds north of 60°S (e.g., in the South Atlantic Ocean, where enounter rates are highest between 54-58°S (Kasamatsu *et al.*, 1996), have not been surveyed. The Weddell Sea (30-55°W, 62-78°S) was also not surveyed (Figure 1 of Branch, In Press), although movement of whales from the Antarctic Peninsular has been demonstrated. The distribution of whales differs greatly across the Antarctic, possibly in a pattern related to the latitude of the Antarctic Polar

Front, since feeding regions where estimated abundance differed the most markedly from associated breeding grounds also had the most northerly front (Branch, In Press).

In order to estimate population trend between circumpolar surveys, Branch *et al*. (In Press) compared areas which had been repeatedly surveyed in different years and applied an upward correction to the second and third surveys to account for un-surveyed areas between the northern boundary of the survey regions and 60°S. The circumpolar estimated rate of annual increase was 9.6% (95% CI 5.8-13.4%), while regional estimates of trend were only significantly greater than zero on the west and east coasts of Australia (Branch, In Press). The correction for unsurveyed areas assumed a similar density of whales up towards 60°S and so may result in a positive bias if humpback density decreases with increasing distance from the ice edge. However humpback whales are not associated with the ice edge in some regions e.g., South Atlantic (Kasamatsu *et al.*, 1996), and in these cases the bias is likely to be negative.

C) Population summary of Southern Hemisphere Breeding Grounds

1. *Southwestern Atlantic Ocean*

i. Distribution and population structure

Breeding ground distribution

The wintering distribution of humpback whales in the southwestern Atlantic (June to December) is concentrated around the Abrolhos Bank region in Brazil (15-18°S), but whales have also been regularly seen along the coast of Espirito Santo and Rio de Janiero States to the south and along the northeastern coast of Brazil as far north as 5°S (Martins *et al.*, 2001; Rossi-Santos *et al.*, 2008; Zerbini *et al.*, 2004). This suggests a coastal distribution between ~3 and 23°S (Figure 1; Andriolo *et al.*, In Press), which may be expanding as humpback whales reoccupy regions formerly decimated by whaling. Offshore sightings have also been documented within oceanic archipelagos such as Fernando de Noronha, Trindade and Martin Vaz and São Pedro and São Paulo (Zerbini, pers comm.). A line transect survey of the coastal waters between 5 and 12°S found the majority of whales (>90%) to be concentrated within 300m of the shoreline, with all whales distributed within 800m of the shore (Zerbini *et al.*, 2004). Photo-identification studies suggest that whales sighted in Abrolhos Bank may travel elsewhere along the coast, with one re-sighting reported at 12°S (Freitas *et al.*, 2004). Genetic studies of whales biopsy-sampled at Abrolhos Bank and Praia do Forte (13°S) also found no genetic differentiation between the two regions (Cypriano-Souza *et al.*, 2010).

There are two documented examples of low-latitude feeding in southern Brazil, revealed in the stomach contents (of shrimp and larval brachyurans) of a single stranding in April 2002 (Danilewicz *et al.*, 2009) and observations from an oil platform (at 19°S) of two whales feeding in August 2005 (Alves *et al.*, 2009). All cases involved juvenile whales (<10m length). The stranding occurred outside the usual humpback wintering period (in April) and geographical range, suggesting this is an uncommon occurrence, but these observations suggest that opportunistic feeding may occasionally occur off the coast of southeastern Brazil, and may be a predominantly juvenile behavior.

Migratory connections

Whales migrate seasonally past coastal waters off the South American coast, the majority travelling offshore towards feeding grounds, departing coastal waters before ~23°S latitude (Andriolo *et al.*, In Press; Zerbini *et al.*, In Press-a), via a narrow (~330nm wide) migratory corridor (Zerbini *et al.*, In Press-a).

Satellite telemetry, photo-identification and genetic studies indicate that most of these whales frequent offshore summer feeding grounds in the South Atlantic, 100-400nm offshore of South Georgia and in the coastal waters of the South Sandwich Islands (Engel and Martin, 2009; Stevick *et al.*, 2006e; Zerbini *et al.*, 2006a). Photo-identification comparisons between Brazil (n=2579 individuals) and Bouvet Island (n=95) yielded no matches (Engel and Martin, 2009). There is also no evidence of migration to the Antarctic Peninsula; mitochondrial DNA suggest significant genetic differentiation between the Antarctic Peninsula population and the Brazilian breeding ground (Engel *et al.*, 2008) and comparisons of photo-identification catalogs have yielded no matches between these regions (Antarctic Peninsula catalog = 375 individuals, Brazil = 983 individuals; Dalla Rosa *et al.*, 2004). All of the noted genetic studies for Brazil populations originate from Abrolhos Banks and Praia do Forte (Cypriano-Souza *et al.*, 2010; Engel *et al.*, 2008). There could therefore be additional unexplored sub-structure within the breeding ground, given the size of the Brazil coast, extent of distribution described above, and results from other breeding regions.

Feeding ground distribution

Large numbers of humpback whales were killed during whaling at South Georgia within 100 nautical miles (nm) of the shore (Mackintosh, 1965). Currently, nearshore density is very low (Moore *et al.*, 1999), but large aggregations of whales are found farther offshore, usually within 300-500nm from the island. This is shown by several lines of evidence, including Soviet catches in the 1960s, sightings from Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) surveys, JSV sightings and satellite telemetry (Kasamatsu *et al.*, 1996; Reilly *et al.*, 2004; Zerbini *et al.*, 2006a). This suggests either a distributional shift in feeding grounds during the last century, or a contraction of traditional feeding grounds to the offshore regions, with humpback whales extirpated from South Georgia and therefore no cultural memory of this feeding location remaining in the population (Clapham *et al.*, 2008).

There is also strong evidence from satellite telemetry and photo-identification studies that humpback whales from the Brazilian wintering ground regularly occur off the South Sandwich Islands (Engel and Martin, 2009; Zerbini *et al.*, 2006a).

Population Structure (between breeding regions)

Brazil is significantly maternally differentiated ($p < 0.05$, F_{ST} and ϕ_{ST}) from the eastern Pacific (Colombian) breeding population and from whales feeding in the Antarctic Peninsula (Engel *et al.*, 2008; Rosenbaum *et al.*, 2009). Nuclear microsatellite genotypes also recovered significant genetic differentiation between Brazil and all breeding grounds in the eastern South Atlantic and western Indian Ocean, with the exception of Angola. This latter was likely due to the small sample size available from Angola for comparison (n=12 individuals, Pomilla *et al.*, 2006).

ii. Abundance

A number of line transect surveys of the wintering ground were carried out between 1999 and 2005; two were boat-based (5-12°S in 1999 and 2000, Zerbini *et al.*, 2004) and five were aerial (12-20°S in 2001-2004, 5-25°S in 2005) (Andriolo *et al.*, In Press; Andriolo *et al.*, 2006). There are also a number of mark-recapture estimates available from photo-identification surveys (Kinas and Bethlem, 1998). Among all estimates, only the 2005 survey covered the entire known (at the time) range of the wintering ground, so this is considered the most current and reliable estimate of population abundance (N=6,251, CV=0.16; Andriolo *et al.*, In Press) available (IWC, 2007a).

Satellite telemetry and photo-identification surveys suggest that most whales remain north of 60°S during the summer. Surveys of the region south of 60°S (20-50°W) estimated very low abundance, e.g. N=168, CV=0.61 in 1997/1998 (Branch, In Press), further supporting the premise that most whales remain north of 60°S during summer feeding.

iii. Genetic Diversity

For an introduction to genetic diversity, see ‘Genetic Diversity’ in the ‘Status of North Atlantic Populations’ section. Between 1997-2001, 171 free-ranging and stranded whales were biopsy-sampled in the region of Abrolhos Bank and Bahia state. Analysis of mitochondrial (maternally-inherited) DNA revealed 61 haplotypes (distinct maternal lineages), which suggests that the Brazilian population is genetically diverse in comparison to other Southern Hemisphere populations (haplotype diversity = 0.972, genetic diversity = 0.025, Engel *et al.*, 2008). Nuclear microsatellite genotypes have been obtained from 275 individuals biopsy-sampled or stranded in Abrolhos Bank and Praia do Forte (Cypriano-Souza *et al.*, 2010). Observed allelic diversity (heterozygosity) was 0.73.

iv. Trends

Systematic surveys conducted off Brazil between 1995 and 1998 (Martins *et al.*, 2001) were used to estimate the population increase rate of the humpback whales concentrated in Abrolhos Bank (Ward *et al.*, In Press). The best model provides an increase rate of 7.4% (CV=0.45) between 1995 and 1998 for the Abrolhos Bank. No surveys have been carried out in the feeding grounds (South Sandwich/ South Georgia region). One other abundance trend has been calculated for the region (31%; Freitas *et al.*, 2004); however the estimate of increase is far above the maximum biologically plausible population growth rate.

v. Habitat or Ecosystem Conditions

Within the main region of humpback concentration (Abrolhos Bank), there is a ~550 nm^2 region (~9% of the Bank) which has been a National Marine Park since 1983 and was declared an area of Extreme Biological Importance by the Brazilian Ministry of

Environment in 2002. The Abrolhos Bank region comprises a shallow-water (mean 30m depth) habitat of coral and algae reefs and mud, and contains an archipelago of islands (Abrolhos Archipelago), with sea surface temperatures averaging between 22-24°C in winter (Martins *et al.*, 2001). Fishing, oil and gas exploration and industrial development are currently highly regulated in this area, while oil and gas exploration are now seasonally restricted throughout Espírito Santo and Bahia States (Engel pers. comm.).

The islands of South Georgia are a partly drowned mountain range system and are a largely uninhabited group of islands found about 800nm southeast of the Falkland Islands. They lie on the South Scotia Ridge, which stretches between Tierra del Fuego and the South Sandwich islands (Headland, 1984). South Georgia is the largest island; around half of it is permanently covered in ice and snow, which provides glacial meltwater to the surrounding sea. The islands are close to the Antarctic Circumpolar Current, so seas are cold and turbulent all year round. The local waters often contain large ice masses, as glaciers calve and break off during storms. Antarctic krill is at high abundance across the northern shelf and shelf-break areas of South Georgia (Murphy *et al.*, 1997).

The South Sandwich Islands are a series of uninhabited volcanic islands located at 56-59°S and 26-28°W. The surrounding seas are fed by the Antarctic Circumpolar Current and are seasonally surrounded by sea ice, but no pack ice. This region has some of the highest chlorophyll levels recorded in Antarctic waters, at similar magnitude to levels at the marginal ice zones and shelves of the Antarctic Peninsula (Perissinoto *et al.*, 1992). Productivity is thought to be driven by glacial meltwater and rainfall runoff from the islands providing increased buoyancy in the surface water and enhanced, stable stratification of layers in the water column (Perissinoto *et al.*, 1992).

Krill found at these islands are not born here but are transported from the Antarctic Peninsula or Weddell Sea via north-easterly flowing ocean currents (Ward *et al.*, 1990). Therefore regional krill abundance is directly influenced by the biological and environmental processes determining abundance in the Antarctic (Murphy *et al.*, 2002), particularly in the Scotia Sea (Fedoulov *et al.*, 1996), and fluctuations in abundance occur in parallel across the South Atlantic (Brierley *et al.*, 1999). High densities of krill are found across the Arc of the Scotia Sea, distributed between the Polar Front and the southern boundary of the Antarctic Circumpolar Current between 20-55°W and 50-60°S (Atkinson *et al.*, 2008).

vi. Threats and Anthropogenic Impacts

A number of oil fields have been developed and are in use in the Campos and Espírito Santo Basins (50-100 miles east of the Brazilian states of Rio de Janeiro and Espírito Santo and south of the Abrolhos Bank, the main area of humpback aggregation), and an expansive offshore oil exploration project is now underway (Dutra, 2004). Such development can present a threat to migratory humpback whales through acoustic disturbance, increased boat traffic, water pollution (e.g. oil spill and chemical waste) and habitat degradation. The biggest effects are likely to be from acoustic disturbance and ship strikes, since humpback whales travel past the region and are not feeding, so may therefore be less subject to the effect of habitat degradation and the poisoning effects of oil spills and pollution. Petrobras have recently been granted two billion USD in funds for further oil and gas development, which may include expansion out to the continental shelf and further impact the humpback whales along their migratory route. The hydrocarbon exploration and production industry is now under development from about 3 to 25°S (Zerbini pers comm.), along nearly the entire Brazilian coast at the shelf break (with the exception of the Abrolhos Bank region), although mitigation measures are currently in place to seasonally restrict seismic survey efforts (see '*Habitat or Ecosystem Conditions*').

Other regional practices that contribute to habitat degradation of the Brazilian calving ground are most concentrated in areas where humpback whales come close to shore, such as northern Bahia State. These include dynamite fishing, industrial shrimp farming and polluting coastal run-off from cities.

Fishing practices may also bring entanglement and ship strike risks. In southern Brazil, numerous interactions between cetaceans and gillnet fisheries have been documented, while surface gillnet (driftnet) fisheries have similar potential to entangle and kill (Young and Iudicello, 2007). Use of driftnets is relatively recent in Brazil but is increasing (Zerbini and Kotas, 1998). A summary of reports from fishermen in the southern pelagic driftnet fishery suggests that humpback by-catch in driftnets and bottom set gillnets has mainly been of calves and juveniles (judged by the small length of these whales), while larger whales are more often released alive with net attached to their bodies (Zerbini and Kotas, 1998). Rio de Janeiro and Espírito Santo were reported regions of most by-catch. Humpback by-catch from the northern driftnet fishery has not been documented. Cases of entanglement have also been documented by photo-analysis, which revealed that 27.5% (30 of 109) individuals had skin lesions indicative of tissue damage (Castro *et al.*, 2008c), 12% (13 of 109) had disseminated bullae and 24% (26 of 109) had wrapping scars, with 8% (9 of 109) having wrapping scars considered to have a high likelihood of being caused by entanglement.

Eighteen humpback strandings were reported from the Brazilian coast between 1980 and 1993; seven of these were calves (39%) and the other 11 were juveniles (<15m), with three calves observed to have been caught in gillnets (summarized in Siciliano, 1995). Humpback strandings are most commonly reported along the north coast of Bahia during winter, with 23 strandings registered between 2000 and 2005 (Neto *et al.*, 2008` and Instituto Baleia Jubarte, pers comm.). As found in other populations, the majority of strandings have been of calves (61% calves, Engel *et al.*, 2006; Neto *et al.*, 2008). In 2002, eight adults stranded along the coast (7 in Bahia / Espírito Santo States, one in NE Rio de Janeiro State); this may be an unusual mortality event since the reports comprise 26% of the total stranding reports (n=37) between 1975 and 2003 (Engel *et al.*, 2006), although observer effort has increased with respect to strandings in recent years. The whales showed no clear evidence of entanglements or ship strikes, and while disease cannot be ruled out (no necropsies were performed), the event has been linked to a seismic survey conducted at 19-20°S during the 2002 breeding season (Engel *et al.*, 2006). Since this time, mitigation measures have been put in place to exclude humpback breeding regions around the Abrolhos Bank from seismic surveys and to prohibit testing during the humpback wintering period of July to November (Engel *et al.*, 2006).

Whale-watch tourism is increasing at an average annual rate of 4% (O'Connor *et al.*, 2009), with 12 boats registered to watch humpback whales, and 3,000-4,000 humpback whale watch visitors to Bahia reported in 2008 (Hoyt and Iníguez, 2008). The industry is currently expanding most rapidly in Praia do Forte due to a developed tourist infrastructure and the close proximity of humpback whales to the coast in this region (Hoyt and Iníguez, 2008). Regulations in place for the burgeoning industry require that boats do not approach whales within 100m and do not remain there for more than 30 minutes. Morete and Bisi (2006) noted differences in mother/calf behavior when whale-watch boats approached to within 300m, with the mother exhibiting increased movement speeds and blow intervals.

Increases in boat traffic, from oil and gas related activities, commercial shipping and tourism all increase the risk of ship strikes and of disturbance from anthropogenic sound. At least three ship strikes have been documented from Brazilian waters between 1999 and 2005 (Marcondes and Engel, 2009). Passive acoustic monitoring of the Abrolhos Bank Marine Park found a negative impact of boat noise on male singing activity (Sousa-Lima and Clark, 2008), suggesting either that males move elsewhere or that they stop singing in the presence of vessels. The impact of such behavior on population fitness is still poorly understood.

Recent humpback population growth (Ward *et al.*, In Press) is likely to have increased the exposure of humpback whales to interactions with fisheries and entanglements in fishing gear (e.g. Siciliano, 1995; Zerbini and Kotas, 1998). Interactions with fishing boats have become a common occurrence, with individuals usually released alive but with nets attached (Zerbini pers comm.). These problems are also likely to worsen with further population increases, particularly as there is some evidence for increases in fishing effort in parallel (Di Beneditto and Ramos, 2001; Zerbini and Kotas, 1998), together with a 35% increase in net size since the 1990s (Di Beneditto, 2003).

The greatest effort in the mid-water trawl fishery for krill is concentrated in the South Atlantic region, off South Georgia, the Scotia Arc and the Antarctic Peninsula (Everson and Goss, 1991; Murphy *et al.*, 1997).

vii. Recovery from Exploitation

Humpback whales have been hunted on a small scale in Brazilian waters since the 17th century (Reeves and Smith, 2006). In the 20th century, the introduction of modern whaling techniques led to catches on an industrial scale, targeted at the main aggregation area in South Georgia. Whaling was carried out from shore stations in Brazil and South Georgia as well as, on a smaller scale, by pelagic fleets (including the Soviet whaling fleet). The total reported catches between 1904 and 1972 (the last year whales were killed) are 27-32,000 (Allison, 2006; Zerbini *et al.*, In Press-b). A Bayesian assessment of the Brazilian humpback whale population using an age and sex-aggregated population dynamic model using the 2005 line transect survey as current abundance, trend data from the 2000-2004 surveys, and available catch data from the 20th century, suggested that the population status in 2006 was at around 27.0% (95% credibility intervals 18.0-38.7%) of pre-exploitation (pre 20th century) abundance (Zerbini *et al.*, In Press-b). A number of alternate modeling scenarios were explored, including various catch allocation hypotheses and indices of abundance available for portions of the breeding ground and on feeding grounds south of 60°S, depensation (reduced population growth rate) at low abundance, constraint on minimum abundance calculated from current genetic diversity, and an uninformative prior on population growth (*i.e.*, excluding trend data). In total, the range of population status estimates for 2006 were 27-34% of pre-exploitation abundance, noting that catch allocations had the greatest effect on estimates and that data for catches from Brazilian land stations in 1929-1946 are still incomplete, which may cause a positive bias to these status estimates (IWC, 2007a). An additional positive bias may be caused by excluding pre-1900 catches (although these are thought to be small) and the lack of catch data from 1929-1946 (Zerbini *et al.*, In Press-b). However the catches during this period are also likely to be small, since the population was severely depleted on the feeding grounds prior to 1929.

2. **Southeastern and central Eastern Atlantic Ocean**

i. Distribution and population structure

Breeding ground distribution

Dedicated surveys, incidental sightings, satellite telemetry and historical whaling records indicate that there is a winter breeding and calving ground located off central western Africa between ~6°S and ~6°N in the eastern Atlantic. This includes the coastal regions of northern Angola (Best *et al.*, 1999; Weir, 2007), Congo, Togo, Gabon (Rosenbaum and Collins, 2006; Walsh *et al.*, 2000), Benin (Van Waerebeek, 2003), offshore islands (Príncipe and São Tomé; Picanço *et al.*, 2009), Pagalu (Aguilar, 1985) and other coastal countries within the Gulf of Guinea (Rosenbaum and Mate, In Review), with a northerly extent that includes occasional sightings and strandings off the coast of Ghana (Van Waerebeek *et al.*, 2009). The northernmost authenticated record comes from a stranding at Assini Mafia (05°N, 3°W) on the eastern Ivory Coast in August 2007 (Van Waerebeek *et al.*, 2007). Periods of peak abundance are found between July and September, with some whales still present as late as December and January in Angola, Gabon and São Tomé (Carvalho and Collins pers. comm. Weir, 2007). Surveys in northern Angola yielded bimodal peaks of sightings (Best *et al.*, 1999), suggesting that at least some whales seen in this region are on migration. However continuous passive acoustic monitoring off Northern Angola (the Congo River Canyon, 6°S) from March through December 2008 recorded humpback whale songs from mid-June through early December, with a clear increase in the hourly number of singers through the first half of July and then a fall-off during November. Relatively consistent singing activity throughout the period suggests that this region may be a previously undescribed breeding area in addition to a migratory route (Cerchio, pers comm.[8]), or that singing and mating

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[8] Also see Cerchio S, Rosenbaum H, Collins T (In Prep) Humpback whale singing activity off Northern Angola as an indication of the migratory cycle and a previously unidentified breeding area.

are occurring during migration, as has been documented in other regions (Clapham and Mattila, 1990).

Small numbers of humpback whales are also regularly sighted during winter in the coastal waters of St Helena island in the southeastern tropical Atlantic (Figure 2, 15°S 5°W), with most sightings consisting of single whales or adults with calves between late June and October (MacLeod and Bennett, 2007). It is not known whether these whales undergo migratory exchange with continental coast breeding grounds to the east or west.

Whaling records from Gabon do not show bimodality (characteristic of a migratory stream) during the winter months, supporting a continuous presence of whales in these waters in winter (Budker, 1952). Aerial surveys carried out in the coastal waters of Gabon (up to 1,000m bathymetry) suggest that whales are most concentrated in the south, between Cap Lopez and the Congo Frontier (Rosenbaum *et al.*, 2004; Strindberg *et al.*, In Press). Encounter rates decreased as depth increased, except around the region of Cap Lopez, where encounter rates were still high at the 1000m survey limit (Rosenbaum *et al.*, 2004). During a boat-based survey of continental shelf waters in Benin, most sightings were made within 10nm of the shore, in water depths of 14-32m (Van Waerebeek, 2003). Satellite telemetry tagging of whales in Gabon reported considerable use of wintering habitats farther north into the Gulf of Guinea and Bight of Biafra, including offshore islands (Rosenbaum and Mate, In Review). Both mother and calf pairs that were satellite tracked used the continental shelf waters north of Bioko Island off Nigeria and Cameroon (Rosenbaum and Mate, In Review); this region was also frequented by early 19th century whalers (Townsend, 1935). Analyses of the group characteristics of whales encountered in Gabon revealed a low percentage of mother-calf pairs (~4.6%) and higher percentage of all-female groups (8% of pairs observed), suggesting that the coast of Gabon is both a breeding ground and a migratory route for whales traveling to other regions in the Gulf of Guinea (Pomilla and Rosenbaum, 2006; Rosenbaum and Collins, 2006).

In northern Angola, the majority of encounters made during yearlong surveys of the northern region occurred in <200m depth, with a drop in encounters outside the shelf break and very low numbers of sightings in waters >1000m (Weir, 2007). The earliest and latest occurrences of humpback whales occurred in May and January respectively. Evidence of population differentiation (see '*Population Structuring*') between whales in Gabon and those in western South Africa indicates that there may be a separate breeding region for western South African whales. Based on the West African regions surveyed and un-surveyed so far, it has been hypothesized that this breeding region may occur in southern Angola; dedicated photo-identification and genetic surveys in the region will be necessary to explore this hypothesis (Rosenbaum *et al.*, 2009).

In coastal waters around São Tomé Island, the humpback whales were observed in the region between August and late November, occurring very close to the shore and in shallow waters (<100m depth) (Picanço *et al.*, 2009). More than 65% of the sightings were of mother-calf pairs, sometimes with very young calves, with extended periods in the region. Competitive groups have been observed on only two occasions (Carvalho, pers comm.[9]). The waters around São Tomé may therefore primarily serve as a calving and nursing area for humpback whales in the region.

Humpback whales have occasionally been observed engaged in repetitive diving behavior characteristic of feeding (with additional observations of schooling fish in one case) near the plumes of rivers and lagoon outlets along the coast of Gabon (Walsh *et al.*, 2000), suggesting that some opportunistic winter feeding may also occur (see '*Habitat and Ecosystem Conditions*').

Feeding ground distribution

Two feeding regions have been identified in association with the southeast and central Atlantic humpback whales. The first is offshore of western South Africa and Namibia, south of the Walvis Ridge at 18°S and associated with the Benguela Current system (see '*Habitat and Ecosystem Conditions*') (Barendse *et al.*, 2006; Best *et al.*, 1995). Summer sightings and whaling catches in Namibia (Findlay and Best, 1995; Townsend, 1935), coupled with observations of feeding, and presence of krill in feces in South Africa (Best *et al.*, 1995) and a sex ratio close to parity (Barendse *et al.*, 2006), suggest persistent usage of this region for feeding by humpback whales. Surveys of whale movement from Cape Columbine (western South Africa) observed three peaks in abundance between October and December but discerned no net direction of movement and observed average swimming speeds slower than those normally observed on other migratory routes (Best *et al.*, 1995), observations indicative of a migratory destination, rather than a migratory stream, for some whales.

Antarctic catches (~5,000 whales) from high latitudes beneath western South Africa (20°W-10°E), observations from surveys and whaling records of multiple 'pulses' in abundance (suggestive of migration) past Cape Columbine and Saldanha Bay (Best *et al.*, 1995; Olsen, 1914) and recent satellite telemetry tracking of whales from Gabon (Rosenbaum and Mate, In Review) suggest a second feeding ground in high-latitude waters.

Migratory connections

Microsatellite genotypes collected in Gabon and western South Africa have recovered 10 re-sights between these regions, four of which occurred within the same year (Carvalho *et al.*, 2009; Pomilla *et al.*, 2006). Three of those recaptured in South Africa were observed feeding, or in association with feeding whales. Since western South Africa may be both a migratory corridor and an offshore feeding ground, the information that these re-sights provide about feeding ground connections is limited. The dates of recapture in western South Africa range between October and January, which is consistent with humpback presence both on migration and during feeding (Carvalho *et al.*, 2009). Satellite telemetry tracking of whales from Gabon revealed a migratory route for two individuals, who travelled offshore at the Walvis Ridge, and passed western South Africa far offshore, close to Bouvet Island, arriving in polar latitudes (~56°S) at around 0° longitude

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[9] Also see Carvalho I, Brito C, dos Santos M, Rosenbaum H (In prep) The West African waters of São Tomé: a calving ground for humpback whales?

(Rosenbaum and Mate, In Review). It may therefore be the case that the migratory route for some humpback whales wintering in the Gulf of Guinea region generally follows the Walvis Ridge offshore, and the feeding area is in the vicinity of Bouvet Island. The degree to which whales that travel past (and can be encountered in) western South Africa are the same or distinct from whales that feed in the Bouvet Island area is not fully known (see below).

Spatial population structuring between Gabon and western South Africa has been revealed by mitochondrial haplotypes (Carvalho *et al.*, 2009; Rosenbaum *et al.*, 2009) and microsatellite genotypes (Carvalho *et al.*, 2009; Pomilla *et al.*, 2006). Some degree of temporal heterogeneity among molecular markers for these two regions has also been found (Carvalho *et al.*, 2009). Significant haplotypic differentiation was found between these regions for all samples (both sexes), and for females (Rosenbaum *et al.*, 2009); this suggests that some portion of the whales in the Gulf of Guinea breeding ground travel elsewhere to feed. Interestingly, comparisons of these regions with whales biopsy-sampled at high latitudes between 20°W-10°E (n=52 whales) found no significant haplotype differences with western South Africa and significant differences with Gabon (Loo *et al.*, 2008). This suggests that whales frequenting the Gulf of Guinea may migrate to several feeding grounds including western South Africa, Bouvet Island (as indicated by telemetry and microsatellite genotype recaptures (Loo, pers comm.,Rosenbaum and Mate, In Review), and possibly other regions of the Antarctic. Microsatellite genotypes suggest a similar pattern of differentiation, while temporal analyses of samples has revealed that females summering in western South Africa are significantly differentiated from females wintering in Gabon (Carvalho *et al.*, 2009). These data in concert suggest that a portion of whales feeding off western South Africa are breeding and calving in a region which has not yet been surveyed; it has been proposed that this may occur north of the Walvis Ridge in Angola (Rosenbaum *et al.*, 2009).

Population Structure (between breeding grounds)

There is significant mitochondrial haplotypic differentiation between Gabon and west South Africa and neighboring Southern Hemisphere breeding grounds in Brazil and the western Indian Ocean (Rosenbaum *et al.*, 2009). Mitochondrial nucleotide differentiation was significant between Gabon (n=477) and Brazil, Mozambique and Madagascar, and non-significant between western South Africa (n=108) and Brazil, Mozambique and Madagascar (Rosenbaum *et al.*, 2009), suggesting a greater degree of migratory interchange between western South Africa and neighboring regions. However, more than one instance of movement between Gabon and Madagascar has been documented (Loo pers comm.; Pomilla and Rosenbaum, 2005), indicating that there must be some occasional inter-annual movement of individuals between the sub-equatorial coasts.

Microsatellite genotype comparisons have detected small, but significant, genetic differentiation among Gabon and western South Africa and Brazil (Pomilla *et al.*, 2006), while photographic catalog comparisons among these regions have revealed no matches (Pacheco de Godoy *et al.*, 2004). Microsatellite genotype comparisons of Gabon and western South Africa with western Indian Ocean breeding grounds show a similar pattern to the mitochondrial haplotypes, with higher levels of gene flow (and no significant differentiation) estimated between western South Africa and most western Indian Ocean breeding grounds, compared to Gabon and the western Indian Ocean breeding grounds, which were significantly differentiated (Pomilla *et al.*, 2006). Song comparisons between Brazil, Gabon and Madagascar also show rapid transmission to neighboring regions, suggesting biological connectivity, either through song exchange on shared feeding grounds, or via male migrations between breeding grounds (Darling and Sousa-Lima, 2005; Razafindrakoto *et al.*, 2009).

ii. Abundance

Breeding ground abundance has been calculated from aerial surveys carried out off the coast of Gabon in 2002 over five days in August, with transects (out to 1000m bathymetry) spanning the region between the border with Equatorial Guinea and south of Mayumba, near the Congo border (Strindberg *et al.*, In Press). The greatest densities of whales were found in the southern stratum, south of Cap Lopez. The overall estimate of abundance for the region was 1,259 whales in 2002 (95% CI 710-2,333). The proportion of whales not detected on the trackline ($g(0)$) was estimated to be between 95% intervals of 0.45 and 0.79; correction for these missed whales therefore provided a corrected mean abundance estimate within the range of 1,594 - 2,798 whales. However this estimate of abundance is likely to be negatively biased for the region, as there was no correction for perception bias, and there is some evidence from sightings near Cap Lopez that more whales might be present offshore of the continental shelf, beyond 1,000m bathymetry. Since the survey was carried out over a five-day period, there may be also additional whales that frequented Gabonese waters but did not travel through the region during this time. It is also unclear whether this estimate of abundance is representative of Gabon, or of whales frequenting other regions in the Gulf of Guinea, since satellite telemetry suggests differential movement of individuals through coastal waters and indicates that some travel widely through the Gulf during the season (Rosenbaum and Mate, In Review; Rosenbaum *et al.*, 2004; Strindberg *et al.*, In Press). The total abundance for the Gulf of Guinea in 2002 is however likely to be greater than the Gabon estimate, for the reasons detailed above.

Mark-recapture estimates of abundance were reported by Collins *et al*. (2008) based on photo-identification catalogs and microsatellite genotypes collected between 2001 and 2006 from Iguela and Mayumba in Gabon. Recaptures in the photo-identification datasets were low, and precision was poor due to small annual sample sizes. The authors considered the larger genetic dataset to be more reliable (since the probability of identity by chance is 2.5×10^{-12}). All genotypic matches were also supported by matches in sex and mtDNA haplotypes. Estimated abundance (using closed models) for Iguela between 2001 and 2004 was 6,560 (CV=0.15) and between 2001 and 2005 was 8,163 (CV=0.12).

iii. Genetic Diversity

For an introduction to genetic diversity, see 'Genetic Diversity' in the 'Status of North Atlantic Populations' section. Mitochondrial genetic diversity has been estimated for Gabon and western South Africa (Appendix 1, Rosenbaum *et al.*, 2009). Haplotype and nucleotide mitochondrial control region diversity estimates were very similar across both regions, with comparably high haplotype diversity (~0.98, Appendix 1), while nucleotide diversity (2-2.1%) was similar to that described for neighboring breeding regions in the eastern Indian Ocean and lower than that described for the western South Atlantic.

Nuclear microsatellite diversity has also been estimated from these regions; Gabon (0.75 +/- 0.01), Angola (0.81 +/- 0.03) and western South Africa (0.76 +/- 0.01) (Pomilla *et al.*, 2006). These values are similar to those obtained from the southwestern Indian Ocean, and slightly (though not significantly) higher than diversity in the southwestern Atlantic.

iv. Trends

No recent trends in abundance are available for this region.

Catch-per-unit-effort data, collected from whaling stations along the coast, showed differing trends in abundance between the Gabon / Gulf of Guinea region (1.8% decline in CPUE with increasing catches) and Angola / Namibia / the South African Cape (0.85% decline in CPUE with increasing catches) (Findlay, 2000). Catches of humpback whales in the latter region (a multispecies hunting ground) showed a rapid decline from 1900-1917 and remained low subsequently until whaling was discontinued in 1963. Catches of humpback whales to the north (a single-species hunting ground) declined during the initial whaling period, resulting in the closure of whaling operations and allowing some population recovery. The population was then exploited again. Four cycles of exploitation and recovery are suggested by catch records from Gabon (Findlay, 2000). The CPUE indices obtained at the end of each of the four whaling periods show a projected increase rate of ~10% per annum between whaling periods, consistent with estimates from other Southern Hemisphere populations (e.g. Hedley *et al.*, 2009; Noad *et al.*, 2008).

v. Habitat or Ecosystem Conditions

In the Southeastern Atlantic, the Inter-tropical Convergence Zone (ITCZ) is several degrees north of the geographical equator, which may explain the distribution of wintering humpback whales north of the equator in this region (Rasmussen *et al.*, 2007). The position of this zone is influenced by the Angolan southwest monsoons and southeast trade winds (Hardman-Mountford *et al.*, 2003). Seasonal northward migration of the ITCZ and an intensification, then reduction, in the southeast trade winds creates a series of winter (July and August) upwellings in the northern Gulf of Guinea (Hardman-Mountford *et al.*, 2003). These are most pronounced between 2-8°E on the northern coast, and south of 2°S on the eastern coast.

The coast of Gabon possesses a uniform and gently sloping continental shelf down to 100m (20-35nm offshore), after which depth increases rapidly (Rosenbaum and Collins, 2006). The shelf narrows in the region of Cap Lopez, where the 1,500m isobath lies within 10nm of the coast (Findlay *et al.*, 2006). Along the coast are multiple shallow lagoons, fed by variable influxes of seasonal freshwater. Some seasonal coastal nutrient enrichment (between July and September) has been identified at Point Noire (Republic of Congo), which may be driven by equatorial surface water mixing in the eastern Atlantic (Hardman-Mountford *et al.*, 2003) and may explain occasional observations of humpback feeding (Walsh *et al.*, 2000).

Saint Helena is a small volcanic island at the tip of a complex of extinct underwater volcanoes and is surrounded by an abyssal plain. To the windward side, island waters are relatively rough for much of the year, while waters on the leeward side are calm; humpback whales have been observed in both regions (MacLeod and Bennett, 2007). Waters surrounding the island are cooled by influxes from the Benguela current (see below).

In northern Angola, the continental shelf is wide (up to 30nm from the coast). In this region, 1,000m bathymetry occurs ~50nm offshore. The shelf narrows west of Luanda and in the region of the Congo Canyon (off Soyo) where water depths of >1,000m occur ~25nm offshore (Weir, 2007). Some seasonal coastal upwelling has been identified at Cabinda and Luanda, likely originating from equatorial eastern Atlantic upwelling, as described for Gabon (Hardman-Mountford *et al.*, 2003). The Congo flows into the sea at this point, creating a massive influx of freshwater and enhanced local productivity in the region of the freshwater plumes. Southern Angola has a narrow continental shelf <5nm wide (1,000m occurs ~8nm offshore).

Angolan coastal waters are fed by the Angola Current, which flows south from the Gulf of Guinea and travels down the coast between 9 and 16°S, forming a front (the Angola-Benguela Front) with the Benguela Current traveling up from the south (Weir, 2007). This front is permanent and tends to migrate northward in winter and south in summer (in concert with the Inter-tropical Convergence Zone), occurring between 14 and 16°S. To the south of the Angolan/Namibia border at ~20°S, the Walvis Ridge is a underwater volcanic ridge which starts at the continental margin and extends to the mid-Atlantic ridge in a southwesterly direction. Satellite telemetry indicates that this ridge may be used as a cue to set the offshore migratory travel direction for Gulf of Guinea whales traveling towards their feeding grounds (Rosenbaum and Mate, In Review).

The Benguela Current is a strong, cold-water northward flow, which originates in the region of Cape Columbine (western South Africa) and is comprised of a coastal branch and an offshore oceanic flow. The Benguela Current is fed by the easterly flow of the South Atlantic current, which in turn is cooled by proximity to the Antarctic Circumpolar Current in places. To the south of the Benguela is another tropical current (the Agulhas), located at around 35°S. In the summer, easterly winds on the Agulhas Shelf cause coastal upwelling and a cyclonic ridge in the vicinity of Cape Agulhas. Southeast trade winds drive a strong offshore movement of the surface water layers near the coast, which creates the belt of coastal upwelling along the coasts of South Africa and Namibia, commencing at Cape Agulhas (16-34°S). The strongest upwelling is found close to Lüderitz on the southern Namibian coast at ~27°S and forms a physical and biological boundary line within the Benguelan system. The Benguela Current is also influenced by the El Niño- Southern Oscillation over a 3-7 yr periodicity. El Niño events are manifested by southward migration of the Angola-Benguela front and associated intrusion of warm waters into the northern Benguela region.

The high latitude feeding region for this breeding ground (Core region 10°W-10°E, possible range 20°W-30°E, Appendix 2) has a patchy distribution of krill (from sampling net data spanning 1926-2003, Atkinson *et al.*, 2004) with the highest mean densities encountered widely distributed across all latitudes south of the polar front in the west (20°W-8°W). In this region, the Weddell Sea shows the greatest extent of winter ice advance and least summer retreat of any region in the Antarctic (Harangozo, 2004). However the rate of ice retreat is rapid (Nicol *et al.*, 2006), which may explain relatively high primary productivity observed to the north and east of the Weddell Sea pack ice in summer (Moore and Abbott, 2000; Nicol *et al.*, 2008). Krill and chlorophyll densities between 10°W and 10°E (central South Atlantic) are minimal (Atkinson *et al.*, 2004; Moore and Abbott, 2000), while in the east (10-30°E), 'hotspots' of krill and chlorophyll density, interspersed with low density regions, are found at the ice edge and close to the polar front (~50°S) (Atkinson *et al.*, 2004; Moore and Abbott, 2000).

vi. Threats and Anthropogenic Impacts

The Gulf of Guinea is an area of intense seismic survey and oil drilling activity and is currently the region of most intense oil drilling worldwide. The waters harbor extensive oil fields, which are being developed by a number of African countries and international companies, with Angola the largest oil exporter in Africa, and extensive production in Nigeria, Gabon and Equatorial Guinea (Findlay *et al.*, 2006; Frynas, 2004). Oil and gas developments have a number of associated risks for humpback whales using the region as breeding and calving habitat (see 'Section VIIa: *Threats: oil pollution, anthropogenic noise, ship strikes*').

Pomilla *et al.* (2004) used cytochrome *P450 1A* (*CYP1A1*) expression as a biomarker to assess the exposure to polycyclic aromatic hydrocarbons, some of the most hazardous components of crude oil, of the humpback whale population wintering off the coast of Gabon. The levels of *CYP1A1* induction detected in humpback whale biopsies were very low. The most plausible explanation reported by the authors is that *CYP1A1* expression correlated to non-accumulating polycyclic aromatic hydrocarbons requires recent introduction of the contaminants with the diet. As the whales do not, or only occasionally, feed off the Gabonese coast, they may not be showing any *CYP1A1* response to the presence of oil-derived pollutants in the water (Pomilla *et al.*, 2004).

The Gulf of Guinea region suffers increasingly from pollution and habitat degradation, both from major coastal cities (Lagos, Accra, Libreville, Porto-Nevo) which dispense raw sewage and untreated toxic waste into the marine environment (United Nations Environment Programme, 1999) and from unregulated foreign trawling and oil and gas developments (Chidi Ibe, 1996). The practice of mining construction materials from the near-shore coastal zone (e.g. sand and gravel) is also common in this region, which contributes to habitat degradation (Chidi Ibe, 1996). There are many entanglement risks for humpback whales in these regions, including a growing commercial shrimp industry off Gabon (Walsh *et al.*, 2000) and an expansion in unregulated fishing by foreign fleets in Gulf of Guinea waters (Collins pers. comm., Brashares *et al.*, 2004; Chidi Ibe, 1996). Entangled swimming humpback whales have been observed in the region (3 whales between 2004 and 2009, Collins pers. comm.) Rapid increases in shipping and port construction throughout the Gulf of Guinea (Van Waerebeek *et al.*, 2007) are likely to increase the risks of ship strikes for humpback whales. Whales are reported as stranding ‘regularly’ in Benin, with wounds suspected as originating from ship strikes (Van Waerebeek *et al.*, 2007). There are no dedicated stranding networks in the region, and ship strikes with oil tankers and other vessels have not been documented.

Aboriginal whaling of humpback whales from rowing boats in Pagalu (southern Gulf of Guinea, 1°S 5°E), has been known since 1855 (Aguilar, 1985). There is no information regarding whaling activity on Pagalu since 1975, although it is assumed to have continued. Catches are made during July and August using harpoons and lances and are focused on small whales (calves, juveniles and neonates), with the mother often set upon in order to separate it from the calf. The number of successful catches is estimated at 1-3 per year, although the additional number of whales maimed or killed but lost during the whaling process is unknown (Aguilar, 1985).

Some strandings data compiled between 2001 and 2005 from South Africa reported 14 humpback strandings on the southern and western coasts and Namibia (IWC, 2002b, 2003b, 2004b, 2005c, 2006c). One fatal entanglement with a rock lobster trap has been reported from western South Africa (Findlay and Best, 1995). The extent of entanglements in this region is unknown. Two whales have been reported as stranding with marked propeller lesions, one in eastern Ivory Coast in 2007 (Van Waerebeek *et al.*, 2007) and the other in Cape Town in 1995 (Best, 2007).

Whale watching in the Gulf of Guinea region is small-scale, with small humpback whale watching industries documented in Benin, Gabon, São Tomé and Príncipe (O'Connor *et al.*, 2009). Whale watching in South Africa is mainly focused on right whales, with humpback whales watched opportunistically. Boat-based whale watching has seen 14% growth in the last decade and is concentrated in the western Cape region; South Africa now numbers among the top ten destinations for whale watching worldwide (O'Connor *et al.*, 2009). There are regulations in place for all whale watching activity in South Africa (Carlson, 2007). Whale watching in Namibia is primarily focused on dolphins and has seen 20% growth since 2008.

vii. Recovery from Exploitation

Population assessment of the recovery of humpback whales in this region is challenged by a paucity of information regarding the unidentified breeding ground associated with the western South African feeding grounds (see ‘*Population Structuring*’). Abundance estimates are available from Gabon (Collins *et al.*, 2008; Rosenbaum *et al.*, 2004), but none are presently available from western South Africa, and in addition the proportion of Gulf of Guinea whales using South African feeding grounds is unknown. Understanding the degree of mixing of breeding whales on feeding grounds is necessary for the accurate allocation of historical catches to each breeding population. There is also uncertainty regarding the degree of mixing of southeastern Atlantic whales with southwestern Indian Ocean whales on the Antarctic feeding grounds directly beneath the African continent (0-40°E), which further complicates catch allocation.

The pattern of historical exploitation also differs between the two southeastern Atlantic regions. Total breeding ground catches for the Gulf of Guinea region were ~15,350 humpback whales, distributed between 1909 and 1959, while catches from western South Africa/Namibia/Angola were ~14,500 humpback whales, with over 70% of all catches made between 1911 and 1914 (Allison, 2006) and 90% of all catches made by 1914 (see '*Trends*'). In addition, ~5,000 humpback whales were killed on feeding grounds directly to the south (20°W-10°E). Previous population assessments of the region have combined all catches from these regions and associated polar feeding grounds at 20°W-10°E, and considered both regions as one population, with Gabon (Rosenbaum *et al.*, 2004) representative of total current abundance (Johnston and Butterworth, 2008). However the lack of recovery in western South Africa suggested by catch-per-unit-effort indices to 1963 (see '*Trends*') suggests greater potential for recovery in the Gulf of Guinea population. There is therefore a need for a population assessment that attempts to capture the degree of depletion and recovery for both regions, as a combined estimate may provide an overly optimistic estimate of recovery for western South Africa. No such population assessment has yet been agreed by the International Whaling Commission Scientific Committee, as a number of key parameters (abundance and trends) are not yet available. Discussion will be focused on this topic during the 2010 IWC Scientific Committee meeting.

3. Southwestern Indian Ocean

i. Distribution and population structure

Breeding ground distribution

At least three winter breeding aggregations of humpback whales have been suggested in the southwestern Indian Ocean from historical whaling records and contemporary surveys (Best *et al.*, 1998; Wray and Martin, 1983). One is associated with the mainland coastal waters of southeastern Africa, extending from Mozambique (24°S, Findlay *et al.*, 1994), to as far north as Tanzania and southern Kenya (e.g., Wasini Channel and Kisite Mpunguti Marine Park, 4°S 39°E) (Berggren *et al.*, 2001; O'Connor *et al.*, 2009; Wamukoya *et al.*, 1996). The second is found in the coastal waters of the northern Mozambique Channel Islands (Comoros Archipelago) (Ersts *et al.*, 2006; Kiszka *et al.*, In press; Kiszka *et al.*, 2007) and the southern Seychelles (Hermans and Pistorius, 2008; Reeves *et al.*, 1991). The third is associated with the coastal waters of Madagascar (15-25°S), best described in Antongil Bay on the east coast (Rosenbaum *et al.*, 1997). Additional sightings of humpback whales in La Réunion and Mauritius suggest a fourth offshore aggregation at 55°E (Corbett, 1994; Dulau-Drouot *et al.*, 2008), although it is not yet clear whether this represents a calving area or a resting area for whales en route to more northerly destinations (August singers have also been recorded in the easternmost island of Rodrigues in 2007 (Vély pers. comm.) but humpback whales in other oceans are known to sing on migration as well as on breeding grounds). The relationship and overlap between these aggregations is not fully clear and only partially investigated (Cerchio *et al.*, 2008; Ersts *et al.*, 2006; Pomilla, 2005; Pomilla *et al.*, 2006), although population structure does exist (Pomilla, 2005; Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009).

In Mozambique, whaling records from Mozambique waters (Mozambique Town and Inhambane; Olsen, 1914) show no temporal bimodality of catches, indicating that this area represents a wintering destination for whales rather than a migratory route. The waters of southern and central Mozambique (18-25°S, between the coast and 183m depth over the continental shelf) were surveyed by yacht over one month (spanning August and September) in 1991 (Findlay *et al.*, 1994). In 2003, a ship-based survey, including additional regions of the coast to the north (between 14-26°S) was carried out over 10 days (spanning August and September, Findlay *et al.*, In press). Transect sightings in both surveys suggest that humpback density is highest in a shallow-banked region in southern Mozambique between 33 and 35°E and 24 and 27°S (between Maputo and Ponta Zavora, Findlay *et al.*, In press; Findlay *et al.*, 1994). While the earlier survey identified a calving area (cow/calf pairs 14.8% of sightings) in the northern Sofala Bank region (Findlay *et al.*, 1994), the later survey observed even densities of calves across the survey region, suggesting a possible recent expansion of the region used by lactating females (Findlay *et al.*, In press).

Boat-based surveys of the islands of the Comoros Archipelago between August and September in 2002 sighted humpback whales distributed across the archipelago, with an average occurrence of 0.42 groups/hr off Anjouan, 0.56 off Mohéli and 0.6 off Grande Comore (Kiszka *et al.*, In press). The most common groups encountered were mother/calf pairs (49%) with competitive groups, escorts and singletons also sighted (Kiszka *et al.*, In press). Surveys were carried out in Mayotte in 2004/2005, with most effort concentrated in the lagoon and reef areas, and some offshore survey also. Humpback sightings were concentrated in the lagoon and reef slope regions (Kiszka *et al.*, 2007). On Geyser and Zélée banks (between Mayotte and Madagascar), humpback whale density and group composition have been investigated (Ersts *et al.*, In press). The densities of humpback whales out to one nautical mile from the surveyed transects, ranged from 0.027 to 0.618 whales/ n.m.^{2} across the three study sites. Females with calves were the most frequently encountered group type in all surveys (Avolio *et al.*, 2002; Ersts *et al.*, In press). Encounter rates ranged from 0.98 to 2.36 groups per hour of search effort (Ersts *et al.*, In press). These results indicate that these shallow reef complexes are likely to be an important area for humpback whales at least during the late austral winter months.

In the southern Seychelles, humpback whales are regularly sighted near Aldabra Atoll between late July and November (Avolio *et al.*, 2002), while sightings farther north in Mahé (575nm to the northeast) have also been reported (Hermans and Pistorius, 2008).

In Madagascar, initial winter surveys in the 1990s have provided acoustic evidence of humpback whales singing on the southern, western and eastern coasts (Best *et al.*, 1998), broadly indicative of a breeding region. Modern whaling off Madagascar took over 6,200 humpback whales (Best *et al.*, 1996), suggesting that the area was frequented by a large number of whales. A line transect survey of abundance carried out on the southern Madagascar coast in 1994 sighted 23.3 whales per day, with an overall encounter rate among all groups of 3.7% cow-calf pairs (Best *et al.*, 1996). Extensive winter surveys have also been carried out in Antongil Bay (northeastern coast) since 1996, documenting all behaviors associated with breeding and calving (Rosenbaum *et al.*, 1997). During a survey of habitat stratification, 12% of encounters were of cows and calves (Ersts and Rosenbaum, 2003), consistent with those on other nursing grounds (Rosenbaum *et al.*, 1997). Humpback breeding characteristics in this region have been described in greater detail by Pomilla and Rosenbaum (2006), and a history of surveys in the region is given by Rosenbaum (2003). Historical catches from this region were uni-modal (characteristic of a migratory destination as opposed to a migratory corridor). In addition, short residency times have been reported from re-sightings in Antongil Bay (3-8 days Cerchio *et al.*, 2009), with inter-annual re-sights occurring with strong temporal regularity (76% of recaptures within 10 Julien days of the date of initial capture) suggesting there may be regular movement through the region during the breeding season (Cerchio *et al.*, 2009). Surveys off Anakao in the southwest of Madagascar have indicated high sighting rates of humpback whales during the winter months (Cerchio *et al.*, 2009) comparable to sighting rates observed in Antongil Bay (Cerchio, pers. comm.). The limits of the breeding ground distribution, the extent that individuals may travel to more northerly locations in Mozambique Channel islands, and the migratory origins of these humpback whales are still largely unknown.

In the Mascarene Islands, humpback whales are observed in La Réunion between early June to early November (Dulau-Drouot *et al.*, 2008). Photo-identification re-sight intervals range from days to two months, suggesting that some individuals may be seasonally resident. However no whales have yet been re-sighted inter-annually (among 29 individuals identified), suggesting a low degree of site-fidelity to this region, or that it may be used as a temporary resting location during migration to northerly calving grounds (Dulau-Drouot *et al.*, 2008). Low encounter rates in nearby Mauritius and a paucity of sightings by local fishermen add further support to this hypothesis (Corbett, 1994).

Migratory connections

At least three migratory pathways for humpback whales in this region have been proposed using a compilation of data from surveys, whaling and acoustic records and sightings (Best *et al.*, 1998). The first pathway (and the one for which the greatest evidence is available) occurs off the coast of eastern South Africa, where humpback whales arrive at the coast from Knysna (33°S 23°E, April onwards) during the northward migration and depart the coast at a similar longitude on the southward migration up until December. Estimates of abundance from 1990 surveys of the northbound and southbound migrations have differed very little, suggesting that a similar proportion of the population uses this migratory route in both directions (Best *et al.*, 1998). The timing of observations of whales along the coast suggests rapid movement towards breeding grounds, with more protracted movement on return to feeding grounds (Best *et al.*, 1998). Other potential migratory paths have been suggested in the central Mozambique Channel and offshore along the Madagascar Ridge (which runs between Madagascar and ~40°S). The Madagascar Ridge has been identified as a potential migratory route based on whaling and sightings data from Walter's Shoal, a location on the Madagascar Ridge, south of Madagascar (Best *et al.*, 1998). The Mozambique Channel route was proposed based on acoustic surveys in 1994, which recorded a few singers in the center of the channel; the same surveys did not detect singers away from the middle of the channel, suggesting that the Channel is not commonly traversed by whales on the eastern African migratory path travelling to Madagascar (Best *et al.*, 1998). However in the Comoros Archipelago, singers are observed every winter season (Kiszka, pers. comm.). The migratory path for whales wintering in La Réunion and Mauritius has not yet been identified.

A summary of connections so far identified between the breeding areas described above is shown in Figure 3. A connection between Madagascar and the Southern Ocean was first identified by Rayner (1940) using Discovery marks (see Glossary). In total, seven Discovery marks were deployed from whaling stations and 125 in the Southern Ocean between 10 and 50°E. Two whales marked >50°S and at 10-50°E were captured in Southern Madagascar, while three other whales marked in the Southern Ocean were also captured in that region (Paton and Clapham, In Press). Additional information on migratory connections has been provided by microsatellite genotyping, which has to date recaptured a whale biopsy sampled in east South Africa at >50°S/5°W, and a whale biopsy sampled in Madagascar at >50°S/59°E (IWC, In Press). The distance between these recaptures, in conjunction with a recent genotypic mark recapture study of movement between these breeding grounds and the Antarctic (Loo, Pomilla *et al*. pers comm.) preliminarily indicates that whales from these breeding grounds may travel to geographically separate feeding grounds to the west and east of the region 5°W-60°E (Loo, pers comm.[10]).

Population structuring

There is significant mitochondrial (F_{ST}) and nuclear (F_{ST} and R_{ST}) genetic differentiation between Madagascar (Antongil Bay) and eastern South Africa (migratory stream travelling to Mozambique), suggesting that interchange between these two regions is restricted (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009). However, given the magnitiude of the F-statistics, a higher degree of undetected exchange is possible. An exhaustive comparison of microsatellite genotypes (coastal eastern South Africa N=179, Madagascar N=718; Pomilla, 2005) has revealed one re-sight between these regions (Pomilla *et al.*, 2006). A photographic identification comparison of 458 individuals from the East African mainland (primarily northern South Africa and southern Mozambique) and 842 individuals from Madagascar collected over seven years yielded two recaptures between regions (Cerchio *et al.*, 2008); a permutation analysis found the observed number of recaptures to be significantly less than expected from a randomly mixing population. This is therefore a second line of evidence for restricted population connectivity between the two regions. Application of a multi-strata recapture model resulted in estimates of exchange probability between mainland East Africa and Madagascar ranging from 0.07 (CI 0.01- 0.38) to 0.13 (CI 0.03 - 0.41) (IWC, 2009a, Cerchio). Thus the East African mainland coast and Madagascar assemblages are neither panmictic (fully connected) nor demographically isolated.

Significant mitochondrial and nuclear (F_{ST}) genetic differentiation has been found between the Comoros Archipelago and the East African mainland but not between the Comoros Archipelago and Madagascar or Mozambique (Pomilla *et al.*, 2006; Rosenbaum

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[10] Also see Loo J, Pomilla C, Olavarría C, *et al.* (In Prep) Genetic structure of feeding aggregations of humpback whales in the Southern Ocean based on mtDNA and microsatellite variation.

et al., 2009), suggesting restricted gene flow between the former two regions. Consistent with the observation of no genetic differentiation between Madagascar and the Comoros Archipelago, there is further evidence to suggest that some whales frequenting the Comoros Archipelago also frequent the east coast of Madagascar; three genotypes, four flukes and two dorsal fins have been recaptured between these regions in different years, suggesting some degree of interchange at least across years (Ersts *et al.*, 2006; Pomilla *et al.*, 2006), which may explain the lack of genetic differentiation between these regions. The affiliation of Cormoros Archipelago whales to the Madagascar population is still under investigation.

Mitochondrial, photo-catalog and microsatellite genotype comparisons have been made between the southwestern Indian Ocean breeding regions and those in Oman (northern Indian Ocean), the eastern South Atlantic and Australia (Minton *et al.*, In press; Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009). Significant mitochondrial haplotype differentiation (F_{ST}) was found among all southwestern Indian Ocean breeding regions and neighboring regions, while significant mitochondrial nucleotide (ϕ_{ST}) and nuclear differentiation was found with the northern Indian Ocean, Gabon (West Africa) and Madagascar (Appendix 1, Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009). To date there have been two instances of a whale visiting both southeastern Atlantic (Gabon) and southwestern Indian Ocean wintering grounds, detected through genotype comparisons (N=722 Gabon and N=480 Madagascar) (Loo pers comm., Pomilla and Rosenbaum, 2005).

All of five major song themes were sung by whales in Gabon and Madagascar in 2003, indicating potentially substantial exchange between males of the two populations (Razafindrakoto *et al.*, 2009), which could potentially occur due to contact either by movement of migrants, exchange on a shared migratory route traveling towards South Africa or song transmission on shared feeding grounds. Only one song theme was shared between Madagascar and Western Australia in 2006, which each had four and six private themes respectively, indicating limited exchange between the populations on either side of the Indian Ocean (Murray *et al.*, 2009). Taken together this suggests greater exchange and interaction between breeding stocks either side of South Africa than those across the Indian Ocean. Acoustic surveys of whales from Brazil and Gabon revealed that they sang all the same themes in 2001 and 2002 (Darling and Sousa-Lima, 2005), suggesting that there may be relatively substantial exchange between these breeding stocks also, either due to movement of migrants or song transmission on shared feeding grounds (e.g. Clark and Clapham, 2004).

ii. Abundance

The most recent estimates of abundance from Madagascar were obtained from surveys of Antongil Bay, using photo-identifications and microsatellite genotypes collected between 2000-2006. Within-year photo-ID recaptures suggested relatively short residency times, with yearly mean recapture periods ranging from three to eight days (Cerchio *et al.*, 2009). Inter-annual recaptures were small for both datasets (less than 5% of individuals recaptured) ranging from zero to four (photo-ID) and zero to six (genotype) recaptures between pairs of years (Cerchio *et al.*, 2009). Abundance for the period 2004-2006 was estimated using closed models for the photo-ID data at 7406 (CV = 0.37, CI = 2106-

12706) and for the genotype data at 6951 (CV 0.33, CI = 2509-11394). For the genotype data, independently determined estimates of genotyping error were incorporated into the recapture models to compensate for missed recaptures. Application of the open Pradel model to all years of data 2000-2006 (excluding 2002 due to a highly truncated season and small sample) resulted in both lower and higher estimates: allowing the model to estimate all parameters yielded an abundance in 2006 of 4936 (CV 0.44, CI = 2137-11692), whereas constraining the parameters of survival and recruitment (to between 0.95-0.98 and 1.06-1.10 respectively) and averaging across all models yielded an abundance in 2006 of 8169 (CV 0.44, CI 3476-19497, Cerchio *et al.*, 2009). Since these estimates are from mark-recapture data over several years, they may represent the abundance of whales breeding off Madagascar, in addition to possibly whales breeding in Mayotte and the Comoros (Ersts *et al.*, 2006), and to a smaller degree from the East African mainland (Cerchio *et al.*, 2008) (see '*Population Structure*').

An earlier survey of abundance was calculated from a month of line-transect surveys of the continental shelf region across the south and southeast coasts of Madagascar in 1994. This produced an estimate of 2,532 whales (CV = 0.27) (Best *et al.*, 1996); this survey did not cover the full extent of humpback distribution in Madagascar, an important consideration in line-transect distance methods of abundance estimation, and thus clearly underestimates the entire population. The degree to which the Antongil Bay mark-recapture abundance estimates represent the total breeding population depends on the degree of movement of whales throughout the breeding grounds in each season, *i.e.*, the probability of equal capture among whales that breed around Madagascar.

A line transect survey of abundance, carried out during August and September in Mozambique in 1991, yielded an estimate of 1,954 whales (CV = 0.38), although no correction for whales missed on the trackline ($g(0)$) was used, so this is considered an underestimate (Findlay *et al.*, 1994). A subsequent line transect survey in 2003 included a larger region of the coast (Findlay *et al.*, In press). Both surveys ranged from coastal waters to the 200m isobath. Two estimates of abundance were generated in 2003, one for all whales sighted (assuming that all unidentified whales were humpback whales) and one for only confirmed humpback whales. The assumption is based on the fact that the only other large whales observed in the region are very low densities of southern right whales to the south. With only humpback whales included, a 2003 abundance of 6,664 whales (CV 0.16) was estimated when data were un-stratified and 5,965 (CV 0.17) when data were stratified by coastal regions (Findlay *et al.*, In press). Estimates with unidentified whales included were slightly greater (by ~150 whales). These estimates were considered negatively biased as an estimate of the Mozambique breeding population, as numerous additional sightings were made to the south while on transit to the survey, and densities in the north were high up to the edge of the northernmost transects, suggesting that a proportion of the population was missed during the survey period (Findlay *et al.*, In press). In addition, no correction for whales missed on the trackline ($g(0)$) was used, so any whales missed on the trackline during survey are unaccounted for (Findlay *et al.*, In press). Neither survey included sighting effort outside the 200m isobath; the near-shore distribution is assumed from whaling records (Townsend, 1935), but sighting surveys outside 200m isobath have not been done, so there may be whales farther offshore and unaccounted for by these surveys.

iii. Genetic Diversity

For an introduction to genetic diversity, see 'Genetic Diversity' in the 'Status of North Atlantic Populations' section. Mitochondrial genetic diversity has been estimated for Mozambique, eastern South Africa, the Comoros Archipelago and Madagascar. Haplotype and nucleotide control region diversity estimates were very similar across all regions, with comparably high haplotype diversity (0.97-0.98, Appendix 1), while nucleotide diversity (2-2.1%) was similar to that described for neighboring breeding regions, western South Africa and Western Australia and lower than that described for Brazil and eastern Australia (Olavarría *et al.*, 2006b; Rosenbaum *et al.*, 2009).

Microsatellite diversity has also been estimated from these regions: Madagascar (0.75 ± 0.00), the Comoros Archipelago (0.75 ± 0.01), Mozambique (0.78 ± 0.01), Southern Madagascar (0.80 ± 0.02) and eastern South Africa (0.76 ± 0.01) (Pomilla *et al.*, 2006). These values are similar to those obtained from the southeastern Atlantic and slightly higher than diversity in the southwestern Atlantic, although the difference is not significant (Pomilla *et al.*, 2006).

iv. Trends

Two trends in relative abundance have been calculated from land-based observations of the migratory stream passing Cape Vidal, eastern South Africa (Findlay and Best, 2006). One spans the period 6-22 July (four surveys between 1988 and 2002, 12.3% per annum), the other spans 6-30 July (three surveys between 1990 and 2002, 9.0% per annum). While the former estimate is high (and outside the biologically plausible range for this species), the latter rate of increase is within the range calculated for other Southern Hemisphere breeding grounds (e.g. Hedley *et al.*, 2009; Noad *et al.*, 2008; Ward *et al.*, In Press). However both rates of increase are considered preliminary and tentative estimates, since these surveys are limited in number and of short duration.

v. Habitat or Ecosystem Conditions

The migratory stream of humpback whales along the African coast travels close to the southward-flowing Agulhas Current, a very narrow, rapid flow which passes close to the southeastern African coast, particularly between Durban and Port Elizabeth. This current occurs throughout the year and is one of the strongest currents in the world (Rao and Griffiths, 1988). The Sofala Bank region, where a high proportion of cows and calves were observed during 1991 surveys (Findlay *et al.*, 1994), is a shallow (20m average depth) coastal bight, characterized by high river run-off and ranging up to 45nm in width from the coast. It is mostly protected from the Agulhas Current by coastal topography (Bakun *et al.*, 1998), which may explain this habitat preference by mothers and calves.

The warm Mozambique current flows southward through the Mozambique Channel, just east of the coast. The larger eastern Madagascar current branches out from the South Equatorial Current and flows south along the eastern coast of Madagascar. These warm currents may explain why breeding grounds on this coast are so far south relative to other

Southern Hemisphere grounds (Figure 3).

The coastline of Mozambique is generally lower-lying than that of most other East African countries and is protected from the open ocean by the Mozambique Channel. This region is the outflow area for 25 eastern African river systems, which creates a swampy, sandy and fairly low-energy coastline characterized by large volumes of river sediment deposits. There are mangrove forests, sandy spits and offshore bars between the Bay of Maputo and the Zambezi River mouth, and north of the Zambezi the coast is characterized by sandy stretches, rocky outcrops and coral islands. There are substantial areas of coral fringed coast, while barrier beaches and islands protect the swampy, sandy coast (Alusa and Ogallo, 1992).

The Comoros Archipelago consists of volcanic islands. Two are surrounded by deep oceanic waters close to the coastline (Anjouan and Grand Comore) while Moheli is surrounded by shallow waters, smaller islets and coral reef complexes out to the 100m isobath (Kiszka *et al.*, In press). Mayotte is entirely encircled by a long barrier reef of around 125 miles length (broken in places by passes arising from ancient river mouths, where humpback whales enter the lagoon), with an additional outer reef barrier in the southwest and an immersed reef complex in the northwest. The island possesses one of the largest interior lagoons in the world, at an average depth of 20m, deepening to 80m towards the ocean entrance. There are multiple islands within the lagoon, themselves surrounded by fringing reefs, and mangrove forests are common across the tidal flats of protected bays of the main island (Kiszka *et al.*, 2007).

Aldabra is a large raised coral atoll located on the southwestern edge of the Seychelles island group (9°S, 46°E, 230 nm north of Madagascar) consisting of four main islands enclosing a central lagoon containing several smaller islands (Hermans and Pistorius, 2008). This site has been designated a UNESCO World Heritage site since 1983 due to the high degree of endemic terrestrial species and unusual abundance of marine species in this region (UNESCO, 1983).

The coastline of Madagascar is mostly sandy on the west coast, with rocky outcrops and extensive fringing reefs and a wide continental shelf boundary. An extensive barrier reef formation, 15 miles in length, occurs offshore of Tuléar on the southwestern coast (Spalding *et al.*, 2001). On the southwestern and southeastern coasts, there are vast sandy beaches, protected by fringing reefs and sand barrier beaches, behind which run a chain of lagoons, connecting with the interior Canal des Pangalanes. The eastern shoreline is mostly rugged and indented, with a narrow continental shelf and steeply shelving bathymetry (Spalding *et al.*, 2001). In this region, Antongil Bay extends 50 miles inland, and contains extensive shallow water regions, with a mean depth of 41.5m across the interior and mean of 23m in the northern section (a focal survey area for humpback whales (Ersts and Rosenbaum, 2003; Rosenbaum and Collins, 2006; Rosenbaum *et al.*, 1997).

The Mascarene Islands are situated on a submarine plateau (depth 1,860 miles) which stretches north up to the Seychelles (Corbett, 1994). La Réunion and Mauritius are volcanic islands with steep offshore continental slopes. In Mauritius, most of the island is fringed by a barrier reef and the 1,000m contour is between1.5-3nm from the coast. La Réunion is slightly less protected, with a discontinuous coral reef system circling <10% of the coast. Humpback whales in La Réunion were mostly sighted at <100m depth, very close to the shore (Dulau-Drouot *et al.*, 2008). The two reported humpback sightings during a general cetacean survey in Mauritius were both within 0.5nm of the shore (Corbett, 1994).

Within the Antarctic feeding grounds associated with this breeding ground (Core region 30-60°E, possible range 10-80°E, Appendix 2), the highest densities of krill (from sampling net data spanning 1926-2003, Atkinson *et al.*, 2004) are found at the eastern and western borders. In the west (10-30°E), areas of higher krill and chlorophyll density are found close to the polar front and ice edge (Atkinson *et al.*, 2004; Moore and Abbott, 2000). Densities of chlorophyll are highest across a range of latitudes in the east (70-80°E, Moore and Abbott, 2000), while estimates of krill density are only high in the vicinity of Prydz Bay (67-70S°) (Atkinson *et al.*, 2004; Moore and Abbott, 2000). This is a region of rapid ice retreat, which may explain the high levels of primary productivity (Nicol *et al.*, 2006). Net survey data from postlarval krill indicate that in the Indian Ocean krill are most commonly found within 100-160nm of the continental shelf break, rather than on the shelf as in the Antarctic Peninsula (Atkinson *et al.*, 2008). This can be seen in Prydz Bay, where the highest densities of krill are found slightly away from the coast (Atkinson *et al.*, 2008). The main concentrations of humpback whale catches were also made slightly offshore, and ~5° to the east of this region (Tynan, 1998), consistent with krill density observations. High krill densities are also found in the sub-Antarctic region close to the coastline of the Prince Edward Island group (46°S, 37°E), where humpbacks are occasionally observed (Whitehead, 1985b) but are not regularly reported as feeding.

vi. Threats and Anthropogenic Impacts

Coastal activities, notably fishing, ports and tourism, have made it attractive for large populations to move to the coast in Madagascar and East Africa. It was estimated in 1992 that 14.6% of the population live in the coastal regions (Alusa and Ogallo, 1992). However the coastal infrastructure is largely undeveloped, with poor infrastructure and limited harbor facilities, so consequently the majority of information regarding fishery activities has been obtained by interviews with fishermen and direct observation during surveys. Similarly, there is an absence of data regarding ship strikes from the region.

A summary of humpback entanglement events, strandings and sightings of entangled whales was compiled for the region via a series of interviews in artisanal fishing communities (Kiszka *et al.*, 2009; Razafindrakoto *et al.*, 2008). There are many gillnet fisheries operating in the near-shore waters of the coasts of mainland Africa and Madagascar. Offshore in the Comoros Archipelago, Mayotte and Mascarene Islands, gillnets are less common as they are hindered by coral reefs and a steep continental slope topography (Kiszka *et al.*, 2009). Stranding reports and observations from Tanzania and Mozambique have mostly implicated gillnets, with most Madagascan entanglements associated with long-line shark fishing (Razafindrakoto *et al.*, 2008). In Mayotte, humpback whales have been observed with gillnet remains attached to them (Kiszka *et* *al.*, 2009), although no fatalities have yet been documented. Among the known breeding grounds, some localized marine protected areas where fishing is prohibited exist in Mayotte, Moheli (in the Comoros Archipelago), Madagascar (northeast coast), Aldabra (under protection as a UNESCO World Heritage Site) and most recently in a 185 mile trans-frontier coastal region between Southern Mozambique and South Africa. While artisanal fishing in La Réunion is limited, with no records of by-catch for humpback whales, the waters of Mauritius are subject to a variety of industrial fishing operations, including longlines and drift longlines on fish aggregation devices, purse seine and midwater trawling. The extent of bycatch and entanglement in these waters is undocumented (Kiszka *et al.*, 2009).

Some strandings and by-catch data compiled between 2001 and 2005 from South Africa reported an estimated 15 humpback whales entangled in shark nets (large-mesh gillnets) in KwaZulu Natal province during this period (only one fatality) while a total of nine stranded whales were reported from the southern and eastern coasts (IWC, 2002b, 2003b, 2004b, 2005c, 2006c).

Whale watching in Mozambique is currently a rapidly expanding yet poorly regulated industry, showing a 34.5% growth in tourist numbers between 1998 and 2008 (O'Connor *et al.*, 2009). Most operators are local, operating motorized boats, recreational fishing boats and dive boats. There is a voluntary code of conduct for operators, but at present this is poorly upheld and no formal regulations or enforcement are currently in place (O'Connor *et al.*, 2009). Whale watching in South Africa is mainly focused on right whales, although the industry at St Lucia in KwaZulu Natal province is focused on southwestern Indian Ocean humpback whales. There are regulations in place for all whale watching activity in South Africa (Carlson, 2007). Recent political instability in Madagascar has reduced the rate of growth of whale watch tourism in this region, although growth between 1998 and 2008 was still in the realm of 15%, with the main industry focused on humpback whales frequenting the Ile Ste Marie / Antongil Bay region and over 14,000 tourists taken on whale watch tours by roughly 13 operators in 2008 (O'Connor *et al.*, 2009). This industry has recently developed some guidelines for the protection of humpback whales, which was passed as legislation in 2000 with local regulations in place in Ile Sainte Marie (Vely pers. comm.) and Antongil Bay (Journal Officiel de la Republique de Madagascar, 2000). Whale watch tourism in Mayotte is small-scale but has expanded rapidly, from no industry in 1998 to 10,000 annual whale watchers in 2008 (O'Connor *et al.*, 2009), with a focus on a range of cetacean species. In the Mascarene Islands, the expanding whale watching industry in La Réunion (3,000 tourists estimated in 2008) is currently unregulated, while in Mauritius large cetacean watching is a minimal component of the whale watch industry and is therefore unlikely to have much impact (O'Connor *et al.*, 2009). An industry for watching humpback whales in Mauritius commenced in 2008 (Vély, pers. comm.).

Until recently, oil and gas reserves in East Africa were largely unexplored. In the last five years a number of offshore seismic oil and gas surveys have been carried out in Mozambique, Tanzania, Madagascar and the Seychelles, which has brought associated threats to humpback whales from seismic noise. Drilling is now either underway or planned in all of these regions, which brings increased shipping traffic and associated risks of habitat degradation from drilling and oil spills and potential for acoustic disturbance and masking of vocal breeding displays on migratory routes and calving grounds (see '*Threats: sound and pollution*'). In Madagascar, offshore development has been concentrated on the northwest coast; in Mozambique it is concentrated in the Mozambique Basin, Zambezi delta region, while development in Tanzania has been most focussed on coastal Zanzibar. Humpback whales are encountered seasonally in all of these regions (see '*Distribution*'). No mitigation strategies for seasonally restricted or marine-mammal observer-regulated seismic surveys have been reported for any of these regions to date.

vii. Recovery from Exploitation

Population assessment of the recovery of humpback whales in this region is complicated by uncertainty surrounding the degree of migratory interchange among the breeding regions and the means of allocating catches from the feeding grounds to each breeding ground, given that feeding grounds are likely to contain a mixture of humpback whales from both southeastern Indian Ocean and southeastern Atlantic breeding grounds.

The great majority of 20th century Antarctic catches were made on the breeding grounds (over 20,000 whales). Feeding ground catches during modern whaling were fewer; 8,150 whales between 30 and 60°E. A similar magnitude of catches were made (~8,000 whales) in the regions where Antarctic feeding grounds are likely to overlap with those for southeastern Atlantic (10-30°E) and southeastern Indian ocean (60-80°E) whales. There is also a degree of uncertainty regarding total catches for the period prior to 1917, since whaling methods used at some whaling stations before this time had a degree of inefficiency (Reeves and Smith, 2006), and many additional whales may have been fatally maimed yet lost prior to capture and inclusion in the catch records.

Given the existing hypothesis based on 'best available data' for restricted gene flow between Madagascar and the eastern African mainland (see '*Population Structuring*') (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009), the IWC recently carried out a population assessment of each breeding ground individually, using current abundance estimates for the migratory stream passing Cape Vidal and for Antongil Bay in Madagascar (Cerchio *et al.*, 2009). It is assumed that most of those whales passing Cape Vidal are traveling to calving grounds in Mozambique and therefore that abundance estimates from Cape Vidal are representative of numbers visiting that breeding ground. There may also be a small component which travels onwards to Aldabra or the Mozambique Channel islands, although the presence of a mid-channel migratory stream (Best *et al.*, 1998) and multiple sightings of whales in both Madagascar and the Comoros Islands (Ersts *et al.*, 2006) suggests that migration towards the Comoros Islands is primarily offshore, either through the center of the Channel or via Madagascar.

A Bayesian age- and sex-aggregated population dynamic model was developed for the population assessment of these two regions (Madagascar and Mozambique), which incorporated a degree of interchange between regions (any whale from each breeding ground has a fixed probability of visiting the neighboring breeding ground in a subsequent year) and allocated Antarctic catches (between 10-60°E) based on the ratio of model-estimated abundances for each region for that year. Probability for the prior on population growth was normally distributed between 0-10.6% for both regions. A number of alternative exploitation scenarios were explored, including one with no interchange between regions, alternate catch scenarios where catches over a wider area were allocated to these breeding regions, struck-but-lost corrections for whales killed between 1900-1916, and alternate means of incorporating abundance estimates within the population dynamic model (either as a normally-distributed value, or as 'raw' mark-recapture data incorporated within the model).

Uncertainty regarding the level of migratory interchange between the two regions was one of the greatest sources of variability in the population assessment. Across the range of sensitivities and catch allocations employed, point estimates for population recovery for Mozambique and Madagascar ranged from 76 to 83% and 65 to 98% respectively in 2006. However, the degree of uncertainty surrounding the point estimates was substantial, with confidence intervals of 43-97% for Mozambique and 38-100% for Madagascar (IWC, In Press).

4. Southeastern Indian Ocean

i. Distribution and Population Structure

Breeding ground distribution

Humpback wintering grounds and coastal migratory routes in the eastern Indian Ocean are found between 15 and 35°S along the coast of Western Australia, with major calving grounds located in the Kimberley Region (15-18°S) and resting areas on the southern migration at Exmouth Gulf (21°S) and at Shark Bay (25°S) (Figure 4, Bannister and Hedley, 2001; Jenner *et al.*, 2001). There are also anecdotal reports and two recent records of humpback strandings (October 2007) farther north in southern Bali (~8°S) in the Indonesian archipelago (Mustika *et al.*, 2009). The body coloration and time of year of the stranding (austral winter) suggests that the whales were Southern, rather than Northern Hemisphere, migrants (Mustika *et al.*, 2009). While there is not a formal stranding network in that region, both stranding events were considered unusual (Mustika *et al.*, 2009), and cetacean surveys in the region have not yielded sightings, suggesting that the number of whales travelling this far north is small.

During the southward migration, whales are found close to shore along much of the coast, mostly remaining within the 200m isobath. During the northward migration, whales tend to be distributed farther offshore, out to the continental shelf boundary (Jenner *et al.*, 2006b; Jenner *et al.*, 2001), with whales spotted as far out as the 1400m isobath in some places, e.g. Northwest Cape (Jenner *et al.*, 2006b).

Aerial surveys in the Perth Basin (Jenner *et al.*, 2001) and whaling data from Albany (Chittleborough, 1965) indicate that northbound whales approach the coast either via the southwestern coast, or arrive at the west coast from offshore farther along the coast in the vicinity of the Perth Basin (Jenner *et al.*, 2001). There are also observations of humpback whales traveling west along the coast from Esperance (33°S, 121°E), and occasionally from as far east as the Great Australian Bight (Bannister pers comm. In IWC, 2006b). On the southbound migration, whales are not observed passing Albany (Chittleborough, 1965), indicating that the majority of southbound whales travel offshore after passing the Perth Basin (Chittleborough, 1965; Jenner *et al.*, 2001).

Boat-based surveys between Jurien Bay and Carnarvon suggest that whales mostly travel >30nm from the coast, with reports from fishermen suggesting that they pass the Abrolhos Islands between May and June (Jenner *et al.*, 2001). Data from whaling stations farther north at Carnarvon and Point Cloates indicate that whales range within the continental shelf break (the great majority were killed within 10nm of the coast), while recent aerial surveys show the greatest density of humpback whales in shallow waters within 15nm of the western islands of Shark Bay (Bannister and Hedley, 2001), with a peak in density around the 90m isobath (Paxton *et al.*, In Press). Increasing sightings in Shark Bay have led to the region being identified as a potential migratory resting area by Bannister (1994); many whales were killed there in the shallow waters of the Bay in the 1950s. At Point Cloates, the 200m continental shelf break comes to within 11nm of the coast; at this point, the migratory path is therefore closest to shore for both northbound and southbound whales. Boat and aerial surveys farther north, off Exmouth, suggest that the migration stream here is within 9nm of the coast, and these surveys indicate that some southbound whales use Exmouth Gulf (21°S) as a resting and nursery region, while others travel farther offshore. Farther north, aerial and boat surveys indicate that whales migrate past the western side of the Monte Bello islands (~20°30'S). At the Dampier Archipelago (~21° 30'S), the northbound migration stream is wider and dispersed farther offshore than the southbound migration stream, which has been subject to boat survey. Aerial surveys also indicate a significant southbound migration stream travelling offshore outside of the boat-based survey in this region. Photographic, aerial and boat surveys indicate that the Kimberley region is the major calving ground for this breeding population between July and October (peaking in September), with high density regions at Frost and Tasmanian Shoals and Camden Sound (~15°S Jenner *et al.*, 2001).

Feeding ground distribution

Summer feeding grounds in the Antarctic (>56°S, 80-110°E) have been inferred from Discovery Mark data (Chittleborough, 1965l; Rayner, 1940) and photo-identification catalogs (Gill and Burton, 1995). Sighting survey data from the Antarctic region between 80-120°E (1987-2004) suggests that the main concentration of humpback whales is found to the east of the Kerguelen Plateau at 90-120°E, between 60 and 62°S (Matsuoka *et al.*, 2006), which supports the hypothesis of a continuous feeding area, although more detailed photo and genotype identification data and satellite telemetry studies will be necessary to determine the degree of interchange and movement across this region. The survey data suggest some degree of habitat expansion from north to south across the transect period, which may suggest either an increase in density or some degree of shift in the feeding area between surveys (IWC, 2007a).

Migratory connections

A large number of Discovery marks (see '*Glossary*') were deployed from whaling stations in Western (n=333) and eastern Australia/Oceania (n=2,712) and in the Antarctic region between 70 and 130°E (n=896) (Chittleborough, 1959a, 1965; Paton and Clapham, In Press; Rayner, 1940). These reveal ten movements between eastern Australia/Oceania and the Antarctic region, with all eastern Australian deployments recovered up to 110°E (nine marks deployed in eastern Australia/Oceania, and one in the Antarctic), suggesting that a small proportion of the eastern Australian/Oceania humpback breeding ground may feed in the same region as the Western Australian whales (Summarized in IWC, 2006b). No marks deployed off Western Australia have been recovered east of 130°E (although the illegal whaling effort in this region was particularly concentrated, Clapham *et al.*, 2009` and marks may not have been reported), nor have whales marked in the corresponding Antarctic region (130-170°E, n=664) been recovered off west Australia (IWC, 2006b).

Population structure (between breeding grounds)

Pair-wise tests of genetic differentiation with eastern Australia were significant ($p < 0.01$) both for haplotypes ($F_{ST} = 0.019$) and for nucleotide distance ($\phi_{ST} = 0.018$) measures (Olavarría *et al.*, 2006b). Pair-wise tests of genetic differentiation with each of the three eastern African breeding areas were significant ($p < 0.05$) for haplotypes (F_{ST} = 0.013, 0.012, 0.011 for eastern South Africa, Mayotte/Comoros archipelago, and Madagascar respectively) but not for nucleotide distance (ϕ_{ST} = 0.003, 0.007, 0.003 respectively) (Rosenbaum *et al.*, 2006).

ii. Abundance

A preliminary analysis of sex ratio using biopsy samples from the wintering ground (collected during August at the Northwest Cape) suggests a ratio of around 2.5-3.5:1 males : females (Jenner *et al.*, 2006a). Assuming that the true sex ratio is 1:1 (see discussion in '*Natural History*'), the negative bias in either capturability or actual presence of females may create an underestimate of abundance for some populations by ~25% (Calambokidis *et al.*, 1997), although note that sex ratios were obtained from small sample sizes and are likely to vary due to temporal segregation of the migration stream according to age and sex class (see '*Natural History*').

A series of aerial surveys (transects up to 40nm from the coast) were carried out from Carnarvon from 1982, timed to encompass the peak of the northward migration past this area (mid-June to mid-August), giving a rate of increase from relative abundance indices (Bannister 1994). Surveys in 1999, 2005 and 2008 were designed to estimate the absolute abundance of the northward migrating whales, with a land-based platform also included in 2005 and 2008 to calibrate estimates from the air (Hedley *et al.*, 2009; Paxton *et al.*, In Press). Poor weather in 1999 and 2005 limited the number of flights made along the transect; however land-calibrated sightings from 2005 (available from the first half of the survey) were used to estimate the proportion of whales missed on the track-line (*g0*) in the 1999 survey. The 2008 survey was carried out with 26 flights used to estimate overall abundance and calibrated within 6.5nm by the land-based counts from shore. Spatial modeling of the aerial data allowed plotting of a 'migration curve' to the daily survey estimates and summing over the survey period. Absolute abundance of northbound whales in 2008 was estimated at 21,750 (95% CI = 17,550-43,000), assuming that only 54% of whales were available at the surface for counting ($g(0) = 0.54$ +/- 0.21) and excluding whales that were not clearly travelling north (Hedley *et al.,* 2009). The 2005 survey estimated 13,145 whales (95% CI 4,984-38,725) (Paxton *et al.,* In Press). Correction upward for whales missed in the 1999 surveys (Bannister and Hedley, 2001) provided a revised estimate of 10,300 whales (95% CI 6,700-24,500) in 1999 (Paxton *et al.*, In Press), which is within the range originally reported using 10-15 minute dive times estimated from other surveys to calculate *g*(0) (mean estimates ranging 8207-13640, Bannister and Hedley, 2001).

Abundance estimates are also available from line-transect surveys of the Antarctic area south of 60°S. Surveys of the region between 70 and 130°E during 2003/2004 yielded an estimated abundance of 31,750 whales (CV=0.11) (Matsuoka *et al.*, 2006). A survey (CPIII) of this region conducted between 1994 and 1999 yielded an estimate of 17,938 (CV=0.18) for 1997/1998 (Branch, In Press). However the degree of mixing of whales from the Western Australian breeding ground with those in neighboring breeding grounds is unknown, although likely to be limited, so these estimates may not be fully representative of the breeding ground.

iii. Genetic Diversity

For an introduction to genetic diversity, see 'Genetic Diversity' in the 'Status of North Atlantic Populations' section. 174 genetic samples were collected from the wintering ground in 1990, 1993, 1994 and 2002. These yielded 53 mitochondrial haplotypes and high estimates of mitochondrial haplotype (h = 0.970 /- 0.004) and nucleotide (π = 0.02 +/- 0.01) genetic diversity (Appendix 1, Olavarría *et al.*, 2007).

iv. Trends

Trend data from the wintering grounds are available from surveys of relative abundance of the northbound migration stream (Bannister and Hedley, 2001), which have been carried out from Shark Bay since the cessation of whaling there in 1963. Surveys from 1982 (and approximately every three years subsequently) were consistent in covering the same area, with the same flight path, aircraft type, pilot and observer (where possible). They covered 10 good flying days in mid-July and were designed to coincide with the maximum number of whales moving northward through the area. Surveys in 1991 and 1994 provided similar annual population increase estimates of ~10% (Bannister, 1994), with the annual estimate from 1982-1994 = 10.15% +/- 4.6% (Bannister and Hedley, 2001). From surveys in 2008, an updated trend in relative abundance was calculated as 9.8% per annum (Hedley *et al.*, 2009). The trend calculated from absolute abundance estimates (see '*Abundance*' section) was very high (14.7%, over the boundary of maximum biological plausibility or this species, see Section Xbvi) and was considered to be too strongly dependent on estimated *g*(0) during each survey.

A trend in abundance has been calculated from the Antarctic region corresponding to the Western Australia feeding ground; however this estimate (18.1%, CI 10.6-25.6% Matsuoka *et al.*, 2006) is outside the range of biological plausibility for the species and suggests that inter-annual changes in the distribution of whales across feeding grounds have a major influence on perceived trend.

Catch-per-unit-effort (CPUE) data were collected during the whaling period, with CPUE values between 1950 and 1962 decreasing from 0.475 to 0.051 respectively and suggesting an extremely marked decline in abundance of 90% (Chittleborough, 1965).

v. Habitat or Ecosystem Conditions

Off southern Western Australia, the Leeuwin Current flows southwards in winter, traveling along the southern Australian coast as far as Tasmania. This is a warm current for this latitude, which warms the continental shelf waters in winter and cools them in summer, fostering at the Abrolhos Islands the most southerly true coral reefs in the world. The Antarctic Circumpolar Current also creates the West Australian Current (commencing in the Indian Ocean) and Southern Australian Countercurrent (commenting at Tasmania). Coastal waters on the southwestern coast tend to be nutrient poor and very clear, while inshore waters along the northwestern and northern coast contain high levels of suspended sediment and are turbid and much higher in amplitude (Environment Western Australia, 2007). As a result of this cline along the coast, there is a wide variety of coastal ecosystems and therefore a high degree of marine species endemism (second in the world), motivating the listing of the Western Australian marine environment as one of the Earth's most biologically valuable eco-regions ('Global 200' Olson and Dinerstein, 2002). However much of this marine biodiversity is still poorly monitored (Environment Western Australia, 2007). Along the southern part of the western coast (north of Perth), there is much sheltered shore habitat provided by embayments, protected bays or offshore fringing reefs, which supports extensive and highly diverse sea-grass beds (Walker, 2003)

Shark Bay is a shallow area of strong carbonate sedimentation, with high turbidity driven by the wind and tides and a large area of seagrass habitat. Further north there are large intertidal mangrove swamps, and coral reefs and atolls offshore. Exmouth Gulf is a large, shallow embayment, which is bordered by intertidal mangrove swamps and arid coastal salt flats to the east and sand beaches to the west, with little coastal run-off from rain or rivers. The main calving area at Kimberley is a drowned river valley (rial) system with large tidal amplitudes, many offshore islands and embayments, mangrove covered tidal flats and a sparse human population (Walker, 2003).

The high-latitude feeding region associated with this breeding ground (Core region 80-110°E, possible range 60-130°E, Appendix 2) includes both the Indian and Pacific oceans and seems to be concentrated to the east of the Kerguelen Plateau (Matsuoka *et al.*, 2006). The Kerguelen Plateau is a large, submerged volcanic plateau. The northernmost point is found at ~67°E, 47°S in the vicinity of the polar front, and the plateau extends >1,190nm to the southeast, ending close to the ice edge at ~78°E 54°S. In the southwestern part of the plateau, the plateau is separated from the Antarctic continental shelf by the abyssal Princess Elizabeth Trough (85°E, 63-66°S). High densities of marine mammals have been reported from the waters of the southwestern Kerguelen Plateau and edge of the Trough, a region where both the southern boundary of the Antarctic Circumpolar Current and the southern water mass boundary are found in close proximity (Tynan, 1997). The eastward travelling Antarctic Circumpolar Current is deflected south around the southern edge of the Kerguelen Plateau. This carries Upper Circumpolar Deep

Water to higher latitudes than it regularly travels to. This feature, coincident with a complex bathymetry, marginal ice zones and the close coincidence of two major frontal zones, is likely to explain the high levels of regional primary and secondary productivity (Moore and Abbott, 2000) and seasonal observations of foraging humpbacks from this region (Tynan, 1997). With the exception of the Kerguelen Plateau, chlorophyll and krill are at low densities in all regions south of the Polar Front, with highest densities of krill found close to the Antarctic coast (90-110°E)(Atkinson *et al.*, 2004; Moore and Abbott, 2000).

vi. Threats and Anthropogenic Impacts

Humpback whales frequenting Western Australian waters are subject to seismic noise and shipping traffic impacts from oil and gas exploration on the migration and calving grounds, as well as general shipping traffic and entanglements risks on the coastal migration corridor. Naval seismic surveys are also regularly carried out on the southern coast, where a proportion of the population regularly passes on migration northward.

Australia is a net energy exporter, and the vast majority of crude oil, liquid petroleum gas and natural gas reserves are concentrated in Western Australia, with the great majority of offshore oil-related seismic activity also occurring in that area (e.g. Geoscience Australia, 2005). The petroleum industry in Western Australia is based on offshore development of reserves in the North West Shelf region, as well as other onshore hydrocarbon basins. There are a large number of oil and gas wells and platforms located on the humpback migratory route between Exmouth Gulf and Dampier (Figure 12 in Jenner *et al.*, 2001), and oil discovery and development of new platforms in this region is ongoing (Geoscience Australia, 2005). A number of mitigation measures are in place to limit the exposure of humpback whales to seismic sound (Department of the Environment, 2008); these include carrying trained observers on deck, surveying outside the humpback migratory/calving period, and when there is a high likelihood of encounters, deploying passive acoustic monitors and/or aerial spotter aircraft prior to seismic activity.

Coastally populated areas are increasing rapidly, with associated development of ports bringing increased risks of ship strikes. All ship strikes in Commonwealth waters (3-200nm) must be reported by law, and a summary of these has been provided to the IWC annually since 2006. Since this time there has only been one report concerning a possible humpback ship strike in Western Australian waters. This occurred in 2008, when a whale (reported as a 'likely' humpback) hit a cruiser and caused $70-80,000 of damage, though the fate of the whale is unknown (IWC, 2009c).

Between 1919 and 1994, 16 strandings have been reported from Western Australia and the Northern Territories. In 2003-2008, 33 strandings were reported, suggesting an increase in stranding rates, which could be due to emerging threats (see '*Threats*') or also to recent population increases and improved reporting of strandings (IWC, 2004a, 2005b, 2006a, 2007c, 2008).

Between 2003 and 2008, 25 entanglement events were recorded from this region, with western rock lobster fishing gear most frequently implicated (Doug Coughran pers comm. IWC, 2004a, 2005b, 2006a, 2007c; IWC, 2008). A rise in marine fishing debris has also been reported for the region (Environment Western Australia, 2007), which suggests that there may be an increasing risk of entanglement from this quarter.

vii. Recovery from Exploitation

Whaling stations operating on the Western Australian coast killed 35,796 humpback whales between 1900 and 1970. In the Antarctic region most closely connected to Western Australia (80-100°E), ~12,750 catches can be assigned based on recent estimates from the IWC (Allison, 2006). However given the likelihood that some whales move outside this area during feeding (IWC, 2007a), a proportion of catches made between 50-130°E may also be of whales from the Western Australian breeding ground. Including all catches made between 50-130°E (all catches within this region assumed to be of the Western Australian breeding population) brings the total feeding ground catches up to 22,751 whales. The total catches made from this breeding population may therefore have been in the region of 48,500 - 58,000 whales. However, Discovery marks indicate that the eastern Antarctic feeding grounds linked with Western Australia are in close proximity with some Discovery mark returns of whales marked in eastern Australia at ~110°E (Chittleborough, 1965; Paton and Clapham, In Press), and satellite telemetry of eastern Australian humpback whales has tracked one whale to ~102°E in Antarctic waters (Gales *et al.*, 2009). It is therefore likely that whales from both breeding grounds share a common feeding region around 100-110°E. Accurate allocation of these feeding ground catches among both tropical breeding grounds is therefore integral to an accurate population assessment of the Western Australian breeding ground.

A preliminary population assessment has been made of whales from this breeding ground, noting that the uncertainty in catch allocation for this stock is substantial, since substantial mixing may occur with eastern Australia and other South Pacific breeding populations on the feeding grounds (IWC, 2007a). In order to determine recovery status of the breeding population subsequent to exploitation, a Bayesian population dynamic model of historical population abundance was developed, incorporating the abundance estimates, genetic diversity and catch data available for this population (Johnston and Butterworth, 2006). The abundance estimate used (N=10,032, CV=0.11) was that reported by Paxton *et al*. (2006), with the two feeding ground catch allocation scenarios considered, including catches between (1) 80-100°E and (2) 50-130°E. The sensitivity of the population model to the following variations was explored: (1) Including catch per unit effort trends from the whaling station (1950-1962), (2) Use of feeding ground trend data, and (3) Depensation at low abundance. Population growth was high (9%), and minimum abundance estimates (median 721-767) were within the minimum abundance range suggested by Chittleborough (1965), for both catch scenarios, while historical effort data fitted the abundance trends well. Historical catch scenarios had a strong influence on pre-exploitation abundance estimates and therefore also on estimated population recovery. Under the conservative scenario that only catches from 80-100°E were of Western Australian whales, pre-exploitation abundance was 17,730 (95% CI 16,380-24,800), with associated recovery to 2006 of 80.4% (95% CI 50.3-90.7%). Under the scenario that a portion of catches from 50-80°E and 100-130°E were also of west Australian whales, pre-exploitation abundance was 22,690 (95% CI 21,152-29,892), with associated recovery to 2006 of 68.9% (95% CI 42-81.2%) (IWC, 2007a).

6. Southwestern Pacific

i. Distribution and population structure

Breeding ground distribution

Humpback whales along the east coast of Australia are thought to breed primarily in the waters inside the Great Barrier Reef (16-21°S) (Chittleborough, 1965; Simmons and Marsh, 1986) and are seen as far north as Murray Island at ~10°S (Simmons and Marsh, 1986). Among groups containing calves observed in the Whitsunday Islands, 47% were seen at <20m depth, while only 5.5% of non-calf groups were observed at this depth (Forestell *et al.*, 2003). An association of mothers and calves with near-shore regions in the Whitsunday Islands was observed, while non-calf groups were more widely distributed offshore (Figure 9 in Forestell *et al.*, 2003). The range of the eastern Australian breeding ground has been hypothesized to include the Chesterfield Reefs (eastern Coral Sea 19-22S, 158-160E, Dawbin and Falla, 1949), although no studies have been conducted there.

Higher inter-annual re-sights have been reported within Hervey Bay (probability of within-region recapture 77%) than within the Whitsunday Islands (probability of within-region recapture 8%), which suggests a higher degree of individual site fidelity to Hervey Bay than to the Whitsunday Islands (Forestell *et al.*, 2003). This result is anticipated, since whales may disperse over a very large area in the breeding grounds throughout winter, while Hervey Bay constitutes a resting area (with a much smaller total area) as part of the southbound migratory route during August to October (Chaloupka *et al.*, 1999).

Northward migration of humpback whales to the breeding ground occurs (*i*) along the Australian mainland coast (and sometimes eastwards through Bass Strait, Paterson, 1991), (*ii*) through New Zealand's Cook Strait, and (*iii*) past Foveaux Strait off the New Zealand southwest coast (Dawbin, 1964; Franklin *et al.*, In Press-b), as suggested by photo-identification catalog re-sightings and Discovery mark returns. A migratory stream of whales passes Byron Bay (28-29°S) while traveling north; this is the most easterly point in Australia. Further north, at Point Lookout (27°S) the migratory corridor becomes very narrow with two series of aerial surveys showing that ~97% of whales pass within 6.2 miles from the coast (Bryden, 1985; Noad *et al.*, 2008). After the migratory stream passes Breaksea Spit off northern Fraser Island (24°S), whales are thought to then disperse through the waters of the Great Barrier Reef, between the outer Reef and the coast, with a unimodal peak in sightings around August (Paterson, 1991).

The southward migration tends to commence from mid-July (Paterson, 1991). Whales initially pass west of Breaksea Spit and enter Hervey Bay (25°S), where they are at peak abundance between August and October (Chaloupka *et al.*, 1999) and most concentrated in the eastern part of the bay (Corkeron *et al.*, 1994). Whales enter and leave Hervey Bay from the north. Group composition in Hervey Bay changes during the season, with mostly immature whales observed early, mature whales observed mid-season and mother-calf pairs, sometimes with escorts, mostly observed September/October (Franklin *et al.*, In Review). Temporally segregated age and sex classes on migration have also been observed along this migratory corridor by Chittleborough (1965) (see '*Natural History*'). On further migration south, many of the whales follow the coastline as far as Eden (37°S, southern New South Wales). Satellite telemetry deployed on humpback whales passing Eden has revealed that some travel offshore at this point towards New Zealand and others travel southeast past the eastern coast of Tasmania (Gales *et al.*, 2009). One whale was also tracked crossing through Bass Strait to the west and traveling southwest from western Tasmania (Gales *et al.*, 2009).

A genetic biopsy study of humpback whales migrating along the eastern Australian coast found a sex ratio strongly skewed in favor of males (2.4:1, Brown *et al.*, 1995), suggesting that a significant proportion of females overwinter in the Antarctic or are more likely to avoid biopsy sampling than males (see '*Section IV-D: Natural History*'). Some sex-specific differences in migratory routes have also been suggested by genetics; a study of individuals sampled during a single migration revealed significant genetic differentiation between males and females (Valsecchi *et al.*, 2010), which may suggest sex-specific use of alternative migratory routes. However, low interchange (4 re-sightings from photo-catalogs of 692 and 1,242 individuals in Oceania and eastern Australian waters respectively) has been estimated to date between eastern Australia and Oceania (Garrigue *et al.*, In Press-b). Nearly all re-sights between eastern Australia and New Zealand / New Caledonia for which sex is known have been males (although a mother and calf pair are the single exception, Franklin *et al.*, In Press-b), although no within season re-sightings have yet been reported. Whether this is due to the greater availability of males for capture (Brown *et al.*, 1995) or sex-specific differences in interchange has not been established.

Migratory connections

Seasonal migratory connections between eastern Australia and the Antarctic are numerous (Figure 6). Most Discovery marks deployed from whaling stations in east Australia were recovered either at 150-180°E or 100-130°E, which were primary locations for summer whaling in 1959 (Chittleborough, 1965). Satellite telemetry has directly tracked eastern Australian humpback whales 60°S between 100°E-175°W longitude, although this distribution was not uniform; most whales arrived in the Antarctic between 140°E-175°W, with one arriving far to the west at 100°E. A small photo-identification catalog (n=11) from the Balleny Islands (67°S, 163°E) has also revealed migratory links with eastern Australia (n=3 inter-region re-sights) (Franklin *et al.*, In Press-a). Considered in combination, Discovery marks and satellite telemetry suggest either that eastern Australian whales feed in a broad swathe of the Antarctic between 100°E-175°W, or that they frequent at least two feeding regions, one which is due south of eastern Australia and stretches out to the east beneath New Zealand, and one which is beneath Western Australia at ~100°E and accessed via migration through Bass Strait. To date, no matches have been found through photo-identification-catalog comparisons of this Antarctic region (70°E-130°E) and eastern Australia (Franklin *et al.*, 2008b), however the Antarctic catalog available for comparison is small (n=35 individuals). Discovery marks indicate that this latter region is also visited by humpback whales breeding in the Western Australian breeding ground, while the former region is visited by humpback whales wintering in the offshore islands of Oceania (Paton and Clapham, In Press).

Population Structure (between breeding grounds)

Mitochondrial haplotype population structuring between eastern Australia and neighboring breeding grounds in Western Australia, New Caledonia, Tonga, the Cook Islands and French Polynesia were all significant (Olavarría *et al.*, 2006b). However nucleotide mitochondrial differentiation was not significant between eastern Australia and Tonga. Interestingly, a small degree of interchange between eastern Australia (Hervey Bay or Byron Bay) and New Caledonia has been documented (all inter-annual resights of four males, Garrigue *et al.*, 2007), while one match to Tonga has also been recorded (Franklin *et al.*, In Press-b). Prior to intense modern whaling, a female Discovery tagged in Fiji was recaptured off Moreton Island (eastern Australia) four years later (Dawbin, 1964). Combined evidence from documented movements and genetic comparisons (Olavarría *et al.*, 2007) suggests a greater degree of migratory interchange of eastern Australian whales with breeding grounds to the east rather than to the west, possibly due to the presence of a partially shared migratory route past New Zealand (Franklin *et al.*, In Press-b). The inferred locations of feeding grounds from satellite telemetry (and Discovery marks, although captures in this case represent regions of whaling effort) also suggest that a larger proportion of the population may come into contact with (and therefore may occasionally mate or migrate with) Oceania whales on feeding grounds directly to the south of eastern Australia.

The hypothesis that eastern Australian whales have more contact with Oceania whales than Western Australian whales is also supported by studies of their songs. Noad *et al.* (2000) showed that song from Western Australian whales could enter and replace that of eastern Australian whales, but this was likely to be uncommon.

ii. Abundance

Land based surveys have been made every 1-3 yrs from Point Lookout, North Stradbroke Island since 1978. Peak migration is between mid-June and mid-July. One set of surveys, carried out at two sites (enabling 'double blind' counts) over 14 weeks across the full duration of the migration, was used to estimate absolute abundance in 2004 by fitting a normal curve to the number of pods passing the survey point during each day and adjusting the curve progressively with Hermite polynomial terms until the best fit to the data was reached (Noad *et al.*, In Press). The best-fitting curve was then used to calculate the number of pods passing both during and outside the survey period (in the 'tails' of the migration). Total 2004 abundance (as a function of total pods, mean pod size, pods passing outside the survey period and pods available but missed during the survey period) was 7,090 +/- 660 (95% confidence intervals) over the full migration period. The proportion of missing pods calculated using the double-blind counts was 10%. A second, stratified random sampling approach to estimating abundance yielded 6,555 whales +/- 389 over the survey period, with the same correction for pods available but missed. Since the Hermite polynomial approach was able to estimate abundance over the full migration period (including tails), the former modeling approach was considered to provide the most inclusive estimate of eastern Australian abundance (Noad *et al.*, In Press). It must be noted that the skewed sex ratio observed for this migratory stream (Brown *et al.*, 1995) means that this is a likely underestimate of the true size of the breeding population in east Australian waters, since a substantial proportion of females may regularly winter in the Antarctic and therefore be unavailable for counting.

The 2004 abundance estimate of 7,090 +/- 660 has been extrapolated forward to 2007 using available trend data (see '*Trends*'), providing a 2007 absolute abundance estimate of 9,683 +/- 612 (Noad *et al.*, 2008). Noad *et al.* (2008), however, also performed double counts using a land station and aerial surveys and used this to estimate that closer to 30% of whales were missed from land. This is somewhat higher than the 10% used to estimate absolute abundance in their previous studies which suggests that these may have been underestimates. Work to reconcile the two estimates of the proportion of whales missed is currently underway (Noad, pers. comm.)

Photo-identification surveys of mark-recapture abundance were carried out in Byron Bay, Hervey Bay and Ballina in 2005. Recaptures between sampling locations during this season were used to estimate 2005 abundance, which was 7,041 (95% CI 4,075-10,008) using model averaging across a variety of closed mark-recapture models (Paton *et al.*, In Press). While many mark-recapture models were closely similar in fit, abundance estimates fell in a fairly narrow range between 6,303 and 7,843 and were congruent with the abundance estimates yielded by land-based counts (detailed above). Since this estimate of absolute abundance is based on one wintering season, it is potentially subject to some degree of negative bias due to a skewed sex ratio (Paton *et al.*, In Press). A multi-year (1999-2005) photo-identification survey of the northward migration passing Byron Bay was also used to estimate abundance using a closed Chapman-modified Lincoln Peterson model with a downward adjustment for mortality (Paton *et al.*, 2009). This estimate (7,390, 95% CI 4,040-10,739 whales) was similar to that obtained for 2005 using one year of multiregional sighting data (Paton *et al.*, In Press). This estimate may not fully capture eastern Australian abundance since many of the sampling periods outside 2005 were of limited duration and the temporal segregation of age and sex classes on migration (Chittleborough, 1965) may mean that demographic groups were unequally captured (Paton *et al.*, 2009).

iii. Genetic Diversity

For an introduction to genetic diversity, see 'Genetic Diversity' in the 'Status of North Atlantic Populations' section. Mitochondrial haplotypic genetic diversity of eastern Australian humpback whales (summarized in Appendix 1) is high (0.96-0.97, Olavarría *et al.*, 2006b; Valsecchi *et al.*, 2010) and similar to that found in other regions of Oceania (Olavarría *et al.*, 2007). Mitochondrial nucleotide diversity is higher (0.026 and 0.023 respectively, Olavarría *et al.*, 2006b; Valsecchi *et al.*, 2010) than that found in other regions of the South Pacific (Olavarría *et al.*, 2007).

iv. Trends

Trends in relative abundance have been calculated using land based counts carried out at Point Lookout on Stradbroke Island since 1978 (see '*Abundance*'). Relative abundance was calculated (either as a rate of whales per hour or a total count of pods) during four, eight or ten weeks covering the peak period of migration every 1-3 years. A regression of these values against time provides a population increase rate of 10.6% +/- 0.48% (1987-2004, Noad *et al.*, In Press). Inclusion of surveys carried out in 2007 gives a slightly revised estimate of 10.9% (95% CI 10.5-11.4%, Noad *et al.*, 2008). These surveys have remained consistent over time, with a strong correlation ($r > 0.99$) between counts and years.

v. Habitat or Ecosystem Conditions

Along the east coast of mainland Australia, the warm-water East Australian Current originates in the Coral Sea and flows southwards along the coast, travelling most rapidly in regions where the continental shelf narrows (e.g. past Point Lookout and Cape Byron). Divergence of this current from the coastal shelf can cause local upwelling, e.g. at Cape Byron and Port Stephens (Oke and Middleton, 2001, 2000). The current forms a series of eddies on making contact with the Tasman Sea to the south. The current, and associated upwellings, are most pronounced during the summer months (Oke and Middleton, 2000).

The Great Barrier Reef extends ~1,400 nm along the coast of Australia, from north of Fraser Island at 25°S to the coast of Papua New Guinea (9°S) (Wolanski, 1994). The outer reefs range between 12-140 nm from the Australian coastline (Simmons and Marsh, 1986). The Barrier Reef is a massive complex of 2,500 individual reefs (Wolanski, 1994), dispersed throughout an offshore lagoon. The northern region (north of 16°S) is very shallow (maximum depth 30m) with densely scattered reefs and shoals (Wolanski, 1994). The central region 16-20°S has the lowest density of reefs, is slightly deeper (most depths less than 40m) and is the freshwater outflow point for a number of rivers.

Hervey Bay is a large (2,500 square miles), shallow (average depth 15m with depths increasing towards the entrance of the Bay), sandy embayment bounded by the Australian mainland and Fraser Island (a sand island which extends along the continental shelf). Narrow, sandy shallows stretch ~12 miles offshore from the northern tip of the bay, forming Breaksea Spit. The Bay has been characterized as an inverse estuary due to high evaporation, low precipitation and very little freshwater input (Ribbe, 2006).

Within the Antarctic feeding grounds associated with this breeding ground (Core region 130-160°E, possible range 110-180°E, Appendix 2), the highest densities of krill (from sampling net data spanning 1926-2003, Atkinson *et al.*, 2004) and chlorophyll (Atkinson *et al.*, 2008) are found between 150 and 170°E along the Antarctic coast and up to the western Ross Sea. In the South Pacific, winter sea ice is found as far north as the polar front in some places (Nicol *et al.*, 2008). The Ross Sea region (165°E-150°W, 65-85°S) has a broad continental shelf and is inaccessible in the far southern reaches (80-85°S) due to the presence of permanent pack ice. Cetacean surveys of the accessible areas of the southern Ross Sea have yielded low encounter rates of humpback whales (70-80°S) (Branch, In Press), suggesting that it may not be preferred feeding habitat. However, much higher encounter rates are found in the northern Ross Sea (65-70°S), a region of rapid ice retreat and high chlorophyll productivity (Moore and Abbott, 2000; Nicol *et al.*, 2006).

vi. Threats and Anthropogenic Impacts

There was an 8.5% increase in whale watch tourism off the coast of Queensland between 1998 and 2008 (O'Connor *et al.*, 2009). Most humpback whales breeding off the eastern coast of Australia are found in the Great Barrier Reef region, which is a protected Marine Park, with some regulated commercial fishery and shipping activity (Australian Government, 2009). Within the Great Barrier Reef Marine Park, mining and oil drilling are prohibited. Whale watching in the park is subject to regulation, although there is no restriction on the number of operators permitted to watch whales in the region (O'Connor *et al.*, 2009). Studies of the effects of whale watching in the region carried out in Hervey Bay by Corkeron *et al.* (1995) suggested that the presence of vessels at ranges of <300m increased the frequency of diving behavior among adults. The effect of such changes in behavior on individual fitness is unknown (see 'Section *VIIav: whale watching*'), although no impacts are observed in terms of calf production between 1992 and 2005, which has been consistently high (Franklin *et al.*, In Review).

Entanglements of humpback whales are regularly documented along the eastern coast. Of 57 eastern Australian humpback entanglements identified between 2003-2008, the most common cause of entanglement was in shark nets (nets placed around beaches to reduce shark attacks on swimmers), with mackerel nets, gillnets and crab and rock lobster gear also implicated (IWC, 2004a, 2005b, 2006a, 2007c, 2008, 2009b). Of these entangled whales, 13 were documented to have died, 30 were successfully released (occasionally still with gear attached) and the fate of the other 14 is unknown. This entanglement total is likely underestimated, since a number of whales included in these reports have not been identified to species level and humpback whales may also self-rescue (Minton, 2004). Shark control nets are common in Queensland, New South Wales and Victoria, and occur close to coasts, which often places them close to the coastal migratory route of humpback whales. Some nets are fitted with acoustic 'pingers', the intent of which is to acoustically alert bycatch species to avoid the nets (McPherson *et al.*, 2001). The effect of entanglements on humpback overall mortality was considered negligible after the introduction of pingers (Gribble *et al.*, 1998); however, levels of marine mammal entanglement and by-catch were low before and after acoustics were introduced, so there is little power to detect any substantial effect on entanglement.

Ship strike reports of 13 incidents with humpback whales between 2003-2008 include direct hits from vessels and observations of whales with severe trauma and/or propeller slashes along the body consistent with ship strike. At least three tourist vessels have been implicated, two in the Whitsundays and a dive boat in Port Douglas. Whales swam away in most strike reports; five deaths attributed to ship strike were reported (IWC, 2004a, 2005b, 2006a, 2007c, 2008, 2009b).

Killer whale predation has been documented in this region, with 17% of photo-identified whales showing some evidence of predatory scarring (Naessig and Lanyon, 2004), comparable to that identified in the Northern Hemisphere (Mehta *et al.*, 2007). The likely population-level impact of killer whale attacks is discussed in Section VIIavii.

Much of the topography of the Great Barrier Reef (see '*Habitat and Ecosystem conditions*') consists of shallow reefs. While whales are mainly found in the deeper waters between the Reef and the mainland, fatal ship strikes are less of a threat in this region as ships generally only enter the Reef to visit a particular port (*e.g.* Hay Point, Mackay, Gladstone, Townsville) with most transit shipping passing outside the Reef. However during coastal migration to and from the summering grounds, humpback whales pass a number of large cities and ports (Sydney, Canberra and Brisbane), which pose increased local risks of ship strikes and pollution effects from increased anthropogenic noise and habitat degradation.

Scientific whaling of humpback whales in the Antarctic waters directly to the south has recently been proposed by Japan, with a catch of 50 humpback whales initially planned for the 2007/2008 season (Nishiwaki *et al.*, 2007). This proposal has been delayed while the IWC conduct meetings on the "Future of the IWC". It is not known if this plan will be resumed after these talks are completed. The impact of whaling on this population is likely to be slight, given the large abundance; however, see Section Xavii.

Recent humpback population increases are also likely to increase the exposure of humpback whales to further interactions with fisheries and entanglements with fishing gear (Noad *et al.*, 2008; Noad *et al.*, In Press) as well as the potential for ship strikes on migration. Conversely, it should also be noted that as the rate of increase of this population is very high, the rate of mortality must be very low. Whatever theoretical or actual threats do exist, they appear to be having little or no impact at a population level.

vii. Recovery from Exploitation

The population status of eastern Australian whales is currently unknown, although the rapid population increase rates suggest strong recovery is underway (Noad *et al*. In Press). Discovery marks, fluke photographs and satellite telemetry all indicate that Antarctic feeding grounds are in close proximity (and therefore overlap) with those identified for whales breeding in Western Australia (see '*Section X: eastern Indian Ocean*') and Oceania (see '*Section X: South Pacific Islands (Oceania)*'). Twentieth century whaling on these feeding grounds (between 110°E-170°W) was enormous, with ~38,800 whales killed. Accurate allocation of these feeding ground catches among the tropical breeding grounds is therefore an integral aspect to population assessment of the breeding grounds. The majority of catches (~70%) were concentrated in the years 1958-1961, which led to the complete collapse of the eastern Australian coastal whaling industry in 1962.

Two preliminary Bayesian population assessments of recovery are available for the region, one accounting for mixing with the Western Australia breeding population on shared feeding grounds (point estimates of recovery level ranged from 29-37% in 2004, 95% probability intervals = 19-52%; Johnston and Butterworth, 2005) and the other accounting for mixing on feeding grounds with Oceania (recovery level was 27-31% in 2008, 95% 15-68%; Jackson *et al.*, 2008, 2009). However catch records differed between these two IWC studies (the most recent Antarctic humpback catch series was made available in 2006; Allison, 2006), as did available estimates of abundance and trend.

Therefore no firm conclusions regarding current population recovery can currently be drawn from these two assessments. The influence of shared feeding grounds on catch allocations (the proportion of catches allocated to east Australia and to breeding grounds in the east and west) needs to be considered when conducting a population assessment of this breeding ground. The IWC intends to carry out a full assessment of this breeding region within the next five years.

7. South Pacific Islands (Oceania)

i. Distribution and population structure

The longitudinal distribution boundaries of humpback whales wintering in Oceania are ~160°E (west of New Caledonia) and ~120°W (east of French Polynesia) between 0 and 30°S (Reeves *et al.*, 1999), a range which includes American Samoa (United States of America), the Cook Islands, Fiji, French Polynesia (France), Republic of Kiribati, Nauru, New Caledonia (France), Norfolk Island, New Zealand, Niue, the Independent State of Samoa, Solomon Islands, Tokelau, Kingdom of Tonga, Tuvalu, Vanuatu, Wallis and Futuna (France). The largest known winter aggregations of humpback whales (and consequently the most surveyed) are located in the coastal waters of Tonga (Abernethy *et al.*, 1992; IWC, 1981), New Caledonia (Garrigue and Gill, 1994), the southern Cook Islands (Hauser *et al.*, 2000) and French Polynesia (Gannier, 2004; Poole, 2002), while similar densities of whales are also encountered in American Samoa (Robbins and Mattila, 2006). Recent surveys in Vanuatu, Niue, the Independent State of Samoa and Fiji suggest low densities of humpback whales in these coastal waters during winter, with singers and cow-calf pairs reported from most survey regions (Garrigue *et al.*, 2004b; Noad *et al.*, 2006; Paton and Clapham, 2002; South Pacific Whale Research Consortium, 2009).

Breeding ground distributions

New Caledonia and local regions

New Caledonia (163-169°E 18-23°S) is 750 miles east of Australia. Humpback whales are encountered throughout New Caledonia and the Loyalty Islands between June and November, with peak abundance occurring in August and September. Newborn calves, competitive groups and singers are frequently encountered, suggesting that part of this region is used as a breeding ground. Incidental sightings suggest that the greatest density of humpback whales is found in the southern lagoon between the main island and Île des Pins (Garrigue and Gill, 1994). Satellite telemetry of whales tagged in New Caledonia has also revealed that a proportion also frequent an offshore seamount (Antigonia Seamount) to the southeast (Garrigue *et al.*, 2010). Photo-identification and genetic biopsy data collected from around Noumea since 1995 has revealed strong site fidelity, with 21% of humpback whales re-sighted during 1999-2004 (Garrigue *et al.*, In Press-a). Average residency times were 17 days for males and 10 days for females (Garrigue *et al.*, 2001).

A survey in the southern islands of Vanuatu (168°E, 17°S) during August 2003 resulted in 16 encounters (0.3 whales/hour, one singer, one mother-calf pair) with the majority of whales sighted around the east coast of Tanna (Garrigue *et al.*, 2004b). Humpback whales are also reported in the waters of Futuna Island (Vanuatu). Humpback whales photo-identified in Vanuatu have been re-sighted in New Caledonia (n=1) and Tonga (n=2) (Garrigue *et al.*, In Press-a; Garrigue *et al.*, In Press-b).

Fiji (178°E 18°S) comprises an archipelago of over 800 islands and islets. It lies due east of New Caledonia. Humpback whales have been observed in the waters of the Lomaiviti Island group during land-based surveys, with an average of 0.02 whales seen per hour during 2002 and 2003 (Gibbs *et al.*, 2006). This estimate is ~5% of those made in the 1950s, when whales were observed from the same watch locations at an average rate of 0.46 between 1956 and 1957 (Gibbs *et al.*, 2006).

Breeding grounds in this region may also extend into the Chesterfield Reefs (eastern Coral Sea 19-22S, 158-160E; Dawbin and Falla, 1949), although no studies have been conducted there.

Tonga and local regions

Tonga (173-177°W, 15-23°S) is an archipelago of 169 islands, divided into four main groups distributed from north to south (Niuas, Vava'u, Ha'apai and Tongatapu, respectively). Humpback whales are found in Tongan waters between late June and early November, peaking in abundance during September (Dawbin, 1966; IWC, 1981). Aerial and boat surveys (July to October 1979) found the greatest density of encounters on the western side of the Ha'apai group, with sightings in the other groups clustered in northern Vava'u and northern Tongatapu (no surveys were made to the south of Tongatapu) (IWC, 1981). A subsequent survey during August and September 1991, mostly within the Ha'apai group, noted 82% of sightings to be in depths of <180m (although 73% of survey effort was concentrated in waters of <180m), with 50% of mother-calf sightings at depths of <36m (Abernethy *et al.*, 1992), suggesting a preference for shallower coastal habitat.

Photo-identification and genetic biopsy surveys of humpback whales in Tonga have been ongoing since 1991 (Abernethy *et al.*, 1992) during August and September, mostly located in the southern waters of the Vava'u group (174°W, 19°S), with occasional surveys in the Ha'apai (174° 30'W, 20°S) and Tongatapu (175°W 21°S) groups. Microsatellite genotype analysis of individuals collected during these surveys revealed an intra-annual re-sighting (or recapture) rate of r=0.34 in 2002; this is much lower than in neighboring New Caledonia (r=1.43) and likely reflects the greater abundance of the Tongan population, see '*Abundance*' section (Olavarría, 2007). A survey of photo-identification re-sightings between 1999-2004 also revealed an inter-annual re-sighting rate of 9% (Garrigue *et al.*, In Press-a), similarly indicative of a relatively large population.

The Independent State of Samoa (hereafter referred to as 'Samoa', 173-170°W, 13°S) consists of a series of seamounts (two main islands, seven small islands) ~45 miles north northwest of American Samoa. Boat-based cetacean surveys (October 2001) were carried out around both main islands (Upolu and Savaii), with effort concentrated on the northeastern coast of Upolu (Noad *et al.*, 2006). Two groups of humpback whales (3 individuals, including one singing male) were encountered during 185 hours of boat survey (0.01 whales/ hr) on the south coast of Upolu, while 41 acoustic detections were made over 14 days during surveys of both islands, mostly near to the south coast of Upolu (Noad *et al.*, 2006). There was no noticeable decline in detections over time, suggesting that whale density remained relatively constant during the survey period. Two presumed cow-calf pairs were also sighted during a 2.9-hour aerial survey. The seasonal occurrence of humpback whales between September and November has also been suggested by anecdotal data (Paton and Gibbs, 2002). This timing of sightings is later than that reported for Tonga, 440 miles to the south-southwest (IWC, 1981). The relative density of encounters was lower than that observed in American Samoa to the east (Noad *et al.*, 2006).

Surveys have also been carried out in the coastal waters of Tutuila (the largest island in American Samoa) between 2003 and 2005 (September and October) (Robbins and Mattila, 2006). Whales have been encountered all around the island, most commonly in the north and west, with an average of 5.5 whales per day. Calves represented 13.5% of all sightings, with one photo-identified lone whale later re-sighted with a calf, suggesting that the birth occurred in these waters (Robbins and Mattila, 2006). Average residency time was 2.9 days, with a maximum re-sight interval of two weeks. The surveys suggest densities of humpback whales frequenting these waters are similar to those on the main South Pacific breeding grounds (New Caledonia, Tonga, French Polynesia). Inter-annual re-sightings between American Samoa and Tonga (Garrigue *et al.*, In Press-a), the Cook Islands, New Caledonia and French Polynesia (Carretta *et al.*, 2010) have been reported despite the small photo-identification catalog (n=150 between 2003-2008) available from this region, suggesting extensive biological connectivity with Tonga and potentially the wider Oceania region.

Cook Islands

Humpback distribution in the Cook Islands (8-23°S 156-167°W, 500,000 square miles of ocean) has mostly been described from the Southern Cook Islands (Palmerston Atoll, Aitutaki and Rarotonga). Whales are regularly encountered between July and November, with peaks in abundance in August and September (Hauser *et al.*, 2000). Whales have also been sighted incidentally in the coastal regions of Mangaia, Atiu (Southern Cook Islands), Manahiki and Penrhyn (Northern Cook Islands) (Hauser and Clapham, 2006). A sighting survey of the principal regions in 1999 noted that whales were distributed at a variety of depths, ranging from close to reefs and abyssal (Hauser *et al.*, 2000). Over 2,911 survey hours (1998-2005), 846 whales were encountered (0.29 whales/hour, Hauser and Clapham, 2006). Within this region, all age and sex classes of whales were sighted, including singers and competitive groups (Hauser and Clapham, 2006). A photo-identification catalog of dorsal fins and flukes revealed no inter-annual re-sightings over the survey period (Garrigue *et al.*, In Press-a; Hauser and Clapham, 2006), although a small number of within-season re-sightings have been made (Hauser and Clapham, 2006).

While the Cook Islands show some characteristics of a humpback breeding ground (for example regular encounters with singers and newborn calves and with competitive groups, though the latter less frequently, Hauser *et al.*, 2000), the low inter-annual re-sighting rate, depth distribution and relatively low density of encounters suggest that this region may primarily represent a migratory route (Hauser and Clapham, 2006). Evidence from satellite telemetry and photo-identification suggests that the major destination for these whales is the Tongan Archipelago. One within-season movement between the Cook Islands and Tonga has been documented using fluke comparisons (Garrigue *et al.*, In Press-a). During a satellite telemetry study carried out in the Cook Islands, all six tagged whales traveled west in the direction of the Tonga Trench (Hauser *et al.*, In Press).

French Polynesia

French Polynesia (8-27°S 134-155°W, covering 3,100,000 square miles of ocean) consists of five island groups (Marquesas Islands, Tuamotu Islands, Gambier Islands, Society Islands and Austral Islands) comprising 118 islands. Most sightings occur from mid-July through to mid-November (Gannier, 2004; Poole, 2002). Sighting rates calculated from boat-based and aerial surveys suggest highest densities in the Windward Group of the Society Islands and the Austral Islands, with scarce sightings in the Tuamotu Islands and Leeward Islands of the Society Islands (Gannier, 2004; Poole, 2006, 2002). Sightings in the Marquesas (the island group closest to the equator) are very rare, with no whales detected acoustically during winter surveys (Gannier, 2004) and only two verified sightings (Poole, 2006).

Surveys concentrated on the north coast of Mo'orea (Windward Islands within the Society Islands) and Rurutu (Austral Islands) reported the majority of encounters within 400m of island reefs (Poole, 2006), while boat surveys of the Windward and Leeward Society Islands reported that the majority of humpback encounters were <1 nm from island reefs (Gannier, 2000), suggesting a habitat preference for coastal regions. Whales have also been observed entering enclosed lagoons at a number of islands via reef passes, so these may constitute preferred habitat for some whales (Poole, 2006). Calves comprised ~10% of all annual sightings in Mo'orea and Rurutu (regions ~350 miles distant) from 1991 to2005; this high proportion suggests calving occurs in or around these waters (Poole, 2006). Humpback residency times around Mo'orea were short, with most whales re-sighted for up to three days. Residency times in Rurutu were much longer, with most whales re-sighted for up to six weeks and cow-calf pairs the longest residents (Baker *et al.*, 2006a). Site fidelity is reasonably high; a survey of photo-identification re-sightings between 1999-2004 revealed an inter-annual re-sighting rate of 13% (Garrigue *et al.*, In Press-a; Poole, 2006). One intra-annual re-sighting between Mo'orea and Palmerston Atoll in the Cook Islands has been documented (sightings one month apart in August and September, Baker *et al.*, 2006a) indicating a migratory movement to the west.

Historical records indicate that use of French Polynesia by humpback whales has occurred relatively recently, since whalers frequently provisioned in Tahitian waters and humpback whales were never mentioned in their accounts (Olavarría *et al.*, 2007). However this breeding ground is genetically diverse, with significant levels of population differentiation (Olavarría *et al.*, 2007) and low interchange rates (Garrigue *et al.*, In Press-a), suggesting limited interchange with other breeding grounds and therefore that this population has persisted for a long time, potentially in less populated regions of Polynesia.

Population structuring and interchange among breeding grounds

Fluke photo-identification catalogs collected in New Caledonia, Tonga, the Cook Islands, French Polynesia (and to a more limited extent in American Samoa, Samoa, Niue, Fiji and Vanuatu) have been compared for survey periods between 1999-2004 in order to document interchange among regions (Garrigue *et al.*, In Press-a). There were 28 instances of interchange between regions (all inter-annual save one) documented in the full dataset of non quality controlled (non-QC) photographs (949 individual whales); Tonga was a re-sighting location in 22 (79%) of these instances, while nine instances (including four with Tonga) involved the secondary survey locations with small associated photo-identification catalogs (Garrigue *et al.*, In Press-a). High numbers of inter-regional recaptures (relative to catalog size) from the small survey regions (located between 160°E-160°W) suggest that most Oceania humpback whales are frequenting the principal survey regions (Tonga, Cook Islands and New Caledonia) in this area of Oceania.

Within-region return rates (0.94-4.28% excluding the Cook Islands) were an order of magnitude greater than between-region re-sightings (0-0.09%), with the exception of Tonga and the Cook Islands (0.39%) (Garrigue *et al.*, In Press-a). Most whales re-sighted in two regions have been sighted only once in each region, suggesting that inter-regional movements may be due to transience rather than permanent dispersal. There is no evidence for sex-biased dispersal; of eight movements of known-sex whales, six were males, but given the possible male sex bias on wintering grounds and small number of whales considered, these data do not indicate a significant sex bias in dispersal (Garrigue *et al.*, In Press-a).

Genetic surveys of the primary wintering regions in New Caledonia, Tonga, the Cook Islands, French Polynesia show significant mitochondrial haplotype differentiation (F_{ST} indicating restricted maternal gene flow) between all regions (Olavarría *et al.*, 2007). Mitochondrial nucleotide differentiation (ϕ_{ST}) was significant between the Cook Islands and New Caledonia, and between French Polynesia and all other regions (Olavarría *et al.*, 2007). These data are therefore consistent with photo-identification-based interchange rates in suggesting restricted movement between regions. The greatest levels of genetic differentiation from neighboring breeding regions were found in New Caledonia and French Polynesia (Appendix 1). French Polynesia was significantly differentiated (both at nucleotide and haplotype levels) from all other breeding regions in the South Pacific (Olavarría *et al.*, 2007). New Caledonia showed significant nucleotide differentiation from the eastern Australian breeding ground to the immediate west, whilst Tonga did not (Olavarría *et al.*, 2006b). New Caledonia and Tonga were significantly differentiated in terms of haplotypes but not nucleotides (Olavarría *et al.*, 2007)

Migratory movements between breeding and feeding grounds

Bimodally-distributed sightings and catches of whales passing through New Zealand waters between May and August (northbound) and between September and November (southbound) indicate that humpback whales migrate seasonally through these waters (Dawbin, 1956a). A less pronounced bimodal distribution of catches was also reported from Norfolk Island ~450 miles due north at 167°E 29°S (Dawbin, 1997). Interchange between New Zealand and other islands in Oceania and coastal eastern Australia has been confirmed through photographic resightings (Constantine *et al.*, 2007; Franklin *et al.*, In Press-b; Garrigue *et al.*, 2000) and Discovery Marks (Chittleborough, 1959a; Dawbin, 1964). A satellite telemetry study in New Caledonia (12 whales) revealed a number of southward migratory movements in the direction of New Zealand and Norfolk Island, with one individual tracked as far as the New Zealand North Island coast (Garrigue *et al.*, 2010), strongly supporting the hypothesis that at least a portion of whales wintering in New Caledonia travel past New Zealand on the east coast of the North Island. A satellite telemetry study of eastern Australian whales on their southbound migration at Eden (NSW) revealed that 50% of the 16 tagged whales travelled towards southwestern New Zealand. Two tags were still active on arrival at the New Zealand coast, and both whales then remained in the Foveaux Strait region for around a week before traveling south. Two whales sighted in Cook Strait (between the North and South Island of New Zealand) were re-sighted in Hervey Bay, eastern Australia, later in the season, indicating that Cook Strait and southwestern New Zealand are migratory (northbound and southbound) routes for a portion of whales from the eastern Australian breeding ground (Garrigue *et al.*, 2007)

Satellite telemetry surveys of whales in the Cook Islands suggest that this region is also used as a migratory route for whales travelling towards Tonga (Hauser *et al.*, In Press). However, significant genetic differentiation between these two survey regions (Olavarría *et al.*, 2007) and the migratory movements that have been revealed between Tonga and Antarctic waters to the southwest (see '*Migratory movements between the breeding and feeding grounds*') suggest either or both of the following possibilities: *(i)* that the Tonga breeding ground is a genetically heterogeneous assemblage of whales frequenting a broad swathe of the Antarctic feeding grounds longitudinally spanning the South Pacific, within which the Cook Islands migratory stream is only one component, *(ii)* that not all Cook Islands whales travel to Tonga and that some have breeding ground fidelity to other regions in the South Pacific.

A number of migratory connections have been made between the breeding grounds of Oceania and Antarctic feeding grounds; these are summarized in Figure 7 and span ~50°E-60°W. One whale sighted in New Caledonia has been recaptured at 171°W through microsatellite genotyping (Steel *et al.*, 2008). Five whales sighted in Tonga have been recaptured (through Discovery marking or microsatellite genotyping) at locations spanning 174°E-114°W (Dawbin, 1966; Steel *et al.*, 2008), one whale sighted in the Antarctic Peninsula (62°W) was recaptured in American Samoa (Robbins *et al.*, 2008a) and a whale satellite-tracked from the Cook Islands traveled to 126°W 65°S (Hauser *et al.*, In Press). Mixed-stock assignment testing of current mitochondrial haplotype distributions in the South Pacific and in the Antarctic regions beneath Australia (60°E-120°E) and eastern Oceania (180-120°W) assigned the majority of 60°E-120°E Antarctic haplotypes (~70%) to Western Australia, and the majority of 180-120°W (~80%) to Tonga (Albertson *et al.*, In press). Limited genetic data available from the Antarctic region between 120°E-180 suggested ~55% and 45% assignment respectively between eastern Australia and New Caledonia (Albertson-Gibb, 2009). These assignments are relatively consistent with the geographical proximity of each breeding ground, although the amount of genetic data available from the Antarctic was low and French Polynesia was not strongly allocated to any Antarctic region (<3%). A comparison of photo-identification catalogs held in French Polynesia (n=439) and the Antarctic Peninsula and Magellan Straits (n=369) also yielded no definitive matches (Albertson-Gibb *et al.*, 2009).

Population structuring with neighboring breeding grounds

Mitochondrial genetic differentiation between eastern Australia and Oceania breeding grounds was significant (F_{ST}) for all regions, suggesting restricted gene flow between breeding grounds (Olavarría *et al.*, 2006b). Comparisons of photo-identification catalogs collected from the eastern Australian breeding ground (n=1242 individuals) and Oceania (692 individuals) have to date yielded four re-sightings between eastern Australia and New Caledonia, the geographically most proximal breeding ground (Garrigue *et al.*, 2007). This corresponds to an interchange rate of ~0.004, one order of magnitude lower than that calculated between breeding grounds in Oceania (Garrigue *et al.*, In Press-a).

Breeding grounds in Oceania were also significantly differentiated (F_{ST} and ϕ_{ST}) from the Colombian breeding ground in the southeastern Pacific (Olavarría *et al.*, 2007).

ii. Abundance

Closed population estimates are available from New Caledonia, Tonga and French Polynesia based on mark-recapture estimates from photo-identification catalogs; these are available for all regions for the period 1999-2004 (1,021 individuals identified) (South Pacific Whale Research Consortium *et al.*, 2006). Models were adjusted for time and heterogeneity and provided estimates of N=472 (CV 0.18) for New Caledonia, N=2,311 (CV 0.22) for Tonga and N=1,057 (CV 0.22) for French Polynesia. Abundance has also been calculated for New Caledonia using photo-identification and genotype data collected between 1995 and 2001; this provided closed model photo-identification abundance estimates of N=327 (CV 0.11) and genotype based sex-specific estimates of males (N=288, CV 0.18) and females (N=248, CV 0.3) as well as for all genotype data combined (N=533, CV 0.15 Garrigue *et al.*, 2004a).

A closed population estimate of combined abundance (using the model M_{th} to account for known heterogeneity in capture probabilities) has also been calculated by pooling encounter histories from the four regions over 1999-2004 (N=3827, CV 0.12) (South Pacific Whale Research Consortium *et al.*, 2006).

iii. Genetic Diversity

For an introduction to genetic diversity, see ‘Genetic Diversity’ in the ‘Status of North Atlantic Populations’ section. Mitochondrial genetic surveys reveal high diversity in all principal survey areas. Average haplotype and nucleotide diversity is lower than that in the Southern Indian Ocean (Appendix 1, Olavarría *et al.*, 2007; Rosenbaum *et al.*, 2009), while both diversity measures decrease linearly from east to west across the regions, with

French Polynesia nucleotide diversity similar in magnitude to that seen in Colombia (Olavarría *et al.*, 2007).

iv. Trends

No trend data are available from this region. No discernable trend in abundance was detected during a capture-recapture analysis of photo-identification data (South Pacific Whale Research Consortium *et al.*, 2006).

v. Habitat or Ecosystem Conditions

Most islands in the South Pacific are either volcanic or composed of coral. The South Pacific sub-tropical gyre (a region of extremely low primary productivity and minimum current flow) lies over western French Polynesia, while Tonga and the Cook Islands sit on the southern edge and New Caledonia flanks the western rim. Continental shelves are absent from the central South Pacific, so waters depth increases rapidly with distance from most islands, outside associated reef areas.

New Caledonia is a long (470 miles), narrow archipelago which runs parallel to the Queensland coast, surrounded by coral reefs, lagoons and islets. To the northeast the Loyalty Islands (mostly atolls derived from fringing reefs surrounding raised limestone or volcanic sea mounts) lie parallel and over a similar length, though they are more scattered. The bedrock of New Caledonia is rich in mineral deposits (including 25% of the known global reserves of nickel). The reefs form the most globally diverse assemblage of structures in one location: fringing reefs, double and single barrier reefs, atolls, sand cays, coral islets and oceanic banks. There are 1,000 miles of barrier reef enclosing New Caledonia and the d'Entrecasteaux and Loyalty Island atolls, the second longest in the world. As a result of multiple submergence and emergences, ancient river canyons form deep water passes through the reefs. The Great South Lagoon contains a diverse coral complex covered with islets, extending up to 32 nm from the shore. Both North and South Lagoons contain a variety of substrates and therefore a huge diversity of marine species (United Nations Environment Programme, 2008). They have been recognized as World Heritage Sites since 2008 (World Heritage Committee, 2009). Prevailing trade winds from the east-southeast create southerly swells in the lagoons. New Caledonia and New Zealand are connected by the Norfolk Ridge, a submarine ridge which also supports a number of seamounts.

The Kermadec and Tonga submarine trenches connect New Zealand, the Kermadec Islands and Tonga respectively and are aligned in a northerly direction. At their confluence in the Kermadec Islands, they meet the Louisville Ridge, a series of seamounts stretching 2,500 miles to the southeast (Ballance *et al.*, 1989). The Kermadecs are a series of volcanic islands occurring along the line of the trench. North of Tonga, the trench turns towards the west just south of Samoa. Tonga is a 560-mile-long tropical archipelago of volcanic islands and coral atolls, which represent the peaks of two parallel submarine ridges. The Tongatapu and Ha'apai groups are low-lying coral limestone islands, while the Vava'u group and many other outlying islands are mountainous volcanoes. The most northerly group (the Niuas) consists of volcanic islands lying close to Fiji to the west and Samoa to the north. Mothers and very young calves have been documented in American Samoa, with the majority of sightings occurring around the volcanic island of Tutuila (Robbins and Matilla 2006), which is dominated by coral reefs in the near-shore habitat.

Regions frequented by humpback whales in the Southern Cook Islands (Palmerston Atoll, Aitutaki and Rarotonga) are all the surface peaks of large seamounts, with coastal waters sloping rapidly to abyssal depths >4000m (Hauser *et al.*, 2000). Palmerston occurs at the margin of a cratered lagoon, protected by a barrier reef system. Rarotonga is a volcanic island, surrounded by a lagoon enclosed within a reef. Outside the reef, water depth drops rapidly. Aitutaki is partly volcanic and partly coral, is surrounded by a barrier reef and contains a large lagoon to the south of the main island. All regions are subject to strong easterly trade winds with rough seas and large swells.

Most islands in French Polynesia are surrounded by a reef, and many are coral atolls where barrier reefs are the only element of the island above the sea surface. Islands are all of volcanic origin, with steep undersea slopes offshore; aside from the Marquesas Archipelago, depths of >500m are attained within 1.1 nm of coastal waters (Gannier, 2004).

Within the Antarctic feeding grounds associated with this breeding ground (Core region 120-180°W, possible range 100°W-160°E, details given in Appendix 2), winter sea ice stretches all the way north to the polar front and the continental shelf is narrow. The lowest densities of primary and secondary productivity are found throughout most of the central feeding range (90-180°W, Atkinson *et al.*, 2008) with higher densities of krill associated with the ice edge to the west and north of the Ross Sea (150-180°E) and in the eastern Bellinghausen Sea and start of the Antarctic Peninsula (east of 80°W). Although this region is located far east of the central breeding grounds for this region, a migratory linkage has been observed between American Samoa and the Antarctic Peninsula, suggesting there may be some movement of Oceania whales to this eastern feeding ground. One small area of very high krill density is also located offshore of Thurston Island (100°W, 70S°, connected to mainland Antarctic by permanent ice), which is located at the confluence of the Bellinghausen and Amundsen seas (Atkinson *et al.*, 2008). Here the southern boundary of the Antarctic Circumpolar Current closely approaches the Antarctic continental shelf (Nicol *et al.*, 2008) and is thus potentially a region of strong upwelling.

vi. Threats and Anthropogenic Impacts

Some local whaling of humpback whales was carried out in French Polynesia (Rurutu), the Cook Islands and Tonga during the 20th century, but this has ceased since 1960 at Rurutu (Poole, 2002) and since 1978 elsewhere (IWC, 1981). Whale sanctuaries (local waters where whaling is prohibited) have since been declared in the Exclusive Economic Zones of French Polynesia, Cook Islands, Tonga, Samoa, American Samoa, Niue, Vanuatu, New Caledonia and Fiji (Hoyt, 2005) while they are protected in New Zealand waters under the New Zealand Marine Mammal Protection Act.

Humpback whales are potentially under threat from unregulated scientific whaling in the Antarctic waters directly to the south. None have been taken to date, but an annual catch of 50 humpback whales was proposed by Japan for the 2007/2008 season (Nishiwaki *et al.*, 2007), as part of its JARPA II research program. This has been held in abeyance while Japan considers that progress is being made by the IWC in its meetings on the "Future of the IWC". It is not known if the proposed take of humpback whales will be reinstated at a future time. Given the variable patterns of recovery observed across the South Pacific (see '*Recovery from Exploitation*') and the inability of whalers to determining the breeding ground origins of whales encountered on the Antarctic feeding grounds, the effect of this level of annual take on regional population recovery could be substantial.

There is whale-watching tourism in all four of the principal survey sites in Oceania, with strong growth in the last decade (O'Connor *et al.*, 2009). French Polynesia (Tahiti, Mo'orea and Rurutu) has seen 38.4% annual growth since 1998, while New Caledonia has seen 14% growth, with the industry mainly focused on humpback whales in South Lagoon. Niue has seen 19% growth, Samoa 12% growth, Tonga 15% growth (mostly in Vava'u) and in Raotonga in the Cook Islands 32% (although much of this figure represents whale watchers on land) (O'Connor *et al.*, 2009). There is no boat-based, dedicated whale watching industry in American Samoa at present.

Whale watching guidelines are in place in Tonga and New Caledonia, while boat-based whale watching in the Cook Islands, Samoa and Niue is minimal (O'Connor *et al.*, 2009). Humpback whales have been at particular risk from excessive boat exposure through whale watching in the South Lagoon of New Caledonia, where there are currently 24 working operators. Levels of exposure have been unusually high (peaking during weekend periods), with boats <100m from calves 40% of the time and each whale exposed to an average of 3.4 boats for two hours daily (Schaffar and Garrigue, 2008). In 2008, commercial tour operators voluntarily signed a code of conduct, and subsequent compliance with this code has significantly reduced the level of daily exposure to boats (South Pacific Whale Research Consortium, 2009).

Surface run-off from nickel strip mines causes habitat degradation and pollution of lagoons in New Caledonia, which is one of the largest producers of nickel globally, yet the effect on the surrounding marine environment has been poorly monitored (e.g. de Forges *et al.*, 1998; Labrosse *et al.*, 2000; Metian *et al.*, 2005).

Raised skin lesions have been reported along the dorsal flanks of humpback whales in American Samoa and are common to the extent that they are seen on nearly all adult whales (Mattila and Robbins, 2008). They appear to be most concentrated around the genital region. They differ morphologically from the 'depressed' lesions caused by cookie cutter sharks and appear to persist for long periods on the skin, rather than either erupting or healing. There are no reports of these lesions in whaling records, suggesting that this phenomenon is recent. The cause of these lesions, and their effect on humpback fitness, is currently unknown (Mattila and Robbins, 2008).

There is little information available from the South Pacific regarding entanglement and ship strikes. Two humpback whales have been observed in Tonga entangled in rope in one instance and fishing net in another (Donoghue, pers. comm.). One humpback mother (with calf) was reported entangled in a longline in the Cook Islands in 2007 (South Pacific Whale Research Consortium, 2008).

vii. Recovery from Exploitation

Subsistence hunting was carried out at Rurutu in French Polynesia, in Tonga and the Cook Islands during the 20th century, with at least nine whales killed in Rurutu (Poole, 2002), at least 114 whales estimated as killed in Tonga (Allison, 2006) and the number of whales taken in the Cook Islands uncertain (Hauser *et al.*, 2000). The impact of the whaling industry on humpback recovery in Tonga cannot be fully described due to a lack of records (IWC, 2006b). Additionally, anecdotal information suggests that Soviet whalers may have hunted whales in Fiji and Tonga in the 1960s (Ivashchenko *et al.*, 2007), though the extent of this hunt is unknown.

Catches of humpback whales on the Antarctic feeding grounds associated with western Oceania and eastern Australia were very large, with ~36,000 taken from 120°E-170°W and ~8,150 killed between 170-110°W. Illegal Soviet whaling in the Antarctic waters associated with the eastern Australia/Oceania region killed over 29,000 humpback whales during 1959-1964 alone (Clapham *et al.*, 2009), with >80% of all catches made during this period. This is likely to have caused a pronounced bottleneck in most populations, with some formerly populated regions (e.g. Fiji, New Zealand) still showing slow recovery. It is very difficult to derive individual population histories for each breeding ground, since the geographical extent of each on the high-latitude feeding grounds (and therefore the level of catch) is unknown.

The degree of population structuring across the breeding grounds is apparently high, with restricted gene flow between Tonga, New Caledonia and French Polynesia (Olavarría *et al.*, 2007). The level of among-region migratory interchange was also low relative to within-region re-sightings (Garrigue *et al.*, In Press-a). The current low density of humpback whales migrating through New Zealand (Gibbs and Childerhouse, 2000; Gibbs *et al.*, 2006) and frequenting Fijian waters relative to pre-whaling years suggests that rates of recovery from exploitation vary across the region, possibly as a result of this demographic segregation.

Bayesian population dynamic models have to date focused on combined recovery in Oceania, grouping catches across New Caledonia, Tonga, the Cook Islands and French Polynesia, taking the combined estimate of abundance for the region and using a 'two-stock' population dynamic model including eastern Australia, since the Antarctic region 120°E-180 is a migratory destination for whales breeding in eastern Australia and Oceania and the large catches from this region must therefore be allocated to both 'stocks' (Jackson *et al.*, 2006; Jackson *et al.*, 2008). A preliminary reconstruction of population history under the two-stock population dynamic model suggests median recovery levels between 23-30% (95% CI 11-41%) of pre-exploitation abundance (Jackson *et al.*, 2009). However, the IWC has not yet completed a Comprehensive

Assessment of this region, which would fully evaluate the sensitivity of the population model to alternative catch allocation hypotheses and estimates of current abundance and migratory interchange.

8. Southeastern Pacific

i. Distribution and population structure

Breeding ground distribution

The wintertime breeding distribution of humpback whales in the southeastern Pacific (May to November) spans the coastline between Costa Rica and northern Peru, with the main wintering areas concentrated in Colombia (Gorgona Island, Málaga Bay and Tribugá Gulf), Panama and Ecuador. Low densities of whales are also found offshore around the Galápagos Islands (Félix *et al.*, 2006), and coastal sightings have been made as far north as Costa Rica (Coco Island and Golfo Dulce, 8°N) (Acevedo and Smultea, 1995; May-Collado *et al.*, 2005). The entire wintering region spans about 1,900 miles latitude between 9°N and 6°S; it is unknown whether the distribution is continuous across this range (Félix *et al.,* 2009b; Flórez-González *et al.*, 1998). Southern Hemisphere humpback whales are only rarely seen north of the equator elsewhere, but the oceanographic equator in the eastern tropical Pacific is 5-10°N of the geographical equator (in the Tropical Surface Water mass) which may explain their more northerly occurrence in this region (Rasmussen *et al.,* 2007), as has also been noted for the southeastern Atlantic breeding ground (see '*Southeastern Atlantic'* in Section XI).

In northern Peru and southern Ecuador, at the southern end of the wintering range, incidental sightings and catch data suggest that humpback whales are distributed up to 200 nm offshore, with the biggest concentrations between 0-100 nm from the coastline (Ramírez, 1988). This may therefore be the location where whales transit from deep offshore waters to the shallower continental coastline. Further north, in northern Ecuador, only 2.5% of all sightings have occurred in waters deeper than 60 m, suggesting a strong preference for continental shelf habitat in this region, which seems to be irrespective of habitat topography (Félix and Haase, 2005). A strongly coastal distribution has also been reported from surveys in Costa Rica (May-Collado *et al.*, 2005). In Colombia, the wintering distribution has been reported as coastal, on the continental shelf. Cow-calf groups have been found associated with depths ≤ 25 m, while adult groups have been found more often in depths > 25 m (Flórez-González *et al.*, 2007). In Panama, cow-calf groups have been observed in shallow waters, usually ≤ 20 m, while adult groups can be found in waters on the continental shelf but at deeper depths (1,000 m) (Flórez-González *et al.*, 2007).

Fluke photo-identification catalogs have been collected in Costa Rica (Acevedo and Smultea, 1995), Ecuador (Castro *et al.*, 2008b), Panama (Rasmussen, 2008) and Colombia (Flórez-González, 1991). Whales have been re-sighted in multiple wintering regions inter-annually (Castro *et al.*, 2008a; Félix *et al.*, 2009b; Flórez-González *et al.*, 1998). Low within-region inter-annual re-sight rates (e.g. 7% in Ecuador, Castro *et al.*, 2008b; 0% in Panama, Rasmussen, 2008) have led some researchers to suggest that whales occupy a broad home range along the coastline (Flórez-González *et al.*, 1998), although Colombia has a relatively high re-sight rate (16 % of whales resighted inter-annually, Flórez-González, 1991). Similar rates of inter-region re-sights (3-4% re-sights between Ecuador and Costa-Rica/Panama and between Ecuador and Colombia Castro *et al.*, 2008a) support this hypothesis, while genetic comparisons of individuals biopsy-sampled in Ecuador and Colombia also found no differentiation between these regions (Félix *et al.*, 2009a). While these observations support a hypothesis of panmixia, there is a degree of breeding ground migratory preference exhibited by whales on their southern feeding grounds (see below) suggesting that the population structuring within this region may be subtle and difficult to detect with the genetic samples currently available. Low within-region re-sights and short residency times in Ecuador also imply that many whales are being captured in transit to more northerly habitats (Félix and Haase, 2001; Félix *et al.*, 2009b) and suggest that the population is much larger than the present regional sampling effort indicates (Félix and Haase, 2001; Rasmussen, 2008).

Migratory connections

Photo-identification matching and genetic comparisons between feeding and breeding regions suggest that summer feeding grounds for southeastern Pacific whales are concentrated in the Chilean Magellan Straits and Western Antarctic Peninsula (Acevedo *et al.*, 2008a; Caballero *et al.*, 2001), with some observations of feeding and possibly summer residency in the more northerly Chiloe Islands and Gulf of Corcovado in Chile (Acevedo *et al.*, 2008b; Galletti Vernazzani *et al.*, 2006; Hucke-Gaete *et al.*, 2006). Whales surveyed in Isla de Chiloe showed residency times of over 20 days, suggesting some degree of fidelity to this region (Galletti Vernazzani *et al.*, 2008). However, historical records of humpback whales in this region are scarce, with no formal records of humpback whaling activities, although there are anecdotal data to suggest whalers occasionally observed them. Therefore it is uncertain whether sightings in this region are related to migration, a recent expansion in distribution from the southerly feeding regions, or a persisting population that has recently been identified by increased sighting effort (IWC, 2007a).

A comparison of breeding ground re-sightings for each feeding area found that a significant proportion of Western Antarctic Peninsula whales were re-sighted in Colombia, while a significant proportion of Magellan Strait whales were re-sighted in Central America, although the sample sizes used in this study were small (Acevedo *et al.*, 2008a). Therefore some Magellan Strait feeders may preferentially migrate towards the northern end of the breeding ground range. However, a few migratory connections have been made between Central America and the Antarctic Peninsula (Rasmussen *et al.*, 2007), so among the humpback whales wintering in Central America there may be individuals with site fidelity to different feeding grounds, as has been documented elsewhere (e.g., in the North Pacific, Calambokidis *et al.*, 2008).

Feeding ground distribution

The Magellan Straits and Western Antarctic Peninsula are separated by the Drake Passage and an intervening distance of ~600 miles. Despite catalog-matching efforts of 1,043 Western Antarctic Peninsula flukes against 92 Magellan Strait flukes, no whales have so far been photo-identified in both feeding regions, which suggests that movement between feeding grounds is rare (Acevedo *et al.*, 2008b). Comparisons of mitochondrial genetic data from the two feeding grounds also revealed significant genetic differences for both nucleotides and haplotypes (ϕ_{ST} = 0.178, F_{ST}=0.201), with much greater genetic diversity in the Western Antarctic Peninsula than the Magellan Straits (see '*Genetic Diversity*') (Olavarría *et al.*, 2006a; Olavarría *et al.*, 2003). These lines of evidence suggest that the two feeding grounds are visited by different aggregations of whales, with very low rates of movement between them. Inter-annual re-sight rates obtained from surveys within the Magellan Straits were high (mean 79%, Acevedo *et al.*, 2006), as is within-season interchange along the Chilean coast / Magellan Straits region (Capella *et al.*, 2008) suggesting high fidelity of a small number of whales to this feeding region (Acevedo *et al.*, 2006).

In the Magellan Straits, humpback sightings between 48°S and 54°S are concentrated in the waters surrounding Isla Carlos III and in the Canal Wide, with residency periods of 2-5 months observed (Gibbons *et al.*, 1998; Gibbons *et al.*, 2003). A review of historical sightings recorded by explorers and whalers indicates that this region has been frequented by humpback whales for at least the last two centuries (Gibbons *et al.*, 2003).

In the Western Antarctic Peninsula region , humpback whales are predominantly found near coastal habitat, particularly in the fjôrds (Dalla Rosa *et al.*, 2008; Thiele *et al.*, 2004), and are strongly linked with regions of marginal sea ice (Friedlaender *et al.*, 2006) and zones of euphausiid density (Murase *et al.*, 2002) (see '*Feeding*'). Whales in the Western Antarctic Peninsula region may move to other, poorly surveyed areas in the Southern Ocean. Photo-identification and satellite telemetry data has revealed both westward and eastward movement of whales from the Western Antarctic Peninsula, towards the Bellinghausen Sea in the west and Weddell Sea / southern Scotia Sea and South Orkney islands in the east (Dalla Rosa *et al.*, 2004; Dalla Rosa *et al.*, 2008).

Incidental sightings of humpback whales off Peru have also been made in summer (Ramírez, 1988), and the highly productive Humboldt Current could provide enough nutrients for humpback feeding (Papastavrou and Van Waerbeek, 1997), but at present there is insufficient data to suggest whether these sightings represents opportunistic feeding at the tail ends of the migration stream or a more permanent feeding ground. A recent summary of incidental humpback sightings in the Galápagos Islands from tourist boats and naturalist guides (177 whales sighted between 1985 and 2000) also revealed a low incidence of summer sightings, which may be associated with summer feeding in this region (Castro and Merlen, 2009).

Population structure (between breeding grounds)

Photo-catalog matching and genetic analyses of neighboring breeding regions (French Polynesia and Brazil) have so far revealed one inter-annual movement to the Colombian breeding grounds (one match with French Polynesia, Donoghue, 2008) and none between French Polynesia and the Antarctic Peninsula and Magellan feeding grounds (Albertson-Gibb *et al.*, 2009), nor between Brazil and the Antarctic Peninsula (Stevick *et al.*, 2004). Other breeding populations in the South Pacific are significantly differentiated genetically from the Western Antarctic Peninsula and Magellan Strait regions (Olavarría *et al.*, 2006a), while Brazil has also been compared to the Antarctic Peninsula and found to be significantly differentiated (Engel *et al.*, 2008). However photo-identification matching between the Western Antarctic Peninsula and South Pacific breeding grounds has also revealed one migratory movement between American Samoa and the Western Antarctic Peninsula (Robbins *et al.*, 2008a), suggesting that this region may be frequented by a small number of whales from neighboring breeding grounds (see '*Habitat and Ecosystem Conditions*').

ii. Abundance

Breeding ground population abundance has been estimated from Ecuador using multiple mark recapture models applied to photo-identification data collected from 1991-2006. The most recent estimate of abundance was 6,504 (CV = 0.21). This was obtained from a closed, Chapman-modified Petersen estimator over the survey period 2005-2006 (Félix *et al.*, In Press).

In the mid 1990s, photo-ID based mark recapture estimates of population abundance for the Colombian breeding grounds were 1,495 (95% CI 919-2,071) for Gorgona Island, 857 (95% CI 547-1,167) for Málaga Bay and between 1,120 and 2,120 whales for the whole Colombian Pacific (Flórez-González *et al.*, 2007).

Heterogeneity in migratory and breeding ground sex ratios (Brown *et al.*, 1995; Calambokidis *et al.*, 1997) can create a negative bias for humpback breeding ground abundance estimates based on fluke captures since sex is not determinable from these data. However the location of these surveys in Ecuador, to the south of the wintering area, means that most whales pass through this region in transit and are therefore likely to be captured.

Feeding ground abundance has been estimated from the Western Antarctic Peninsula (Stevick *et al.*, 2006c) using photographs collected between 1994/1995 and 2001/2002 and considering three photo-catalog collections from the region as separate samples of the population. Using this approach to the Chapman's two-sample estimator yielded abundances ranging from 1,960-3,260 (95% CI range 900-4,500). However, the three photo surveys were likely to have frequented the same high-use regions of the feeding areas, which makes the sampling approach non-independent. A regional estimate of humpback whale abundance with greater spatial coverage was carried out by CCAMLR in January and February 2000, using visual line transect surveys. These surveys yielded abundance estimates of 6,991 (CV=0.32) for the Antarctic Peninsula and 2,493 (CV=0.55) for the Scotia Sea. Abundance from the wider Antarctic region between 50-110°W was also estimated from circumpolar surveys, at 3,310 whales (CV=0.21) in 1996/1997 (Branch, In Press).

Overall abundance over breeding grounds (Ecuador, Colombia and Costa Rica) and feeding grounds (Western Antarctic Peninsula) was calculated by pooling photo-IDs from all breeding grounds (collected over 1991 to 2004) and using the feeding ground dataset as a second sample, in order to minimize the effect of capture bias by sampling different habitats (Stevick *et al.*, 2006b). Pooling samples violate the assumptions of open population models, so mean abundance estimates for each time span were regressed, after filtering for low sample bias. Abundance was estimated at 3,850 whales (95% CI 3,700-4,000) in 1997 (Stevick *et al.*, 2006b).

iii. Genetic Diversity

For an introduction to genetic diversity, see 'Genetic Diversity' in the 'Status of North Atlantic Populations' section. Genetic analysis of 148 biopsy samples collected in Colombia between 1991 and 1999 revealed 27 mitochondrial haplotypes (Caballero *et al.*, 2001; Olavarría *et al.*, 2007). Genetic and haplotypic diversity was lower than that found elsewhere in the South Pacific ($h = 0.900$+/- 0.016, $\phi = 0.019$ +/- 0.96) (Olavarría *et al.*, 2007). In addition, a genetic survey off Ecuador (including the offshore Galápagos Islands) between 2002 and 2007 obtained 103 biopsy, sloughed skin and stranding samples, which revealed 29 mitochondrial haplotypes and slightly lower genetic and haplotypic diversity than that reported for Colombia ($h = 0.893$+/- 0.023, $\phi = 0.018$ +/- 0.01) (Félix *et al.*, 2009a). Both studies suggest that the southeastern Pacific stock has the lowest genetic diversity among Southern Hemisphere breeding populations (excluding the Northern Indian Ocean, see Appendix 1) (Olavarría *et al.*, 2007; Rosenbaum *et al.*, 2009).

A genetic study of the feeding regions revealed a substantial difference in mitochondrial genetic diversity between the relatively diverse Western Antarctic Peninsula region ($n = 89$, $h = 0.915$ +/- 0.018, $\pi = 0.018$ +/- 0.01) and the Magellan Straits ($n = 52$, $h = 0.339$ +/- 0.08, $\pi = 0.010$ +/- 0.005), where only four haplotypes have so far been found (Olavarría *et al.*, 2005; Olavarría *et al.*, 2006a).

iv. Trends

There is some evidence for a population increase over time suggested by the abundance estimates reviewed in '*Abundance*' above (Stevick *et al.*, 2006c). However, no trends are yet available for this population. Annual rates of population increase have been calculated using sightings from three circumpolar surveys of the Antarctic region (Branch, 2006) and suggest a 4.6% annual increase for the region surveyed between 100W and 50W, but the variance is very large (95% CIs between -3.4 and 12.6%) and the degree of mixing of southeastern Pacific humpback whales with those from other breeding grounds in this Antarctic region is still unknown.

v. Habitat or Ecosystem Conditions

The wintering ground includes both sub-tropical and tropical climates and the major oceanic-atmospheric interaction of the equatorial front, which comprises a complex system of surface currents and sub-surface counter-currents driven by north and south trade winds. To the south, the Humboldt Current brings cold water north along the coast from Chile to Ecuador until deflected off to the west by the equatorial front off Ecuador.

In Ecuador, wintering ground habitat is composed of a large bight, bordered by the mainland coast and Isla De La Plata in the west. The mainland continental shelf is about 25 nm wide on average, up to a maximum of 40 nm. West of Isla De La Plata, the shelf drops to >3000m. The sea floor is mainly composed of sand, gravel, rocky outcrops and coral reefs. In Ecuador and Colombia, occurrences of mothers and calves are significantly associated with shallow waters (20m or less) throughout the winter season (Félix and Haase, 2001; Flórez-González, 1991; Flórez-González *et al.*, 2007). In Ecuador, mothers and calves were mainly observed at Puerto Cayo (mainland coast), while larger groups of adults and subadults were observed offshore at La Plata and Bajo de Cantagallo islands (Félix and Haase, 2005).

In western Panama, the Gulf of Chiriquí is a shallow region (>300m) bordered by two peninsulas and containing many island groups. Most humpback sightings occur near island groups, while effort in open water between islands has yielded fewer sightings. Sightings of calves occur close to island groups, rocky outcrop or mainland (Rasmussen, 2008). Historical whaling records (Best, 2008) and recent acoustic deployments (Oviedo *et al.*, 2008) also indicate that humpback whales are distributed elsewhere along the coast in winter, particularly within the Gulf of Panama.

Golfo Dulce, southern Costa Rica, is a 10-mile-wide estuarine embayment with a steeply sloped inner basin and shallow outer basin. Isla del Coco is an offshore volcanic island with a 180m contour line ranging 1-10 miles from shore (Acevedo and Smultea, 1995). A small number of sightings of singletons and mother-calf pairs have been made in these areas both in winter and summer, suggesting that it is an occasional habitat for whales from both Northern and Southern Hemisphere populations (Acevedo and Smultea, 1995).

The Galápagos Archipelago is located 620 miles west of mainland Ecuador at 1°S and consists of 13 major islands and 50 minor ones, all volcanic in origin. The central region between islands is shallow, and the archipelago is surrounded by narrow shelves with abrupt continental slopes, with depth increasing rapidly to 3,000m on the west and south. During dedicated surveys, a mother with a small calf was observed in the shallow northern waters in this region, suggesting that it has been used as an occasional nursery habitat (Félix *et al.*, 2006), but no male singing has been detected acoustically, confirming that breeding density is low in this region. There is high cold-water primary productivity on the western side (including Isabela Island), which supports a high abundance and diversity of other marine mammals (Banks, 2002).

The waters of the Gulf of Corcovado are fed by the eastern South Pacific Ocean. At this location the Antarctic Circumpolar Current reaches South America and diverges to form the Humboldt Current to the north and Cape Horn Current to the south. Fjords on the eastern side subtend Moraleda Channel and lead to Continental Chile, which feeds the eastern waters with fresh water from glacial ice-melt and river influxes. Incidental sightings and dedicated surveys between 2001 and 2006 have produced a total of 145 humpback sightings, mainly in the summer months and mainly concentrated in the Gulf of Corcovado, but also on the west coast of Chiloé Island and in fjords south of 50S (Hucke-Gaete *et al.*, 2006). Sighting surveys off Isla de Chiloé between 2006 and 2008 found a low density of humpback whales (n=52), some of whom were feeding (Galletti Vernazzani *et al.*, 2006). The timing of sightings suggests that they were not on migration further south this late in the season.

The Magellan Strait region is highly varied topographically. In the north it is composed of the Patagonian fjords (external channels connected with the Pacific Ocean and internal channels and fjords connected with the Southern Ice fields), which are characterized by cold water and low salinity due to high rainfall, glacial ice melt and influxes from rivers. Sighting surveys find concentrations of humpback whales in the Canal Wide within this region (Gibbons *et al.*, 2003). The Magellan Strait is a 350-mile channel which links the Pacific and Atlantic Oceans and is subtended by a series of sounds (or 'inner seas'). The region is fed by water masses from both oceans as well as a great deal of fresh water from precipitation and river influxes and is therefore a region of rich habitat diversity (Panella *et al.*, 1991). Within the Straits, humpback whales are regularly found at high densities in the vicinity of Carlos III island (Gibbons *et al.*, 2003). To the south, the Fuegian fjords are topographically similar to the Patagonian fjôrds but receive influence from the Atlantic Ocean. Few humpback whales have been sighted in this region (Gibbons *et al.*, 2003).

The Western Antarctic Peninsula spans roughly 13,670 square miles out to the shelf break, from the tip of the Peninsula to Alexander Island at the base. The Antarctic Peninsula shelf is broad, and is characterized by very high levels of primary production and phytoplankton biomass during spring and summer. Running northeast up to the tip of the Peninsula, Bransfield Strait is bordered by the mainland and South Shetland Islands to the northwest. To the south of this, Gerlache Strait is a much narrower channel bordered by the mainland and Brabant and Anvers Islands to the northwest, with extensive freshwater input from glacial meltwater. Primary production is highest in the Gerlache Strait region (Varela *et al.*, 2002). The two straits are demarked by a hydrographic front, which separates the more freshwater Gerlache from the more saline Bransfield Strait (Varela *et al.*, 2002). To the west of both of these, at the western shelf break, is the frontal zone of the Southern Boundary of the Antarctic Circumpolar Current (Garcia *et al.*, 2001). Further to the south along the Peninsula, Marguerite Bay is a large embayment (60 miles wide) with a complex bathymetry and rapid coastal currents, which may be forced by sea melts, gyres and eddies. The southern boundary of the Antarctic Circumpolar Current flows northwest here, contributing warm water throughout the year (Thiele *et al.*, 2004). A study of humpback density against acoustic backscatter (in the upper 100m of the water column, indicative of zooplankton) in outer Marguerite Bay found a significant relationship between whales and prey abundance, proximity to the ice edge and high slope bathymetry (which correlates strongly with zooplankton abundance) (Friedlaender *et al.*, 2006). This may not necessarily be indicative of environmental inter-relationships in the inner waters and channels of the Antarctic Peninsula. Surveys of the inner regions have found high densities of humpback whales in fjords and close to coastal habitat and ice edge boundaries (Thiele *et al.*, 2004).

vi. Threats and Anthropogenic Impacts

Disturbances from seismic sound may impact this population, as yearly multi-national naval deployment exercises are carried out by UNITAS throughout the humpback breeding season during a five-month circumnavigation of the South American coast.

In the South of Ecuador lies the Gulf of Guayaquil, which is the main port and, since 2005, also under development as a region of offshore oil and natural gas production (Félix and Haase, 2005), a major source of anthropogenic noise, habitat degradation and additional ship strike risks for migratory and nursing whales. Recently developed commercial routes also pass through the near-coastal waters off Salinas and around La Plata Island in Ecuador, areas which currently support a high density of whales (Félix and Haase, 2005).

The Panama Canal is one of the most highly travelled shipping routes in the world (Kaluza *et al.*, 2010), traversed by over 12,000 ships every year. The cumulative impact of this level of shipping traffic on the calving grounds in the Gulf of Panama (Best, 2008) is unknown, though the impact of ship strikes on calves is likely to be disproportionate, as observed in other regions (Capella Alzueta *et al.*, 2001). While some stranding reports indicate a degree of mortality from ship strikes (Capella Alzueta *et al.*, 2001; Castro *et al.*, 2008c), no ship strikes have yet been directly reported for humpback whales to date from the southeastern Pacific region, although burgeoning coastal development coupled with some evidence of population increases means fatalities from this source are likely to increase in the coming years.

In the southeastern Pacific, the main fishery interactions suggested by studies of strandings, photographs and recorded entanglement events seem to be entanglement and/or death after contact with gillnets and purse seine nets (Alava *et al.*, 2005; Capella Alzueta *et al.*, 2001; Castro *et al.*, 2008c; Félix *et al.*, 1997).

In Ecuador, the size of the artisanal fishing fleet was estimated at 15,000 vessels in the late nineties (Alava *et al.*, 2005). Vessels are small, and fishing techniques include long-lines (mostly deployed in the north) and surface and deep-water gillnets (mostly central and southern regions). Cases of entanglement have been documented for Ecuador by photo-analysis, which revealed that 19% (8 of 43) individuals had skin lesions indicative of entanglement (Castro *et al.*, 2008c). A 29% (95% CI 11-53%) rate of fishery interaction was reported from a summary of 2001-2002 stranding events by Alava *et al.* (2005), who found that surface gillnets were the fishery device most commonly linked to entanglements and estimated the average rate of stranding at 1.55 whales (range 1-4) per year since 1994. The pelagic purse seine fishery was also implicated in earlier strandings in the region (1994-1996 Félix *et al.*, 1997). An unusually high number of humpback strandings was also reported in 2004 (five calves and three adults), but cause of death has yet been established (Félix *et al.*, 2004).

Reports from Colombia showed a rise in the numbers of dead and entangled whales reported over two decades, with 18 reported between 1996-2000, as opposed to six each in 1986-1990 and 1991-1995 (Capella Alzueta *et al.*, 2001). Of these recent deaths, 10 were attributed to entanglement and three to vessel strikes (one was of unknown cause and the other a failed hunting attempt). The majority of reports concerned calves (54%), a significantly high value relative to the average ratio of calves to adults in the population and consistent with entanglement observations from other breeding grounds (Engel *et al.*, 2006; Neto *et al.*, 2008). The most frequent reports were in the Negritos Bank area (54%), followed by the Gorgona mainland (21%) (Capella Alzueta *et al.*, 2001).

There are whale-watching industries in all of the South and Central American countries bordering humpback wintering and summering habitat. Whale watch regulations are currently in place in Panama, Ecuador and Costa Rica, while industries in Peru, Colombia and Chile are not yet subject to guidelines (Hoyt and Iníguez, 2008). The fastest industry growth has occurred in Costa Rica (56%) and Panama (53%), while whale watching in Peru and Chile is mainly focused on other species and whale watching in Colombia is not strongly developed, possibly as it overlaps with the rainy season and tourism has been low as a result of political turmoil (O'Connor *et al.*, 2009).

In Isla de la Plata (Machalilla National Park, Ecuador), the tourism industry has been growing rapidly in recent years, as it is the prime whale watching area in Ecuador (O'Connor *et al.*, 2009). Across Ecuador, whale-watching tourists increased at the rate of 17.8% annually between 1998 and 2006 (Hoyt and Iníguez, 2008). A theodolite-based study of the effects of the burgeoning industry at La Plata found that vessel approaches increased humpback swimming speeds significantly and that whales reverted to more direct travel paths after vessels departed (Scheidat *et al.*, 2004), suggesting that even with regulations in place, vessel interactions are negatively influencing humpback behavior.

Documented interactions with killer whales (*i.e.*, rake marks and bites) and potentially also false killer whales and sharks are high in this region, with two recorded sightings of killer whale attacks (Flórez-González *et al.*, 1994; Scheidat *et al.*, 2000) and 6.4% identified from photographic catalogs with bite marks and parallel scars (Félix and Haase, 2001). There are also recorded interactions with sharks in whaling records, which seem to be mostly after hunting injuries have occurred (Best, 2008). Such interactions may also occur after entanglement injury, but studies of this interaction have not been done.

Humpback whales in the Straits of Magellan feed in proximity to a major shipping route for vessels travelling between the Pacific and Atlantic Oceans (Kaluza *et al.*, 2010; Morris, 1988). This traffic is mostly composed of large container ships and oil tankers. The route is also notoriously perilous to navigate, so risks of running aground are higher and the isolation of the region makes subsequent clearing of pollutants difficult. For example, a supertanker spill of 51,500 tonnes of crude oil occurred in 1974, and was not subsequently cleared (see Section VIIaiv) (Morris, 1988). The impact of this shipping traffic on the Magellan Strait humpback population has not been documented (Olavarría, pers comm.). More recently, the development of many fjords for aquaculture and salmon farming may reduce and degrade available productive habitat for whales feeding in this region.

Declines in sea ice extent along the Western Antarctic Peninsula during the last century correlate with a major decline of Antarctic krill (Atkinson *et al.*, 2004), which will potentially reduce the feeding success (and therefore carrying capacity) for southeastern

Pacific whales, or drive a change in prey species. There is also a growing fishery for krill in this region (Everson and Goss, 1991).

Whale watching in Antarctica grew at a rate of 16.4% per annum between 1998 and 2008, with the Antarctic Peninsula the region most frequently visited and large cruise liners the predominant mode of transport. A study of the travel patterns of tour ships shows the highest traffic in the Gerlache Strait, an area which also boasts particularly high primary productivity (see '*Habitat and ecosystem conditions*') (Lynch *et al.,* In Press). However, the extreme weather conditions faced in the Antarctic region means the risks of vessel damage and sinking are greater, particularly as there are currently no regulations concerning vessel construction for tourism activities in these regions. Each accident poses enormous logistic challenges for rescue and creates environmental pollution from oil, debris and other waste. One major oil spill resulting from a tourist vessel sinking in the Antarctic Peninsula region has been documented (Eppley and Rubega, 1990); fuel leakage is apparently ongoing (Janlot *et al.*, 2003). Recently an ice-strengthened cruise ship (the *Explorer*) struck an iceberg and sank in November 2007 close to the South Shetland Islands. Legislation surrounding vessel safety has been reviewed by the Antarctic Treaty Meeting of Experts, which has recommended mandatory standards of vessel design and construction in order to reduce the risks of future accidents in the Antarctic region (Secretariat of the Antarctic Treaty, 2009).

vii. Recovery from Exploitation

Humpback whales have been hunted in Chile since at least 1870 (American style shore whaling; Reeves and Smith, 2006). However, the region encompassing the Western Antarctic Peninsula and western South America was most heavily exploited during the modern 20th century whaling period. Over 2,000 whales were killed in the South American coastal region north of 40°S, and around 15,000 were killed south of 40°S and between 50 and 100°W (Allison, 2006). In order to determine recovery status of the entire region subsequent to exploitation, a Bayesian population dynamic model of historical population abundance was developed, incorporating the abundance estimates, genetic diversity and catch data available for this population (Johnston *et al.,* In Press). The sensitivity of the population model to the following variations was explored: (*1*) increased Antarctic catch allocations from further to the west of the region (100-130°W) and by assuming a degree of feeding in more distant Antarctic areas, (*2*) estimates of recent abundance from the feeding (Hedley *et al.*, 2001; Stevick *et al.*, 2006c) and breeding (Félix *et al.*, In Press) grounds, respectively, (*3*) depensation (reduced growth rate) at low population abundance, (*4*) using available trend data from the Brazilian population as a prior on population growth, and(*5*) weighting the model with trend data from Antarctic surveys (Branch, 2006). The model outcome was found to be relatively insensitive to catch allocation, as the number of additional catches between 100-130°W is low (around 300 whales). Estimates of abundance had a strong influence on model outcome, with the breeding ground abundance estimate yielding a pre-exploitation recovery of median 56% in 2006, while the feeding ground abundance estimates yielded median recovery levels between 49-78% (IWC, 2007a; Johnston *et al.,* In Press).

Since the feeding ground estimate reported in Stevick *et al.* (2006c) had a notably narrow coefficient of variance of 0.02, and certain methodological aspects of the paper required further discussion, the International Whaling Commission agreed that the best available estimate of recovery for this population ranged between 30-70% of pre-exploitation abundance (IWC, 2007a), while noting that these estimates are made somewhat unreliable by the absence of trend data from the region.

It should be noted that this estimate of population recovery includes catches from both the Magellan Straits and Western Antarctic Peninsula feeding grounds (Allison, 2006). However multiple strands of evidence suggest that these feeding grounds are visited by different groups of whales (Acevedo *et al.*, 2008b; Olavarría *et al.*, 2006a), so population assessments of each region separately would be useful to tease apart this overall recovery estimate. While catch data are available separately for each feeding ground (Allison, 2006), to date no estimate of abundance is yet available for the Magellan Straits to permit a population assessment of this region.

XIII FIGURES

Figure 1. Seasonal humpback breeding and calving grounds off Brazil (June to December) in the Western South Atlantic. Soft grey shading indicates humpback wintering habitat (patchy shading does not imply a discontinuous distribution, but that humpbacks are less commonly seen). Dashed arrows indicate approximate satellite telemetry tracking of whales towards feeding grounds east of South Georgia and the South Sandwich islands (Zerbini *et al.*, 2006a). Markers A and B (with dashed lines) denote four inter-annual photo-identification matches between Abrolhos Bank and the South Sandwich Islands (Engel and Martin, 2009), and one with South Georgia (Stevick *et al.*, 2006a).

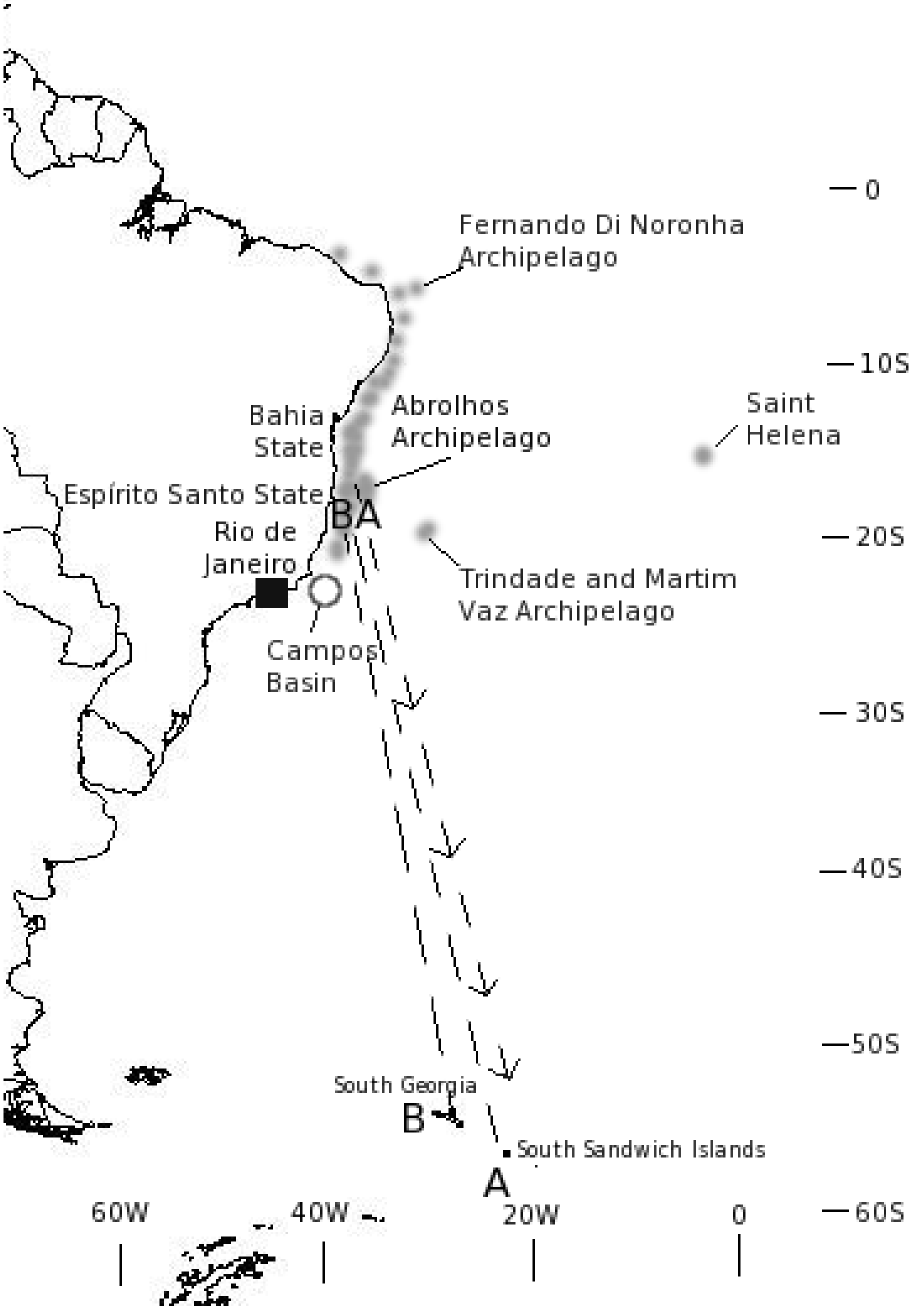
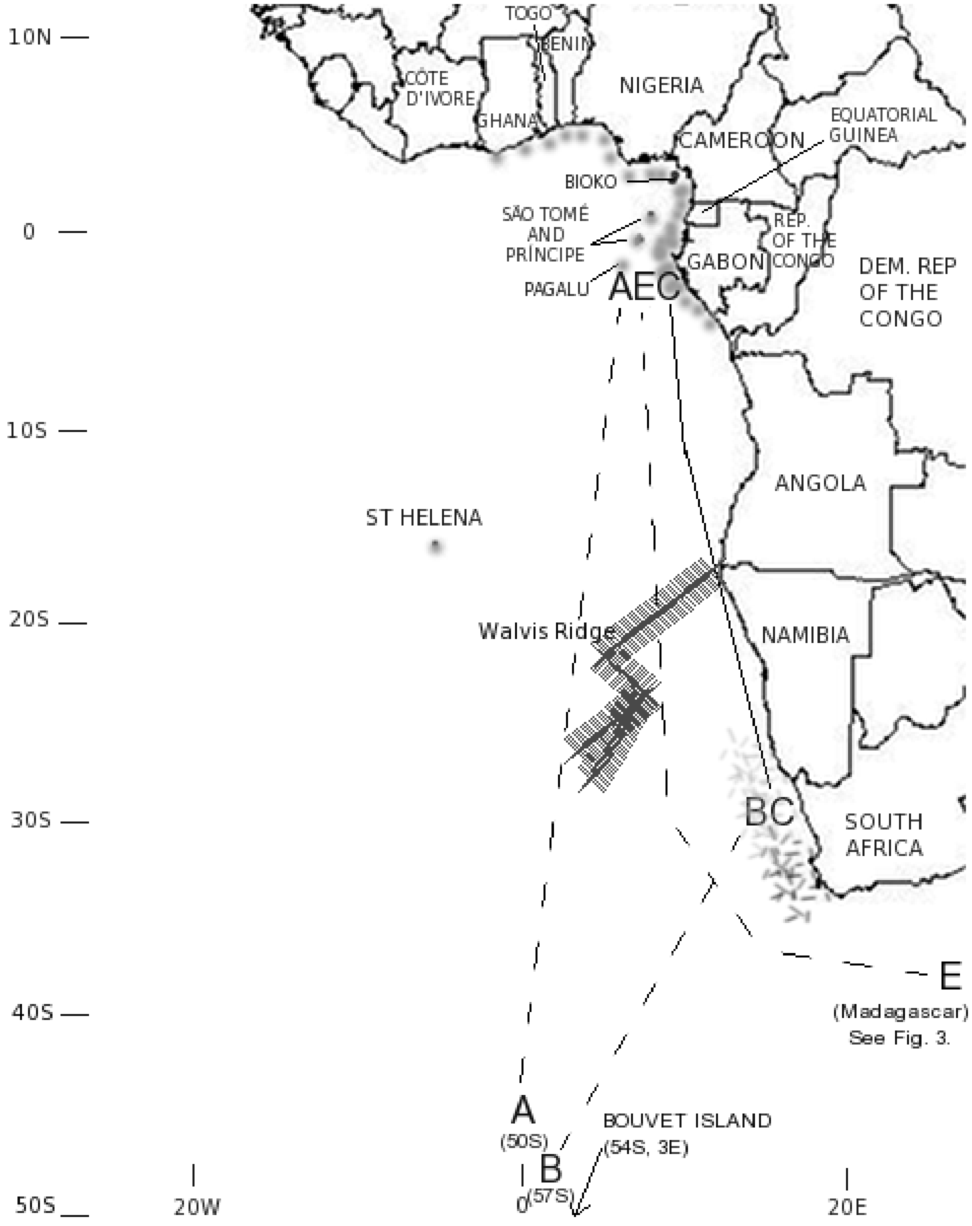


Figure 2. Seasonal humpback breeding, calving and continental feeding grounds off southwestern and central Africa (~6°S-6°N, July to January) and St Helena (June to October) in the eastern South Atlantic. Soft grey shading indicates humpback wintering habitat, grey stipple indicates summer feeding habitat. Markers A-C indicate genotype connections identified between breeding and feeding habitats (inter-annual re-sights are dashed lines, intra-annual re-sights are solid lines), marker E indicates two genotype recaptures between breeding habitats (Carvalho *et al.*, 2009; Pomilla and Rosenbaum, 2005; Pomilla and Rosenbaum, 2006).[11]



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[11] Satellite telemetry tracks showing migratory movement offshore at Walvis Ridge not shown, but forthcoming in Rosenbaum and Mate (In Review)

Figure 3. Humpback breeding and calving grounds in the southwestern Indian Ocean (July to January). Soft grey shading indicates humpback wintering habitat. Seasonal migratory routes are indicated with a thick gray arrow. Markers A and B represent genotype recaptures (Loo pers commIWC, In Press), while markers C and D (grey lines) represent Discovery Mark returns (IWC, 1998; Paton *et al.*, In Press; Rayner, 1940; Rosenbaum and Mate, In Review). Markers E and F indicate genotype recaptures between breeding grounds (Ersts *et al.*, 2006; Pomilla and Rosenbaum, 2005) while Marker G indicates photo-identification and genotype recaptures between a breeding ground and migratory route (Cerchio *et al.*, 2008; Pomilla *et al.*, 2006).

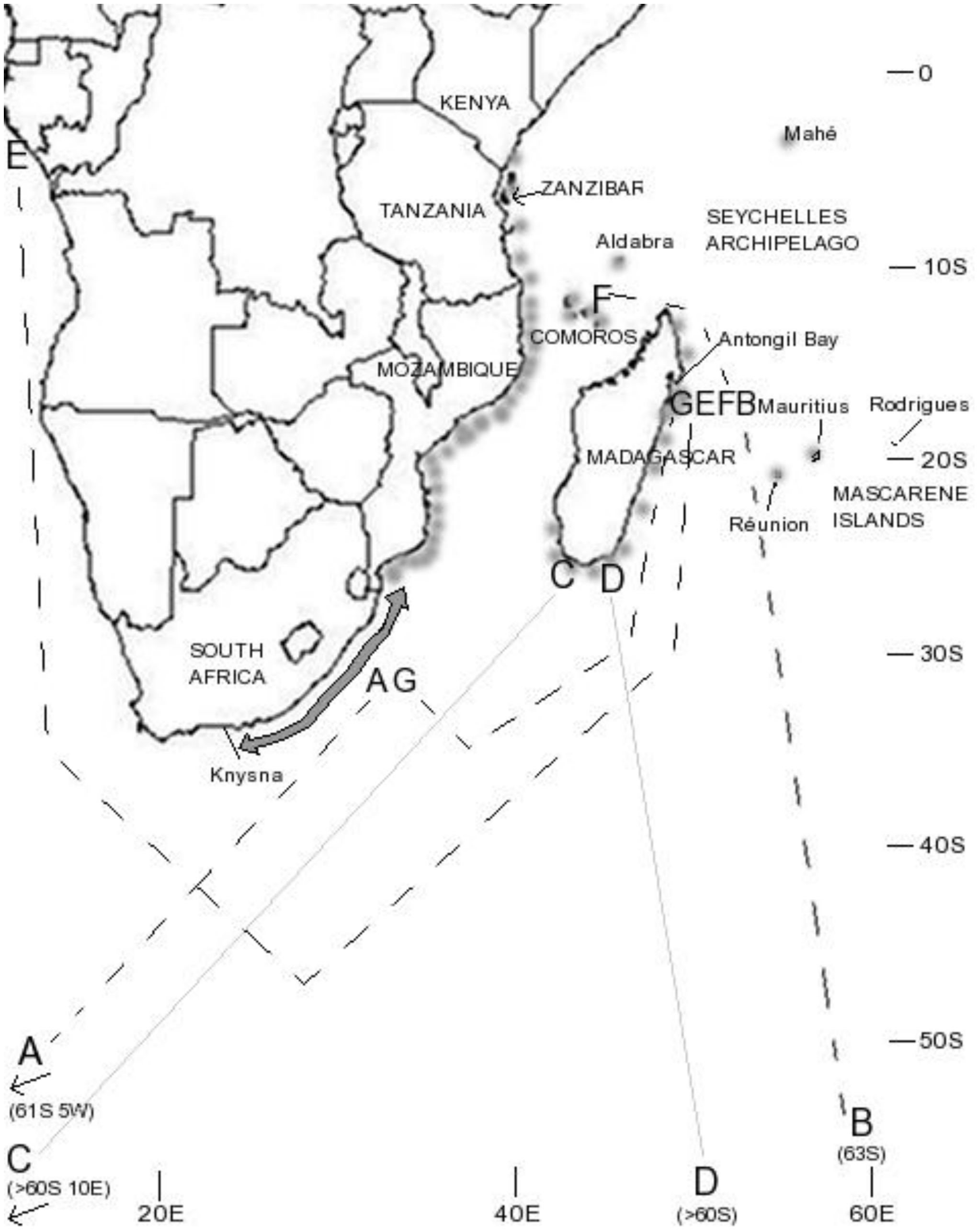


Figure 4. Humpback breeding grounds in the southeastern Indian Ocean. Soft grey shading indicates humpback wintering habitat. Seasonal migratory routes are indicated with a thick grey arrow. Discovery mark recaptures (Chittleborough, 1965; Paton and Clapham, In Press; Rayner, 1940) are shown as grey lines. Marker A indicates a photo-ID recapture between breeding and feeding grounds (Gill and Burton, 1995). Marker B represents two Discovery mark recaptures between breeding grounds (Chittleborough, 1965).

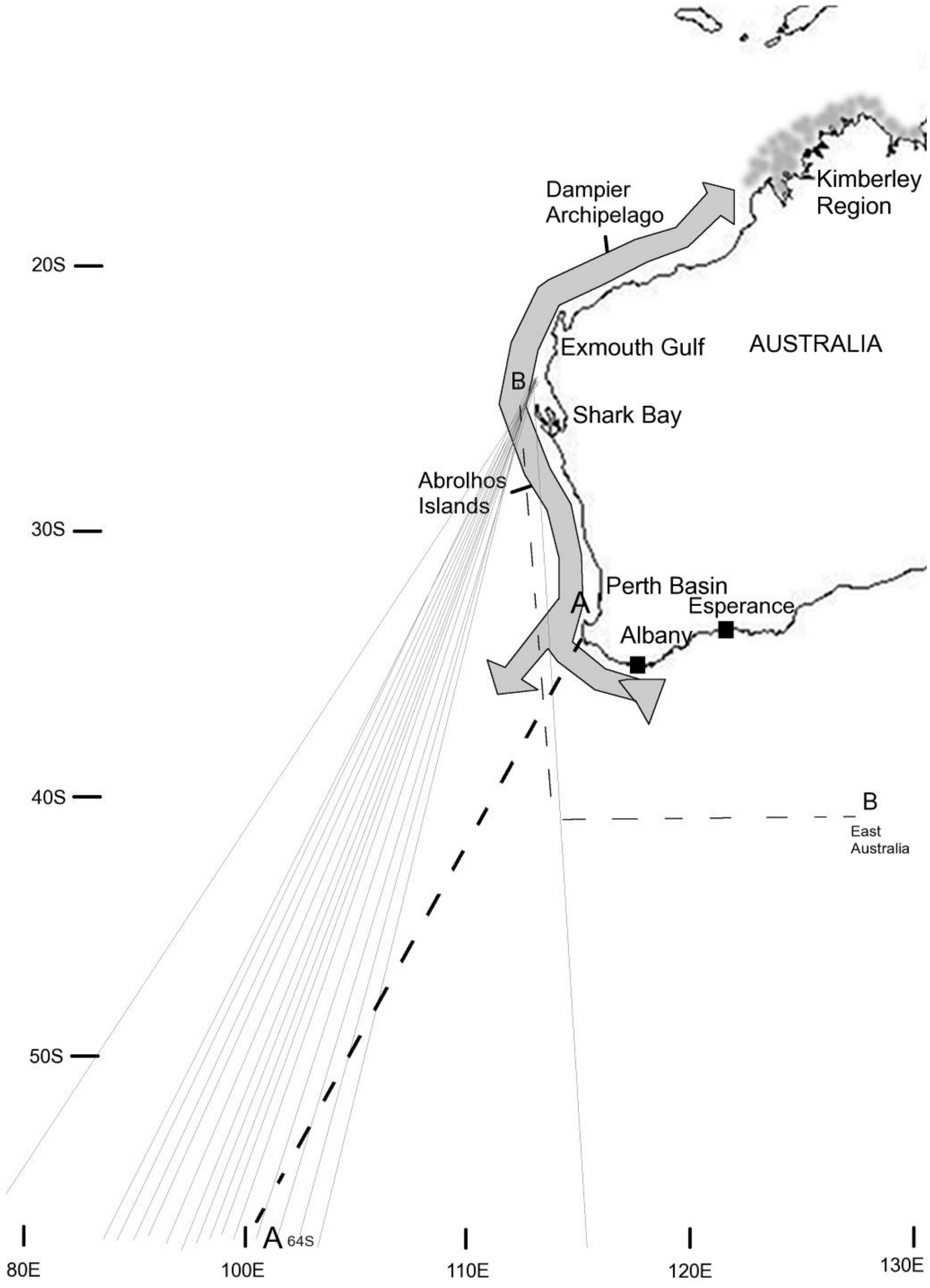


Figure 5. Humpback breeding, feeding and calving grounds in the northern Indian Ocean (shown in grey, after Minton *et al.*, In press). Soft grey shading indicates humpback wintering habitat. Incidental sightings, strandings and acoustic detections are shown as crosses (Gore, pers. comm., Braulik *et al.*, 2010; Reeves *et al.*, 1991; Whitehead, 1985a)

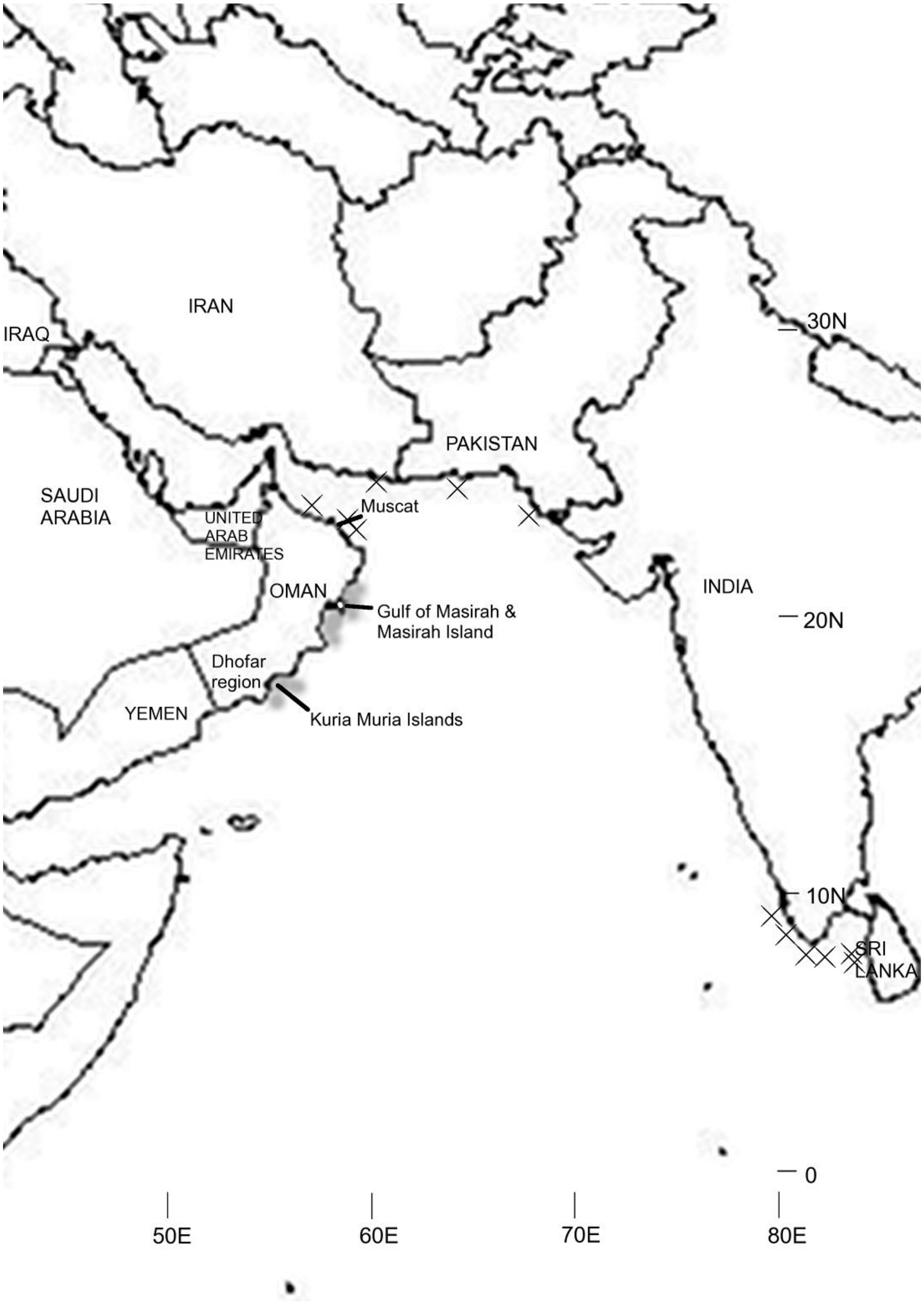


Figure 6. Humpback breeding and calving grounds along the eastern coast of Australia. Soft grey shading indicates humpback wintering habitat. Discovery mark connections between breeding and feeding grounds and shown in gray (Chittleborough, 1965; Paton and Clapham, In Press). Approximate satellite telemetry tracks (Gales *et al.*, 2009) are shown as dashed arrows. Photo-identified re-sights between breeding and feeding regions (A-F) and breeding grounds and migratory routes (G) are described in (Franklin *et al.*, In Press-a; Franklin *et al.*, In Press-b; Rock *et al.*, 2006). Within-season migratory movement between New Zealand and Australia (solid line with arrow) has been documented by three photo-IDs (G) (Franklin *et al.*, In Press-a). Inter-annual exchange between breeding grounds is shown by markers H and J (3 and 1 re-sights respectively, Franklin *et al.*, In Press-a; Garrigue *et al.*, In Press-b; Garrigue *et al.*, 2010).

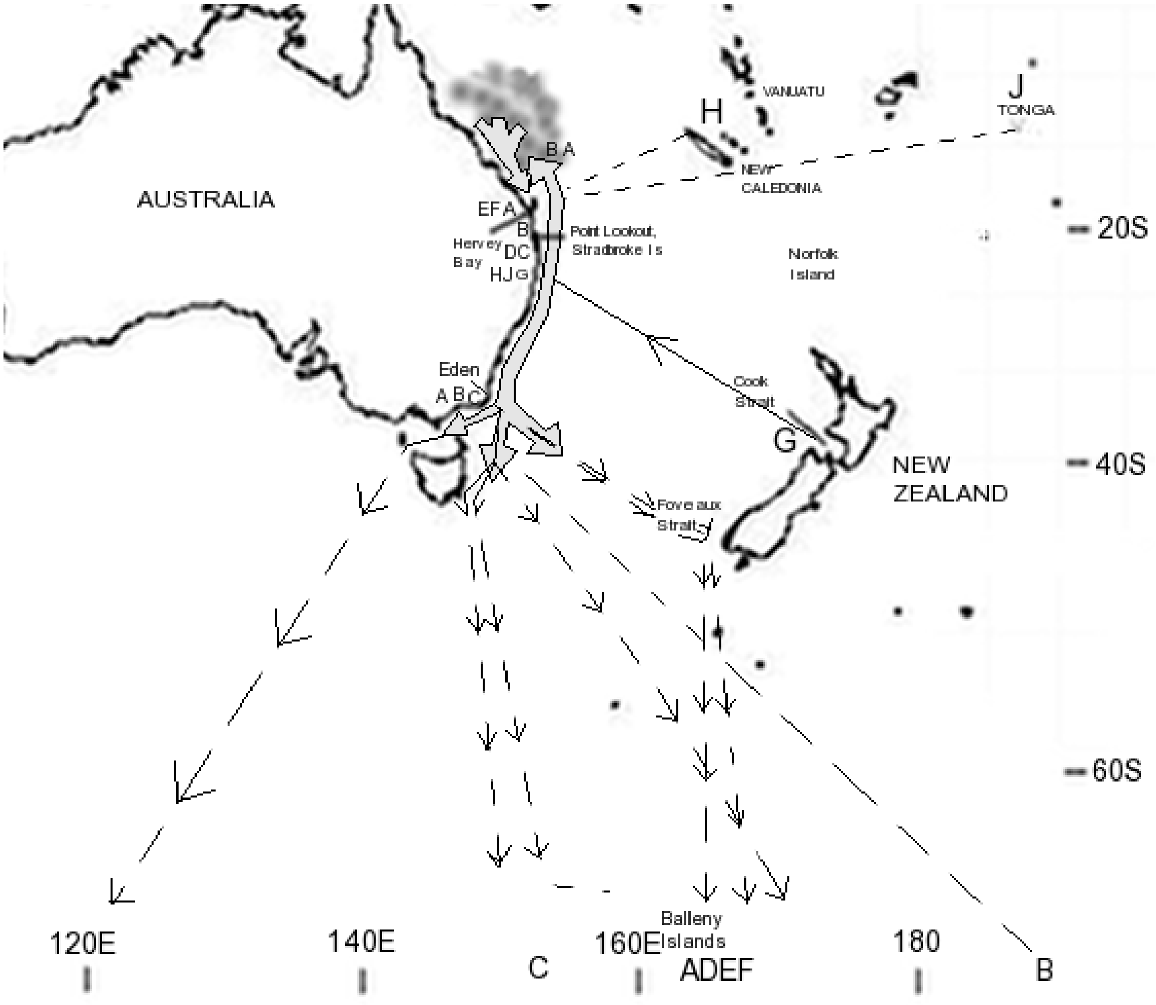
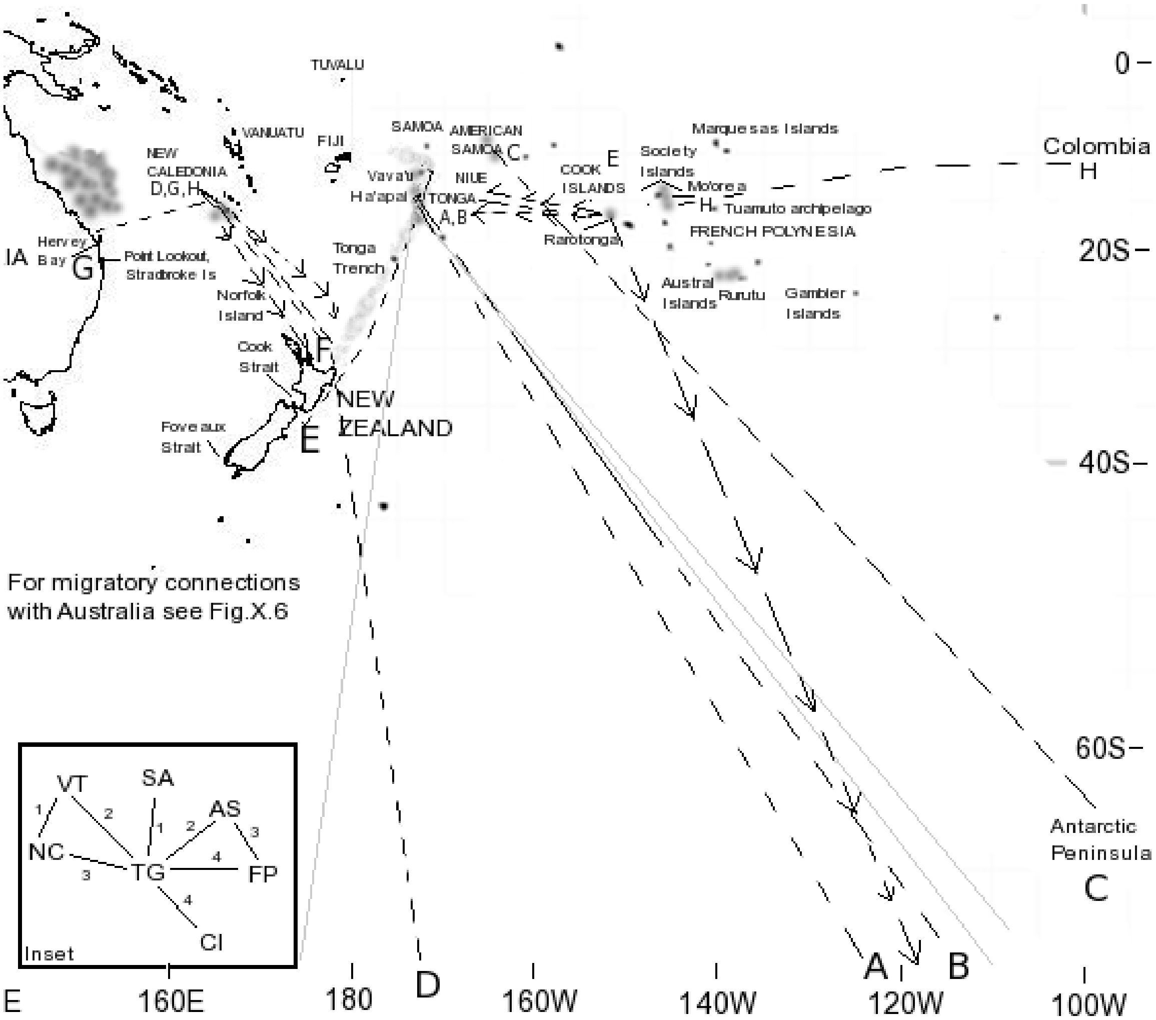


Figure 7. Humpback breeding and calving grounds in the South Pacific (Oceania) region. Soft grey shading indicates humpback wintering habitat. Discovery mark connections are shown in gray. Approximated satellite telemetry tracks from the Cook Islands towards Tonga and the Antarctic (Hauser *et al.*, In Press) and from New Caledonia towards New Zealand and the Tonga Trench (Garrigue *et al.*, 2010) are shown as dashed lines with arrows. Photo-identification matches between breeding grounds are shown as marker G (see Fig.X.6, Franklin *et al.*, 2008a; Garrigue *et al.*, In Press-b; Garrigue *et al.*, 2010), H (see Fig. X.7, Donoghue, 2008) and in inset box[12] (quality controlled re-sights 1999-2004, Garrigue *et al.*, In Press-a). Markers A, B and D are genotype re-sights (Steel *et al.*, 2008), Markers C, E and F are photo-ID re-sights (Constantine *et al.*, 2007; Robbins *et al.*, 2008a).



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[12] NC=New Caledonia, TG=Tonga, VT=Vanuatu, AS=American Samoa, SA=Samoa, FP=French Polynesia, CI=Cook Islands

Figure 8: Humpback breeding, calving and continental feeding grounds in the southeastern Pacific (May to November). Soft grey shading indicates humpback wintering habitat, stipple indicates summer feeding habitat. Photo-identification re-sights between the breeding and feeding grounds are too numerous to summarize in the figure; solid lines show migratory destinations for each breeding ground (but do not indicate migratory route) based on *comparative* levels of exchange between the Central and South American coasts and the Magellan Straits and Antarctic Peninsula (Acevedo *et al.*, 2008a), and also from photo-identification re-sightings between Central America and the Antarctic Peninsula (Rasmussen *et al.*, 2007). Marker A (dashed line) indicates one photo-ID based inter-annual breeding ground re-sight reported with French Polynesia (Donoghue, 2008).

Figure 9: Reproduced from SPLASH data (Calambokidis *et al.*, 2008). Lines indicate photographic matches between breeding and feeding areas. Lines are color coded by breeding area origin from Asia (blue), Hawaii (yellow), Revillagigedos Islands (brown), Baja California (green), mainland Mexico (lavender) and Central America (red). Photographic matches between breeding areas are shown in dotted black and photographic matches between feeding areas are shown in purple.

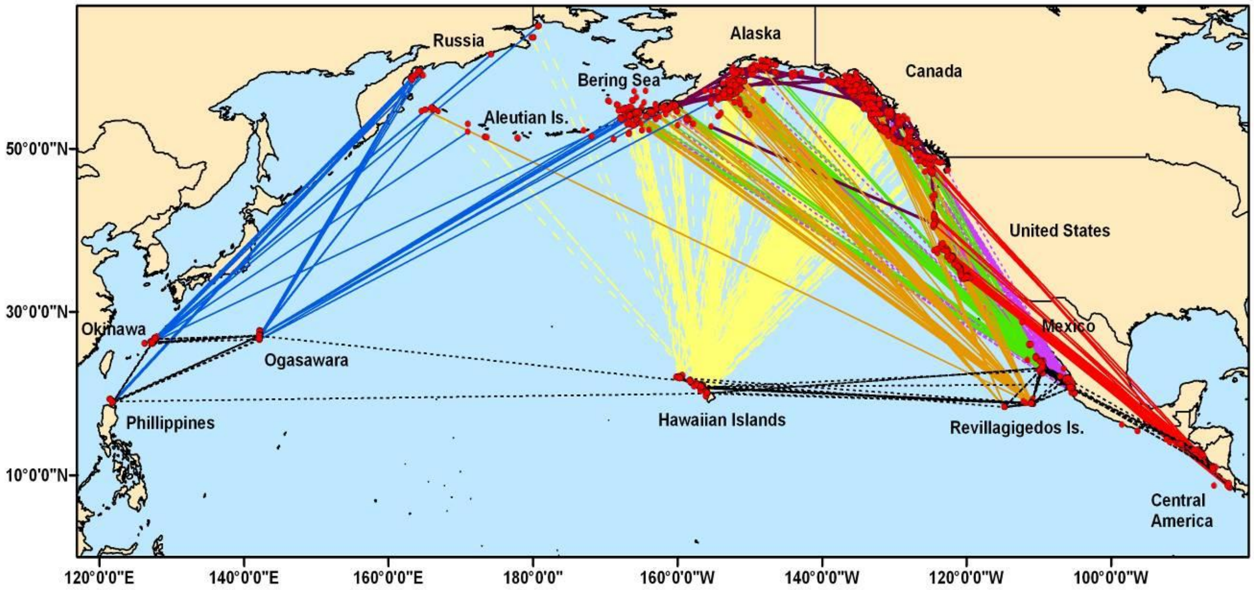
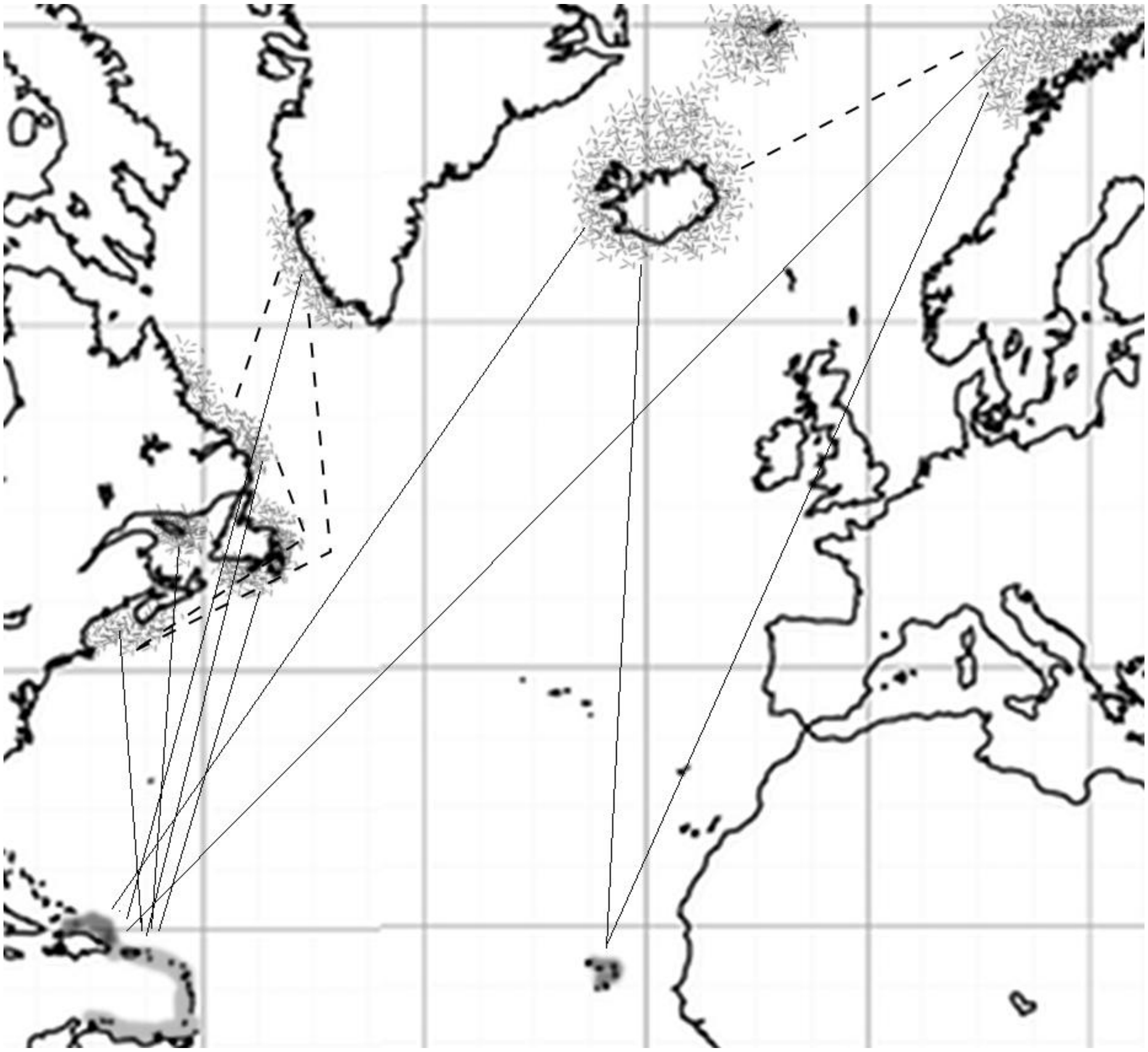


Figure 10: Humpback breeding and feeding grounds in the North Atlantic. Grey shading indicates humpback wintering habitat, stipple indicates feeding habitat. Solid lines show migratory destinations for each breeding area based on photographic and genetic matches. Dashed lines indicate resights between feeding areas.



XIV APPENDICES

A) APPENDIX 1. Genetic Diversity and Population Differentiation in the Southern Hemisphere

TABLE 1. Global estimates of genetic diversity by breeding ground

Breeding ground	Sampling Region	Sampling period	Number of samples	CR length (bp)	Number of haplotypes	Haplotype diversity	Nucleotide diversity	Reference
Southwestern Atlantic	Abrolhos Bank, Brazil	1997-2001	171	400	61	0.972 (0.004)	0.025 (0.013)	(Engel *et al.*, 2008)
	Abrolhos Bank, Brazil	1997-2001	164	486	66	0.974 (0.004)	0.025 (0.013)	(Rosenbaum *et al.*, 2009)
Southeastern Atlantic	Gabon and Cabinda	1998-2002	477	486	100	0.980 (0.002)	0.021 (0.011)	(Rosenbaum *et al.*, 2009)
	West South Africa	1993-2004	108	486	52	0.9766 (0.006)	0.020 (0.010)	(Rosenbaum *et al.*, 2009)
Southwestern Indian Ocean	Mozambique and east South Africa	1991, 1999-2003	151	486	65	0.979 (0.004)	0.020 (0.010)	(Rosenbaum *et al.*, 2009)
	Mayotte and Geyser, Comoros	1997-2003	78	486	32	0.974 (0.006)	0.021 (0.001)	(Rosenbaum *et al.*, 2009)
	Madagascar	1996-2001	511	486	93	0.978 (0.002)	0.021 (0.011)	(Rosenbaum *et al.*, 2009)
Northern Indian Ocean	Oman	2001-2002	38	486	8	0.691 (0.052)	0.018 (0.009)	(Rosenbaum *et al.*, 2009)
Southeastern Indian Ocean	West Australia	1990, 1993-1994, 2002	174	470	53	0.970 (0.004)	0.020 (0.010)	(Olavarría *et al.*, 2007)
Southwest and Central South Pacific	East Australia	1992	135	371	42	0.968 (0.004)	0.026 (0.013)	(Valsecchi *et al.*, 2010)
		2002-2003	156	470	42	0.962 (0.005)	0.023 (0.012)	(Olavarría *et al.*, 2006b)
	New Caledonia	1995-2002	250	470	61	0.974	0.021	(Olavarría *et al.*,

						(0.003)	(0.011)	2007)
	Tonga	1991, 1994-2002	310	470	48	0.962 (0.004)	0.020 (0.010)	(Olavarría *et al.*, 2007)
	Cook Islands	1998-2002	131	470	23	0.923 (0.010)	0.019 (0.010)	(Olavarría *et al.*, 2007)
	French Polynesia	1997-2002	99	470	21	0.913 (0.012)	0.019 (0.010)	(Olavarría *et al.*, 2007)
Southeast Pacific	Colombia	1991-1999	148	470	27	0.900 (0.016)	0.019 (0.010)	(Olavarría *et al.*, 2007)
	Ecuador	2002-2007	103	469	29	0.892 (0.023)	0.018 (0.009)	(Félix *et al.*, 2009)
North Atlantic	Dominican Republic (Worldwide consensus)	1992-1993	20	288	11	0.884 (0.040)	0.030 (0.016)	(Palsboll *et al.*, 1995; Baker and Medrano, 2002)
	Dominican Republic (North Atlantic consensus)	---	9	283	--	0.889 (0.091)	0.022 (0.013)	(Baker and Medrano, 2002)
North Pacific	Basin	2004	1856	500	28	--	--	(Baker *et al.*, 2008)
	Philippines	2004	13	500	--	0.628	--	(Baker *et al.*, 2008)
	Okinawa	2004	78	500	--	0.648	--	(Baker *et al.*, 2008)
	Ogasawara	2004	173	500	--	0.864	--	(Baker *et al.*, 2008)
	Hawaii	2004	229	500	--	0.714	--	(Baker *et al.*, 2008)
	Mexico-Revillagigedo	2004	115	500	--	0.857	--	(Baker *et al.*, 2008)

Mexico-Baja	2004	118	500	--	0.890	--	(Baker *et al.*, 2008)
Mexico-Mainland	2004	63	500	--	0.893	--	(Baker *et al.*, 2008)
Central America	2004	37	500	--	0.755	--	(Baker *et al.*, 2008)

TABLE 2: Global estimates of genetic diversity by feeding ground[1]

Feeding ground	Sampling Region	Sampling period	Number of samples	CR length (bp)	Number of haplotypes	Haplotype diversity	Nucleotide diversity	Reference
Eastern South Pacific	Antarctic Peninsula	1989, 1996-1999, 2002	89	470	25	0.915 (0.018)	0.018 (0.009)	(Olavarría *et al.*, 2006a)
	Antarctic Peninsula (west of 60°W)	1999-2000	46	360	17	0.913 (0.021)	0.023 (0.012)	(Engel *et al.*, 2008)
	Antarctic Peninsula (east of 60°W)	1999-2000	31	360	14	0.916 (0.029)	0.025 (0.013)	(Engel *et al.*, 2008)
	Magellan Straits	2003, 2005	52	470	4	0.339 (0.080)	0.010 (0.005)	(Olavarría *et al.*, 2006a)
North Atlantic	Basin	---	63	283	37	0.891 (0.025)	0.021 (0.011)	(Baker and Medrano, 2002)
		1988-1991	246	288	25	0.881 (0.015)	0.023 (0.012)	(Baker and Medrano, 2002; Palsboll *et al.*, 1995; Larsen *et al.*, 1996)
	Norway	1992-1993	35	288	4	0.533 (0.084)	0.008 (0.005)	(Larsen *et al.*, 1996; Baker and Medrano, 2002)
	Iceland (North Atlantic consensus)	1992-1993	90	288	10	0.737 (0.047)	0.015 (0.008)	(Larsen *et al.*, 1996; Baker and Medrano, 2002)
	Iceland (Worldwide consensus)	---	3	283	--	0.667 (0. 314)	0.024 (0.019)	(Baker and Medrano, 2002)
	Eastern Greenland	1992-1993	9	288	--	0.722 (0.098)	0.025 (0.014)	(Baker and Medrano, 2002)

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[1] Analyses of all feeding ground regions are forthcoming in Loo J, Pomilla C, Olavarría C, *et al.* (In Prep-b) Genetic structure of feeding aggregations of humpback whales in the Southern Ocean based on mtDNA and microsatellite variation.

	Western Greenland	1992-1993	44	288	17	0.868 (0.032)	0.027 (0.014)	(Palsboll *et al.*, 1995; Baker and Medrano, 2002)
	Newfoundland	1992-1993	17	288	--	0.816 (0. 082)	0.016 (0.009)	(Baker and Medrano, 2002)
	Gulf of St Lawrence	1992-1993	25	288	15	0.937 (0.032)	0.026 (0.014)	(Palsboll *et al.*, 1995; Baker and Medrano, 2002)
	Gulf of Maine (Worldwide consensus)	---	34	283	--	0.897 (0.028)	0.023 (0.012)	(Baker *et al.*, 1987)
	Gulf of Maine (North Atlantic consensus)	1992-1993	23	288	10	0.822 (0.066)	0.023 (0.013)	(Palsboll *et al.*, 1995; Baker and Medrano, 2002)
North Pacific	Basin	2004	1856	500	28	--	--	(Baker *et al.*, 2008)
	Russia	2004	72	500	--	0.837	--	(Baker *et al.*, 2008)
	Eastern Aleutians	2004	9	500	--	0.972	--	(Baker *et al.*, 2008)
	Bering Sea	2004	117	500	--	0.800	--	(Baker *et al.*, 2008)
	Western Aleutians	2004	36	500	--	0.848	--	(Baker *et al.*, 2008)
	Western Gulf of Alaska	2004	98	500	--	0.845	--	(Baker *et al.*, 2008)
	Northern Gulf of Alaska	2004	231	500	--	0.779	--	(Baker *et al.*, 2008)
	Southeast Alaska	2004	185	500	--	0.480	--	(Baker *et al.*, 2008)
	Northern BC	2004	109	500	--	0.547	--	(Baker *et al.*,

							2008)
Southern BC-Washington	2004	51	500	--	0.831	--	(Baker *et al.*, 2008)
California-Oregon	2004	123	500	--	0.827	--	(Baker *et al.* 2008)

TABLE 3a: Levels of mitochondrial control region genetic differentiation among breeding grounds and migratory corridors in the North Pacific (Information currently unavailable for North Atlantic)

All values shown are pair-wise F_{ST} values for frequencies of control region haplotypes of humpback whale mtDNA. **Bold** indicates significance at 0.05 while empty fields indicate inadequate sample sizes for this comparison.

North Pacific

	Philippines	Okinawa	Ogasawara	Hawaii	Mex-Revillagigedo	Mex-Baja	Mex-Mainland	Central America
Philippines	--							
Okinawa		--						
Ogasawara		**0.032**	--					
Hawaii		**0.236**	**0.142**	--				
Mex-Rev		**0.128**	**0.046**	**0.043**	--			
Mex-Baja		**0.120**	**0.044**	**0.054**	0.003	--		
Mex-Main		**0.202**	**0.093**	**0.084**	**0.032**	0.005	--	
Cent. America		**0.454**	**0.328**	**0.282**	**0.223**	**0.148**	**0.068**	--

(From Baker *et al.*, 2008)

TABLE 3b: Levels of mitochondrial control region genetic differentiation among breeding grounds and migratory corridors in the Southern Hemisphere.

Above diagonal shows F_{ST} values, below diagonal shows ϕ_{ST} values (using unadjusted pair-wise distances) over 5,000 non-parametric random permutations of the data matrix (20,000 permutations used for (4)). Values shown in bold are significant ($p < 0.05$), while values on the diagonal represent the sample size for each comparison. Boxes shaded red indicate comparison not done.[2]

	BR	GA	WSA*	MOZ	COM	MAD	OMN	WA*	EA*	NC	TG	CI	FP	COL	ECU
Abrolhos Bank, Brazil (BR)^{1,2}	N=164^{1}	**0.007**^{1}	**0.010**^{1}	**0.015**^{1}	**0.017**^{1}	**0.012**^{1}	**0.147**^{1}		🟥						🟥
Gabon and Cabinda (GA)^{1,2}	**0.004**^{1}	N=477^{1}	**0.003**^{1}	**0.006**^{1}	**0.008**^{1}	**0.007**^{1}	**0.130**^{1}		🟥						🟥
West South Africa* (WSA)^{1,2}	0.004^{1}	0.000^{1}	N=108^{1}	**0.006**^{1}	**0.006**^{1}	**0.005**^{1}	**0.128**^{1}		🟥						🟥
Mozambique and east South Africa (MOZ)^{1,2}	0.004^{1}	**0.005**^{1}	0.002^{1}	N=151^{1}	**0.005**^{1}	**0.003**^{1}	**0.126**^{1}		🟥						🟥
Mayotte and Geyser, Comoros (COM)^{1,2}	0.007^{1,2}	0.002^{1}	0.000^{1,2}	0.002^{1}	N=78^{1}	0.002^{1}	**0.118**^{1}		🟥						🟥
Madagascar (MAD)^{1,2}	0.004^{1}	**0.004**^{1}	0.003^{1,2}	0.000^{1}	0.000^{1}	N=511^{1}	**0.116**^{1}		🟥						🟥
Oman (OMN)^{1,2}	**0.103**^{1}	**0.094**^{1}	**0.106**^{1}	**0.095**^{1}	**0.096**^{1}	**0.080**^{1}	N=38^{1}		🟥						🟥
West Australia* (WA)^{2,2}								N=174^{2}	**0.019**^{3}	**0.014**^{2}	**0.016**^{2}	**0.028**^{2}	**0.039**^{2}	**0.058**^{2}	🟥

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[2] A complete analysis of all Southern Hemisphere breeding grounds is forthcoming in Rosenbaum HC, Pomilla C, Olavarría C, *et al.* (In prep) A comprehensive analysis of mtDNA sequences from humpback whales for breeding stocks A-G and X..

	BR	GA	WSA*	MOZ	COM	MAD	OMN	WA*	EA*	NC	TG	CI	FP	COL	ECU
East Australia* (EA)[3]								**0.184**[3]	N=174[3]	**0.011**[3]	**0.019**[3]	**0.042**[3]	**0.052**[3]	**0.062**[3]	
New Caledonia (NC)[2,2]								0.007[2]	**0.006**[3]	N=250[2] N=251[3]	**0.009**[2]	**0.032**[2]	**0.046**[2]	**0.055**[2]	
Tonga (TG)[2,2]								**0.012**[2]	0.002[3]	0.004[2]	N=310[2] N=354[3]	**0.022**[2]	**0.031**[2]	**0.058**[2]	
Cook Islands (CI)[2,2]								**0.014**[2]	**0.010**[3]	**0.013**[2]	0.004[2]	N=131[2,3]	**0.025**[2]	**0.073**[2]	
French Polynesia (FP)[2,2]								**0.032**[2]	**0.030**[3]	**0.028**[2]	**0.025**[2]	**0.020**[2]	N=99[2,3]	**0.079**[2]	
Colombia (COL)[2,2]								**0.038**[2]	**0.047**[3]	**0.041**[2]	**0.044**[2]	**0.054**[2]	**0.045**[2]	N=148[2,3]	0.002[4]
Ecuador (ECU)[4]														0.002[4]	N=103[4]

[1] (486bp, Rosenbaum *et al.*, 2009)

[2] (470bp, Bonferroni correction for multiple comparisons, Olavarría *et al.*, 2007)

[3] (470bp, Olavarría *et al.*, 2006b)

[4] (469bp, Félix *et al.*, 2009)

Table 4a: Levels of differentiation between breeding and feeding grounds in the Northern Hemisphere (**bold** indicates significance at 0.05) All values shown are pair-wise F_{ST} values for frequencies of control region haplotypes of humpback whale mtDNA. **Bold** indicates significance at 0.05. Empty fields indicate inadequate sample sizes for this comparison. (From Baker *et al.*, 2008)

North Pacific

	Russia	W. Aleutians	Bering	E. Aleutians	W. Gulf of AK	N. Gulf Of AK	Southeast Alaska	N. BC	S. BC-Washington	California-Oregon
Philippines	--	--	--	--	--	--	--	--	--	--
Okinawa	**0.031**		**0.200**	**0.283**	**0.130**	**0.198**	**0.577**	**0.497**	**0.127**	**0.360**
Ogasawara	0.002		**0.101**	**0.118**	**0.042**	**0.111**	**0.326**	**0.253**	**0.029**	**0.297**
Hawaii	**0.135**		**0.029**	0.025	**0.033**	0.000	**0.096**	**0.065**	**0.097**	**0.252**
Mex-Rev	**0.042**		0.010	0.008	-0.006	**0.021**	**0.234**	**0.162**	**0.048**	**0.206**
Mex-Baja	**0.042**		0.015	0.002	0.000	**0.032**	**0.246**	**0.176**	**0.045**	**0.152**
Mex-Main	**0.088**		0.018	-0.002	**0.031**	**0.059**	**0.366**	**0.272**	**0.095**	**0.079**
Central America	**0.302**		**0.168**	**0.109**	**0.218**	**0.250**	**0.625**	**0.527**	**0.303**	-0.014

North Atlantic

Values shown are F_{ST} expressed as percent variance and permutation probabilities. (From Baker & Medrano, 2002)

	Variance %	**Permutation Probability**
Among stocks by region [Norway, Iceland] [E.Greenland, W. Greenland, Gulf of St Lawrence, Gulf of Maine]	14.62	0.000
Regions within stocks	5.66	0.000
Among regions (North Atlantic consensus)	20.28	0.000
Among regions (Worldwide consensus)	1.40	0.245
Among stocks	17.17	0.000

TABLE 4b: Levels of differentiation between breeding grounds and feeding grounds in the Southern Hemisphere[3]

	Antarctic Peninsula (AP) N=46[1], 89[2]	Magellan Straits (MS) N=52[2]	Antarctic IWC Area IV 60-120°E (IV)	Antarctic IWC Area VI 180-120°W (VI)
Abrolhos Bank, Brazil (BR)[1] N=171	**0.054[1]**	NA	NA	NA
West Australia* (WA)[2,] N=174[2], 132[4]	**0.044**[2]	**0.292**[2]	0.001[4]	**0.022**[4]
New Caledonia (NC)[2] N=250[2], 368[4]	**0.043**[2]	**0.281**[2]	**0.006**[4]	**0.043**[4]
Tonga (TG) [2] N=310[2], 354[4]	**0.046**[2]	**0.283**[2]	**0.011**[4]	**0.045**[4]
Cook Islands (CI) [2] N=105[4]	**0.057**[2]	**0.325**[2]	**0.035**[4]	**0.058**[4]
French Polynesia (FP) [2] N=99[2], 113[4]	**0.064**[2]	**0.342**[2]	**0.048**[4]	**0.057**[4]
Colombia (COL) [2] N=148[2], 97[4]	0.001[2]	**0.181**[2]	**0.058**[4]	0.001[4]
Ecuador (ECU)[3] N=103[2]	0.002[3]	**0.167**[3]	NA	NA

[1] (Engel *et al.*, 2008)
[2] (Olavarría *et al.*, 2006a)
[3] (Félix *et al.*, 2009)
[4] (Albertson *et al.*, In press)

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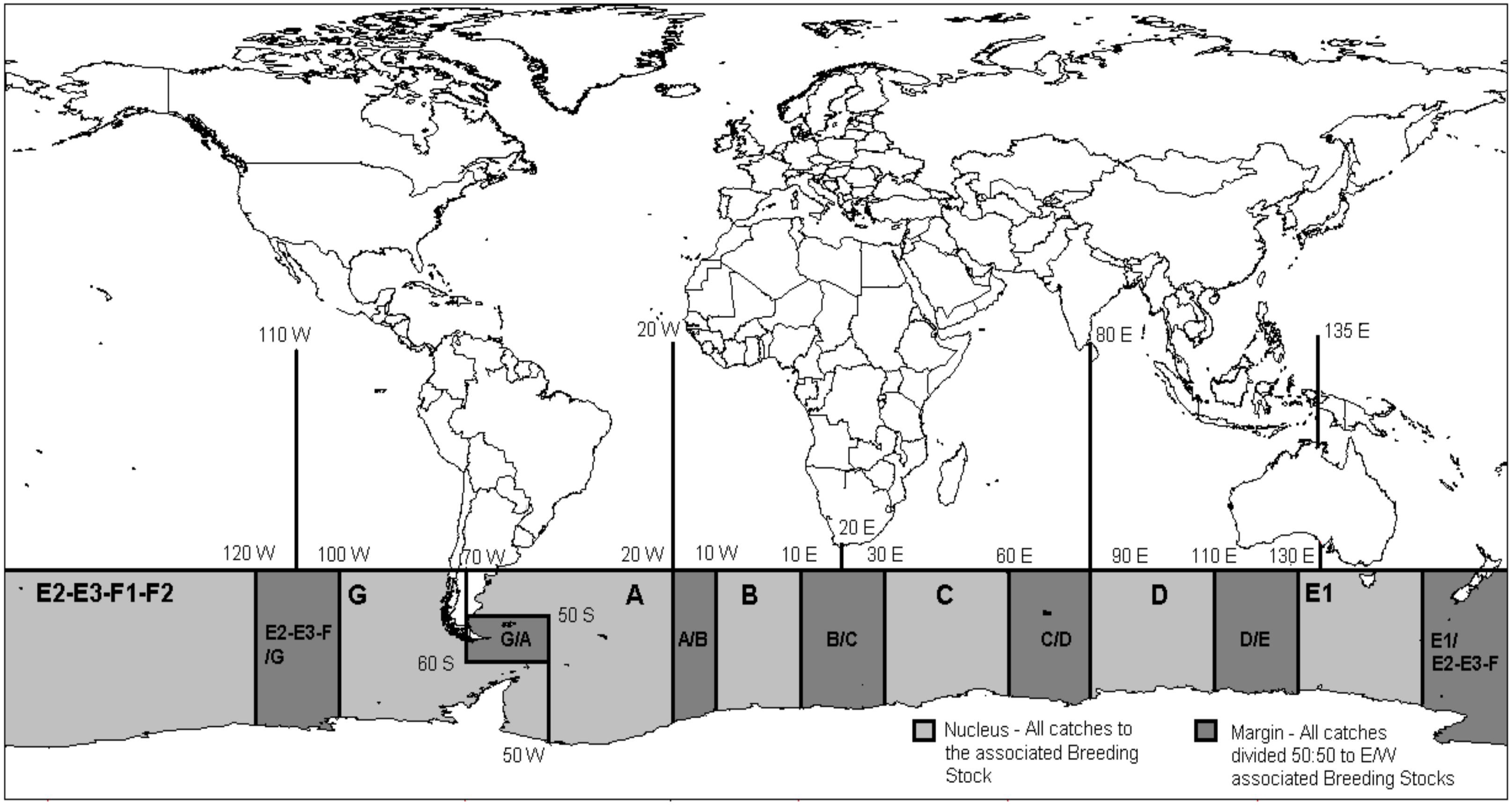
[3] A complete analysis of differentiation between Southern Hemisphere breeding and feeding grounds is forthcoming in Loo J, Pomilla C, Leslie M, *et al.* (In Prep-a) Connectivity between Feeding Areas and Breeding Regions of humpback whales in the Southern Hemisphere based on mtDNA and microsatellite variation.

Table 5: Levels of differentiation between Feeding Areas (**bold** indicates significance at 0.05) (From Baker *et al.*, 2008)

North Pacific

	Russia	W. Aleutians	Bering Sea	E. Aleutians	W. Gulf Alaska	N. Gulf Alaska	Southeast Alaska	N. British Columbia	S. British Columbia/WA	California/ Oregon
Bering	**0.094**		**--**							
E. Aleutians	**0.114**		-0.012	**--**						
W. Gulf Alaska	**0.039**		0.012	0.010	**--**					
N. Gulf Alaska	**0.105**		0.013	0.007	**0.014**	**--**				
Southeast Alaska	**0.389**		**0.242**	**0.343**	**0.220**	**0.116**	**--**			
N.British Columbia	**0.293**		**0.174**	**0.245**	**0.148**	**0.080**	0.003	**--**		
S. British Columbia/WA	**0.038**		**0.088**	**0.104**	**0.035**	**0.076**	**0.314**	**0.223**	**--**	
California/ Oregon	**0.268**		**0.157**	**0.108**	**0.202**	**0.229**	**0.478**	**0.401**	**0.268**	**--**

B) APPENDIX 2. Figure reproduced from (IWC, In Press) showing Southern Hemisphere locations of stocks A to G. Longitudinal boundaries encompass Antarctic feeding areas considered associated with those stocks.



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XV LITERATURE REVIEW

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