

## WHY DO BALEEN WHALES MIGRATE?<sup>1</sup>

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### ABSTRACT

The annual migrations of baleen whales are a conspicuous but unexplained feature of their behavioral repertoire. Some hypotheses offered to explain whale migration focus on direct benefits to the calf (thermoregulation, calm water) and some do not (resource tracking, and the “evolutionary holdover” hypothesis). Here, we suggest that a major selective advantage to migrating pregnant female baleen whales is a reduced risk of killer whale (*Orcinus orca*) predation on their newborn calves in low-latitude waters. Killer whale abundance in high latitudes is substantially greater than that in lower latitudes, and most killer whales do not appear to migrate with baleen whales. We suggest that the distribution of killer whales is determined more by their primary marine mammal prey, pinnipeds, and that following the baleen whale migrations

<sup>1</sup> Through his teaching and writing, Ken Norris inspired us to ask the “why” questions about nature; thus we dedicate to Ken our effort to understand why baleen whales migrate. During our literature search we were delighted to find an unpublished manuscript by Norris, written in the early 1980s, that anticipates some of the ideas reviewed here. We include two insightful quotes from that manuscript, titled “Broad Patterns of Cetacean Zoogeography and Evolution.” Our answer to the migration question provides another link to Norris—an observation by one of us (Connor) in the spring of 1982, during Ken Norris’s Natural History of California Field Class, that forcefully brought home the magnitude of the threat killer whales present to baleen whales and their young. Hiking along Donner Ridge, over 200 m above the Big Sur coast line, we spotted a group of killer whales milling close to shore. Just what the killer whales were doing was unclear until, some minutes later, a bloodied gray whale surfaced in their midst. Ken, waylaid by a nasty flu, staggered up to the cluster of undergraduates glued to their binoculars, and still had enough presence of mind to remark that the unfortunate gray was unusually far out from the kelp bed. On their return migration north after breeding in protected Mexican lagoons, the gray whales, with newborns in tow, must run a gauntlet of killer whales to return to their summer feeding grounds. As we witnessed, not all make it through safely. Those same killer whales, we argue in this review, may provide the primary selection pressure for the migration itself.

would remove them from their pinniped prey. There are problems with all current hypotheses, most of which stem from a lack of directed research. We explore variation in migratory habits between species, populations, and individuals that may provide a "natural laboratory" for discriminating among the competing hypotheses.

Key words: mysticetes, migration, predation, *Orcinus orca*.

Migration involves persistent movement between two destinations. The migrations of baleen whales include the longest known annual movements of any mammal (Stone *et al.* 1990) but remain poorly understood. What makes baleen whale migrations particularly interesting is that, for at least a few species, nutritional resources cannot be invoked as the primary reward for arriving at one of the two destinations. In contrast, such resources (food, water or particular nutrients) are typically held to be of primary importance for arrivals at both destinations in the long-distance seasonal migrations of terrestrial mammals (*e.g.*, Fryxell 1995, Murray 1995).

In general, baleen whale migrations are seasonal movements between productive high-latitude feeding grounds and low-latitude breeding grounds. The selective forces favoring baleen whales' use of polar feeding grounds are easily understood and not controversial (Norris 1967, Laws 1985, Tynan 1998). The component of baleen whale migrations that has eluded satisfactory explanation is why some whales travel to warm-water breeding grounds. We consider separately explanations relating to adult behaviour and calf survivorship. Before evaluations of the various hypotheses, we consider whether there is a cost to whales that migrate.

#### IS MIGRATION COSTLY?

"The great migratory distances covered by most baleen whales are probably of only modest importance to their energetics today. The animals, because of their large body size, conserve heat easily, and whether they swim wholly at the poles, or in a migratory path, may involve much the same expenditure for locomotion."

Kenneth S. Norris<sup>1</sup>

As Norris recognized, although baleen whales may travel considerable distances during migration, it remains unclear whether this is physiologically demanding compared to the alternative of not migrating. This issue was brought to our attention by Giuseppe Notobartolo di Sciara,<sup>2</sup> who suggested that there may be no additional energy cost to migrating in a straight line compared to the likely alternative, which is travel in many directions.

Undisturbed fin whales, *Balaenoptera physalus*, on the Mediterranean summer feeding grounds average 4 km/h (Notobartolo di Sciara *et al.* 1997), far faster than the average daily speed (1.5 km/h), but slower than the fastest recorded

<sup>2</sup> Personal communication from Giuseppe Notarbartolo di Sciara, Istituto Centrale per la Ricerca Applicata al Mare, Via di Casalotti 300, 00166 Rome, Italy. Communication by e-mail, 26 April 1998.

daily speed (5.9 km/h) of a fin whale satellite-tracked off Iceland (Watkins *et al.* 1996). We are unaware of any direct measurements of the migrating speeds of individual fin whales, but 4 km/h is comparable to the speeds of individual humpback whales, *Megaptera novaeangliae* (4–4.5 km/h, Mate *et al.* [1998]), and gray whales, *Eschrichtius robustus* (4–5 km/h, Mate and Harvey [1984], and 5.9–6.3 km/h, Swartz *et al.* [1987]) on migration.

However, it is important to consider what alternative behaviors might whales engage in while “traveling in many directions.” Instead of migrating to resource-poor, low-latitude lagoons or islands for the benefit of a newborn calf (reproductive effort), pregnant baleen whales could travel to areas with sufficient resources to feed (somatic effort). It is possible that individuals of species such as the blue whale, *Balaenoptera musculus*, whose winter migratory destinations are poorly known, do just that (*e.g.*, Reilly and Thayer 1990). If the alternative to migrating to breed is traveling to feed, then there is a clear opportunity cost associated with migration to resource-poor areas.

#### BENEFITS TO MIGRATING ADULTS

##### *Brodie's Hypothesis*

The most popular explanation for mysticete migration has been that of Brodie (1975). This hypothesis, aspects of which were further developed by Kshatrya and Blake (1988), holds that mysticetes' energy budgets are optimized by migrating to warm waters during the winter, when prey is relatively scarce and temperatures are at their lowest in polar waters. Other modelling studies do not support Brodie's original hypothesis (Lavigne *et al.* 1990, Ryg *et al.* 1993, Watts *et al.* 1993) and indicate that most mysticetes do not optimize their energy budgets by migration.

##### *Evolutionary "Tradition"*

Evans (1987) suggested that migration is a vestigial behavioral left over from a past era when continents were closer together and noted that this “postulates that there are no strong selection pressures favouring breeding in equatorial waters.” Observations that some individuals of migratory species do not migrate every year allow us to dismiss this hypothesis, as selection will operate on such behavioral variation. Some female humpback whales (Brown *et al.* 1995, Craig and Herman 1997) southern right whales, *Balaena glacialis australis* (Payne 1986), and juvenile humpback whales of unknown sex (Straley 1990, Clapham *et al.* 1993, Swingle *et al.* 1993) do not undertake a complete migration to low latitudes each year. There are several records of minke whales within the antarctic pack ice over the winter (Taylor 1957, Ribic *et al.* 1991, Hobson and Martin 1996, Gill and Thiele 1997). Earlier this century, fin whales were killed off the west coast of Norway in winter (Ingebrigtsen 1929). There were early reports of blue, fin, and humpback whales wintering on the Grand Banks, off Newfoundland (Millais 1906, cited in Jonsgård 1966). Blue,

fin, or humpback whales were sighted south of the Antarctic Convergence in winter (Mackintosh and Brown 1956).

### *Resource Tracking*

Payne (1995) suggested that whales can reduce their period without food by feeding on plankton in mid-latitudes, which become (or remain) available in these latitudes when food is unavailable in polar waters. This hypothesis may apply to right whales, which apparently feed during the breeding season in at least one area (Payne 1995), and perhaps some of the larger balaenopterids whose breeding habits and location remain unknown (*e.g.*, Reilly and Thayer 1990). It seems less plausible for the two species whose migration is most well known, the gray whale (Nerini 1984) and humpback whale (Clapham 1996), which rarely feed on or near breeding grounds. This hypothesis is also weakened as a general explanation by the recent observations that some minke whales (Taylor 1957, Ribic *et al.* 1991, Hobson and Martin 1996, Gill and Thiele 1997) and humpback whales (Christensen *et al.* 1992) are in polar waters over winter.

### *Calf Growth and Survivorship*

The remaining hypotheses assume that parturition drives migration. From what is known about calf mortality in mysticetes, it appears likely that the calves are at greatest risk during the first couple of weeks *postpartum* (*e.g.*, Eberhardt and Norris 1964, Pacheco 1998) while newborn whales are still in or near their birth location. Although most mating occurs on or near breeding grounds in many species, there is no obvious reason why mating could not take place at high latitudes. Thus the focus of our inquiry is how females benefit from giving birth in warm, low-latitude waters instead of on or near high-latitude feeding grounds. From the female's point of view, migration will be favored if she has more grand-offspring by migrating than if she does not. Males are not the focus of this review but are likely to migrate for the opportunity to encounter estrous females on the breeding grounds. Animals ovulating *postpartum* can account for a significant proportion of the female population—approximately 18% of the pregnant population in fin whales (Locker 1984).

We review the remaining hypotheses for baleen whale migration: calf thermoregulation and the need for calm water. Additionally, we suggest that a neglected factor favoring migration to low-latitude waters is a reduced risk of predation on neonates by killer whales, *Orcinus orca* (*e.g.*, Payne 1995).

*Calf thermoregulation*—A common variant of Brodie's hypothesis focuses on thermal benefits of migration to calves rather than mothers (*e.g.*, Norris 1967, Horwood 1987, Clapham 1996, Dingle 1996). Physiologically, the benefit to calves of migrating mothers could range from survival—if calves are physiologically incapable of living in polar waters (*e.g.*, Kshatrya and Blake 1988)

to more rapid development, because energy that could be expended for heat production by neonates in cold water is used in warm water for growth.

Although some species of smaller odontocetes give birth in polar waters, Dingle (1996) suggested that such species "have evolved efficient heat-conservation mechanisms in the young, unlike mysticetes." This statement is less than satisfying, because it implies that there is some unknown constraint on mysticete thermoregulation. Alternatively, heat production may be higher in small odontocetes that have higher active metabolic rates related to their diet. Another factor may be a lower cost of travel for large-bodied mysticetes that renders migration more efficient than the cost of employing some "other mechanisms." However, such differences between odontocetes and mysticetes may be irrelevant in view of recent models of calf thermoregulation.

Over 30 yr ago Kanwisher challenged the thermoregulation hypothesis, "The young of the largest species [of baleen whales] are theoretically insulated sufficiently for the coldest seas" (Kanwisher and Sundnes 1966). More recent modelling supports Kanwisher's assertion. Baleen whale calves larger than those of minke whales, *Balaenoptera acutorostrata*, (almost all baleen whales, Leatherwood *et al.* 1983) should be thermoneutral in the coldest marine waters on earth (Watts *et al.* 1993).

The models predicting "lower critical temperatures" for baleen whale neonates are somewhat sensitive to estimates of parameters such as insulation capacity and metabolic rates. For example, lower than expected metabolic rates would increase the "lower critical temperature" estimates in the models of Watts *et al.* (1993), possibly to the point where birth in cold water would necessitate diverting energy from growth and development to heat production in favor of the calf thermoregulation hypothesis. Data on neonate metabolic rates and thermoregulation could be obtained from neonates held for rehabilitation (Heyning and Mead 1997) and anatomical work on calves stranded or taken by indigenous fisheries (*e.g.*, George *et al.* 1994).

*Calm water—*

"It is worth noting that very few cetaceans seem wholly free of the need to inhabit at least relatively calm waters during their calving season . . . the great whales may undergo migratory movements that may bring them into relatively calm water at this time."

Kenneth S. Norris<sup>1</sup>

Norris and others have recognized that a preference for giving birth in relatively calm low latitudes could favor migration in baleen whales (Whitehead and Moore 1982, Payne 1995). Humpback whale females with calves in the Caribbean appear to prefer waters in the lee of coral reefs, which may provide an easier environment for calves to swim in (Whitehead and Moore 1982). Female-calf pairs occurred in shallower waters near shore than did other whales off Hawaii (Smultea 1994). While high-latitude storms might present a threat to calf survival (see description in Payne 1995) the hypothesis can be made more general by invoking energy savings to calves surfacing in calm versus stormy waters (Whitehead and Moore 1982).

We raise two questions regarding the viability of the "calm water" hypoth-

esis. The first, based on the observation that some smaller odontocetes live in high latitudes, parallels an argument against the "calf thermoregulation" hypothesis. Is it reasonable to suggest that the benefit to a calf born in calmer tropical waters versus stormy high latitudes outweighs the travel costs for large whales but not smaller odontocetes that live, and in some cases give birth, in high latitudes? Second, why travel to tropical or equatorial waters for a resource which may be on the feeding grounds? Suitable protected areas may be available in polar waters around the pack ice edge, or in cold-temperate waters in the lee of land or rocky reefs.

*Killer whale predation*—We suggest that reduced predation risk from killer whales, which are abundant at high latitudes, provides the primary fitness benefit to female baleen whales leaving polar waters to give birth in the tropics. This idea has been suggested previously (*e.g.*, Payne 1995) but remains undeveloped. Other known baleen whale predators including the great white shark, *Carcharodon carcharias*,<sup>3</sup> tiger shark, *Galeocerdo cuvier*, (PJC, personal observation of Queensland Museum specimen JM7303 [Paterson and van Dyck 1991, figure 5]), and false killer whale, *Pseudorca crassidens*, are absent from polar waters (Leatherwood *et al.* 1983, Last and Stevens 1994).

Predators such as tiger sharks and false killer whales may threaten newborn calves of baleen whales in tropical waters. Thus, more specifically, we are suggesting that the risk of predation on newborns calves from high-latitude killer whales is sufficiently greater than the risk from warm-water predators to favor migration to the tropics for parturition. However, the relative risk from tropical sharks versus killer whales may change with size, and baleen whales span a large size range. Minke whales reach sexual maturity at approximately 7 m, (Stewart and Leatherwood 1985), little larger than a newborn blue whale (6–7 m, Yochem and Leatherwood 1985). Blue whales may be much more effective than minke whales at defending their calves from large sharks but only marginally better at defending calves from group-hunting killer whales. If so, then the relative benefit of migration—of trading the threat of killer whales for tropical sharks—may be greater for larger than smaller species.

The problem of estimating the global threat to baleen whales from killer whales is exacerbated by the phenomenon of dietary specialization among populations of killer whales. Two genetically distinct, sympatric populations of killer whales in the waters off British Columbia exhibit pronounced dietary differences. The "transient" form specializes on marine mammals, but "resident" killer whales are piscivorous (Bigg 1982, Baird *et al.* 1992). An apparently similar pattern has been reported from the Southern Hemisphere (Mikhalev *et al.* 1981).

Densities of killer whales in polar waters appear substantially higher than in tropical waters. Hammond (1984) gives estimates from vessel-based line transect surveys in antarctic waters of 180,000 (179,708, SD = 106,323) killer

<sup>3</sup> Personal communication from Steven Burnell, Department of Veterinary Anatomy, University of Sydney, Sydney, NSW 2006, Australia. Communication by e-mail, April 1997.

whales in 6,929,995 km<sup>2</sup>, a density of approximately 26 whales per 1,000 km<sup>2</sup> (figures taken from Hammond, tables 3 and 4, areas converted to km<sup>2</sup> from nm<sup>2</sup>). Using similar techniques in the eastern tropical Pacific (ETP), Wade and Gerrodette (1993), estimated there were 8,500 killer whales (CV = 0.368) in 19,148,000 km<sup>2</sup>, or approximately 0.44 whales per 1,000 km<sup>2</sup>. Although we cannot distinguish mammal from fish-eating specialists in these estimates, the huge disparity in abundance suggests a greater risk to baleen whale young in high latitudes.

Why don't mammal-eating killer whales follow the whale migrations to feed on this seasonal abundance of neonates? Some may do so. Soviet whaling data suggest that some killer whales undergo annual migrations to at least temperate latitudes (Budylenko 1981, Mikhalev *et al.* 1981). Three "transient" killer whales are known to have moved 2,660km along the Pacific coast of North America, from 58°41'N to 36°48'N over three years (Goley and Straley 1994). Killer whales are observed occasionally off the coast of southeast Queensland, Australia, at the same time that humpback whales migrate through the area (Paterson 1987).

Movements of killer whales along the North American west coast may be at least partially in response to the presence of migrating gray whales. There are several reports of killer whales attacking gray whales, including females with calves, while on migration (*e.g.*, Rice and Wolman 1971, Baldrige 1972, Poole 1984, Goley and Straley 1994). Gray whale females and neonates occupy the innermost reaches of the breeding lagoons (Swartz 1986), which, coupled with migration, appears to be a generally effective strategy for removing neonates from the threat of killer whale predation during the first few weeks of life. We are aware of two records of gray whale deaths in the calving lagoons due to killer whale attacks, (Scammon 1874, cited in Rice and Wolman 1971, Jones and Swartz 1984). Observations of dead stranded gray whales in the Chukchi and Beaufort Seas suggest that killer whales preferentially prey on younger animals in Arctic waters (George and Suydam 1998).

It seems unlikely, however, that hundreds of killer whales descend upon breeding grounds to prey upon baleen whale neonates. We suggest two reasons for this. Travel costs decrease with increasing body size, so migrating a given distance will be more energetically demanding for killer whales than for the larger baleen whales. More important we suspect, is the primary dependence of mammal-eating killer whales on pinnipeds. Thus the distribution and abundance of pinnipeds (especially pups) will dictate the distribution and movements of mammal-eating killer whales (*e.g.*, Baird *et al.* 1992). Pinnipeds are relatively rare in tropical waters and are common in lower latitudes only in productive areas. However, millions of pinnipeds occur in polar and cool temperate waters (Ridgway and Harrison 1981*a, b*).

We suggest that pursuit of migrating baleen whales into tropical waters would take killer whales away from their primary pinniped prey. Currently, the proportion of polar populations of killer whales that migrate or the extent of their migrations is unknown. However, some killer whales overwinter in polar waters (Taylor 1957, Leatherwood *et al.* 1984, Heide-Jørgensen 1988,

Gill and Thiele 1997), and large populations of killer whale prey (Leatherwood *et al.* 1983) remain in high latitudes over the winter.

We surmise that if calving occurred in polar waters, killer whales would preferentially feed on young baleen whale calves, as the calves would represent a large individual prey item that is relatively easy to subdue. Large mammalian predators change prey preferences in response to changes in prey vulnerability, (Corbett and Newsome 1987, Mills *et al.* 1995), and the idea that smaller baleen whales are more at risk of predation by killer whales than are larger whales is not new (Chittleborough 1953, Dolphin 1987).

We also point out that, although migration between high and low latitudes is the focus of this paper, other regions of the ocean may offer a similarly reduced risk of killer whale encounter. The biologically unproductive regions in the oceanic gyres in temperate latitudes might be readily accessible to large balaenopterids such as fin and blue whales whose widely dispersed nature would not present an attractive target to killer whales. However, breeding locations for these species remain to be established.

#### TESTING HYPOTHESES

What data are needed to assess the predation hypothesis? We identify critical variation in species, populations and possibly individuals within populations that might provide natural "field tests" of hypotheses for whale migration.

##### *Variation Between Species: the Bowhead Whale*

Bowhead whales are the prominent exception to the general pattern of baleen whales calving in warm, calm water. Bowheads are further distinguished from similar sized right whales (their nearest relatives) by their strong association with ice (Moore and Reeves 1993), thicker blubber layer (Lowry 1993), slow growth rates, later maturation (Zeh *et al.* 1993) and a very long lifespan (George *et al.*, in press). Bowhead whales may also feed more during late autumn and winter months than other species (Schell and Saupe 1993). How do these unique characteristics of bowheads mesh with hypotheses for migration?

While most other large Northern Hemisphere baleen whales are wintering in warm temperate or tropical waters, Bering Sea bowhead whales remain in areas with heavy ice cover (Moore and Reeves 1993). Bowhead whales are preyed upon by killer whales (Philo *et al.* 1993). Mitchell and Reeves (1982) have suggested that killer whale predation may account for the failure of one bowhead population to recover from whaling. The ability of bowheads to travel under ice and to break through ice at least 20 cm thick for breathing may provide them with a partial refuge from killer whales (Nerini *et al.* 1984, Philo *et al.* 1993). To be an effective alternative to migration does not require that ice cover confer immunity to killer whale attack, only that it reduces the risk. George *et al.* (1994) have suggested that the springtime bowhead mi-



gration from the highly productive Bering sea to the Beaufort sea may be to escape killer whale predation. Females should seek well-protected areas (perhaps polynyas?) in which to give birth, but relevant observations are non-existent (Moore and Reeves 1993). The general association between the distribution of bowheads and ice cover declines to a minimum 2–5 mo after the peak birthing period (Moore and Reeves 1993). This suggests a peak period of vulnerability that may be similar to that faced by gray whale calves on the return migration up the California coast (Goley and Straley 1994). Support for the ice-as-alternative-refuge hypothesis would come from observations of ice-seeking behavior by bowheads that detect killer whales (*e.g.*, Reeves and Mitchell 1988) and of mothers with newborn calves remaining in closer association with ice than other whales. However, such evidence does not answer the question of why bowheads do not migrate to warmer latitudes in the first place.

Late maturation and a long lifespan is expected to correlate with reduced exposure to environmental challenges such as predation risk (Austad and Fischer 1991). A reduced predation risk on large bowhead whales could account for their unusual life history characteristics but would be irrelevant for the predation hypothesis which focuses specifically on predation risk to young calves.

An adaptation to lower levels of energy for growth and reproduction might also explain bowhead life history characteristics, if age-specific reproductive effort is reduced (Austad 1997). This could be due to either a lower rate of energy intake, a greater metabolic expenditure for thermoregulation and possibly a greater energy expenditure dealing with rough seas. A lower energy intake would increase the relative costs (if there are any) of migration compared to other species, but whether this was a factor originally disfavoring migration, or a strategy favored once year-around pagophilly was established, would be difficult to determine.

The “calf thermoregulation” hypothesis predicts that newborn bowhead whales will have a thicker blubber layer than newborn right whales, a more rapid growth of the blubber layer (probably at the expense of rapid growth in length), and other anatomical and physiological adaptations for thermoregulation. There are insufficient data on the masses and blubber layers of neonatal right and bowhead whales upon which to draw conclusions.

#### *Variation Between Populations: Right Whales*

Interpopulation variation in migratory habits might allow researchers to distinguish among the hypotheses for whale migration. For example, the wintering grounds of southern right whales occur across more than 20° of latitude, from the Auckland Islands south of New Zealand (51°S) to the Head of the Great Australian Bight (31°30'S). Although one is well south of the other, both are close to (relatively small) sea lion colonies (Reeves *et al.* 1992, Dennis and Shaughnessy 1996), as is at least one other wintering ground (Península Valdés, Argentina 42°30'S [Lopez and Lopez 1985]). Predators have been ob-

served in these areas: killer whales at Península Valdés (Payne 1995) and great white sharks at the Head of the Bight.<sup>3</sup> These sites, along with the calving grounds in South Africa (approximately 34°30'S) vary in their distance to the large populations of killer whales in antarctic waters. Water temperatures and sea conditions vary between these sites, from approximately 23°C and 6–7 m/sec (17–20 km/h, wind velocity used as an indicator of sea state) at the Head of the Bight to 10°C and 8–9 m/sec (22–25 km/h) at the Auckland Islands (NOAA 1998). Between-sites comparisons of calf growth rates, use of calm waters, and predation rates in their first year of life offer an opportunity to test hypotheses.

*Variation Within a Population? Humpback and Fin Whales off Northern Norway*

In the early days of modern whaling, humpback and fin whales were killed in the late winter and early spring off Finnmark, northern Norway (approximately 70°N; Ingebrigtsen 1929). Ingebrigtsen (1929) recorded two humpback fetuses from females shot on 10 March 1898, as 12 and 14 ft (3.7 m and 4.3 m) in length. As humpback whales are born at 4.1–4.3 m (Lockyer 1984), at least the second fetus must have been very near term. Ingebrigtsen (1929) cited Collett (1912) recording a 14-ft (4.3-m) fetus from a fin whale in March, and that “newly born calves 20 ft [6.1 m] in length were observed in April and June with their mothers.” Fin whales are born at around 6.4 m (Lockyer 1984). As Ingebrigtsen described both humpback and fin whales as “very fat,” it seems unlikely that these were females in poor condition trading off a higher risk of calf predation for possible energy savings. These reports seem to have been ignored in discussions of the reasons for whales’ migrations, yet they raise serious problems for all hypotheses. We address issues relating to humpback whales, as these animals are now well studied in the North Atlantic.

Ingebrigtsen assumed that humpback whales migrated between Finnmark and Iceland. This has been discounted by recent research demonstrating that whales in these two areas are distinct matrilineal groups and that some animals from Finnmark migrate to the Caribbean (Larsen *et al.* 1996, Stevick *et al.* 1998). Humpback whales, including calves, have been observed off the Cape Verde Islands (in the eastern tropical Atlantic) in winter (Reiner *et al.* 1996), another area identified as a possible wintering ground for whales from the eastern North Atlantic (Larsen *et al.* 1996). Could the female humpbacks killed with apparently near-term fetuses migrate to tropical waters in time to give birth? The fastest recorded migration of a humpback whale from feeding to breeding grounds is 39 d, from photo-identification of an animal in the Pacific (Gabriele *et al.* 1996), at an assumed speed of approximately 4.74 km/h. This is comparable to speeds maintained by whales satellite-tagged in the same region (approximately 4.5 km/h, Mate *et al.* 1998). Given these rates of travel, it is difficult to imagine that the females could have reached tropical waters (either the Caribbean or Cape Verde islands) in time to give birth,

especially as calves in the Caribbean are mostly born in February and March (Whitehead 1982). We suggest that the females with near-term fetuses were skipping migration to tropical waters to calve in high latitudes.

Is there any reason to discount Ingebrigtsen's data? More recent work supports some of the other anomalous aspects of his paper. Incidental sightings demonstrate that humpback whales occur in the waters between Bear Island and northern Norway between January and March (Christensen *et al.* 1992). Fin whales with out-of-phase fetuses were found in the Icelandic whale fishery relatively recently (Martin 1982). We consider that there is no reason to ignore Ingebrigtsen's data. These data present problems for all hypotheses regarding migration, unless it is assumed that the observations represent "mistakes" that selection will weed out (by calf death).

The Gulf Stream eddies to the waters off Finnmark, and so the sea is not frozen there as it is at comparable latitudes elsewhere (*e.g.*, off Siberia or Alaska) in winter. However, water temperatures off Finnmark in late winter and early spring (3°–4.5°C) are extremely low when compared with those of known humpback whale calving grounds, for example in Caribbean waters in January–March (Whitehead and Moore 1982, Clapham *et al.* 1993), where sea surface temperatures are in the mid-20s. Wind strengths off Finnmark in late winter and early spring are around 7–8 m/sec, comparable to 6–7 m/sec in the West Indies in January–March (NOAA 1998). However, wind strengths are probably poor indicators of the availability of calm water off both the West Indies and Finnmark. The protection for calves offered by islands and rocky reefs off Finnmark may be comparable to that provided by coral reefs in the West Indies.

The Finnmark observations appear to contradict the predation-hypothesis prediction that killer whales should seek out baleen whale neonates born in polar waters. We are unaware of data on predation by killer whales on neonates in Finnmark waters late last century. Although recent work on killer whales elsewhere in Norwegian waters suggests that marine mammals are an insignificant component of their diet (Similä *et al.* 1996), the distribution of mammal-eating whales off the entire Norwegian coastline at present and in the latter part of last century is unknown.

Unfortunately, all aspects of the Finnmark ecosystem have been perturbed. Baleen whales were hunted to low numbers (*e.g.*, Christensen *et al.* 1992), killer whales in Norwegian waters were hunted until the early 1980s (Øien 1988), herring stocks off Norway have been heavily fished (Similä *et al.* 1996) and the Barents Sea capelin (*Mallotus villosus*) stock, on which the humpback whales were feeding (Ingebrigtsen 1929) crashed in the mid-1980s (Christensen *et al.* 1992). Currently there are no reports of whales off the Finnmark coast in late winter and early spring.<sup>4</sup>

<sup>4</sup> Finn Larson, Danish Institute for Fisheries Research, Department of Marine Fisheries, Charlottenlund Slot, DK-2920 Charlottenlund, Denmark. Communication by e-mail, 12 March 1998.

*Other Non-migratory Balaenopterids*

Non-migratory balaenopterid populations exist in the tropics, subtropics and enclosed seas. Bryde's whales, *Balaenoptera edeni* (Cummings 1985), at least one population of humpback whales (Whitehead 1985, Mikhalev 1997), and fin whales in the Mediterranean Sea (Forcada *et al.* 1996), do not undertake migrations across ocean basins. What rates of predation do these populations experience? How does their reproductive success compare with that of their migratory relatives? How do their calves' growth rates compare with those for migratory animals? Answering these questions should throw further light on factors selecting for migratory behaviour.

## CONCLUSION

We draw two general conclusions from our review of baleen whale migration. First, we reject all of the hypotheses that pose benefits to adults as the primary factor driving migration in well-known species such as the humpback and gray whale. We emphasize that benefits of migration to particular classes of individuals, such as males seeking mates, depend on existing female migration and thus cannot be considered primary factors driving migration. Resource tracking may be a viable hypothesis for poorly known species such as the blue whale.

Second, among hypotheses that focus on calf growth and survival, the two leading candidates are the killer-whale predation hypothesis, developed here, and the calm water hypothesis suggested by Whitehead and Norris. We also caution that the calf-thermoregulation hypothesis, which has fared very poorly in recent models, cannot be considered totally discredited until measurements of neonate insulation capacity and metabolism are made.

We have argued that variation, both between and within species, should be a primary focus for further research into the causes of baleen whale migration. The extent of annual movements varies considerably among baleen whale species, from the relatively sedentary, pagophillic bowheads, through the more mobile right whales to the balaenopterids and gray whales. This variation may, for example, reflect a range of responses to predation: from ice-dependent migrations of bowheads, through the migration of right whales to very shallow temperate waters, to the movement by humpback and gray whales to relatively shallow tropical waters. It is also clear that some species exhibit "partial migration" (see Dingle 1996). Data on the sex, age, condition and behavior of non-migrants will advance our understanding of baleen whale migration considerably.

As baleen whale species vary in many aspects of their life history and behavior, the extent to which each selective force impacts individuals of particular species will differ. While it is certainly possible that some of the factors discussed here and presented as competing hypotheses actually act in concert to favor whale migration, only by developing critical tests that distinguish among the various hypotheses will progress in the understanding of whale

migration be achieved. We have raised some initial suggestions for hypothesis testing that we hope will provide the stimulus for refining tests.

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