

## WHY DO BALEEN WHALES MIGRATE?

### A RESPONSE TO CORKERON AND CONNOR

In an effort to stimulate debate, Corkeron and Connor (1999) provide a valuable summary and critique of existing hypotheses regarding the long-standing mystery of why some baleen whales undertake extensive seasonal migrations into biologically unproductive waters. More or less convincingly, they dismiss existing arguments and propose instead that migration evolved as a predator-avoidance strategy. They suggest that, by migrating to tropical or subtropical waters during the winter calving season, whales remove themselves and their vulnerable offspring from the high-latitude range of most killer whales (*Orcinus orca*). Here, I examine this idea further and suggest that predation is unlikely to be the primary force influencing mysticete migratory behavior.

Since a great deal more is known about the migratory patterns of humpback whales (*Megaptera novaeangliae*) than those of any other mysticete (Clapham and Mead 1999), I use this species as the exemplar in the following discussion, with the North Atlantic taken as a representative population. However, I recognize that major ecological differences exist among species and that generalizations from humpbacks to other members of this taxon may not be appropriate.

As noted by Corkeron and Connor (1999), humpback whales undertake a well-documented migration from summer feeding areas in temperate or polar waters to tropical or subtropical wintering grounds, where they calve and mate. Although not all individuals migrate every year (*e.g.*, Brown *et al.* 1995), it is clear that a large proportion of the population generally does. The migration includes whales of both sexes and all maturational classes (Chittleborough 1965, Dawbin 1966). In the North Atlantic, humpbacks segregate in summer to specific high-latitude feeding grounds, including the Gulf of Maine, the Gulf of St Lawrence, Newfoundland/Labrador, Greenland, Iceland, and Norway. In winter, whales from all six feeding grounds mix spatially and genetically on a common breeding range in the West Indies (Katona and Beard 1990, Palsbøll *et al.* 1997).

The predation hypothesis advanced by Corkeron and Connor (1999) hinges upon two primary assumptions. First, that the abundance of transient-type killer whales (*i.e.*, those which feed on marine mammals, Bigg 1982) is sufficiently low in low latitudes to minimize the probability of predatory encounters in winter; and second, that humpbacks are a regular target of killer whales, and that lethal attacks occur with sufficient frequency for this predation to have become a selective force.

I do not disagree with Corkeron and Connor that killer whales are more abundant in high latitudes, where the biomass of potential prey is considerably greater than elsewhere. However, their presence in tropical and even equatorial waters is well established (Leatherwood and Reeves 1983, Katona *et al.* 1988, Flórez-González *et al.* 1994, Smith and Whitehead 1999). The available information suggests that those killer whales found in the humpback whale's primary North Atlantic breeding grounds (the West Indies) are transient-type animals (Katona *et al.* 1988, Mitchell and Reeves 1988). If humpback whales truly represent a significant diet item for this species, it is difficult to explain why killer whales are rarely, if ever, observed in association with major humpback aggregations in winter. To take the most obvious example, the spectacularly high seasonal abundance of humpbacks and humpback calves on Silver Bank (see Winn *et al.* 1975, Whitehead and Moore 1982, Smith *et al.* 1999) should make this habitat the restaurant of choice for any mysticete predator. The reduced abundance of killer whale prey in the tropics should be all the more reason for killer whales to seek out aggregations of humpback whale calves. Furthermore, since humpback song is virtually ubiquitous in the region during winter (Winn and Winn 1978), this should represent a powerful acoustic cue to killer whales regarding the location of large aggregations of whales. Yet little interaction occurs between the two species.

There is little doubt that humpbacks are sometimes attacked by killer whales, although the key point here is the frequency with which serious (*i.e.*, potentially lethal) attacks occur; this is not at all clear. Teeth marks or bites consistent with the dentition of killer whales are commonly observed on humpback whale tails, and occasionally on other body parts; Katona *et al.* (1980) found these features on a third of the humpbacks photographed in the western North Atlantic. However, observations of actual attacks are extremely rare in the North Atlantic or elsewhere. In the Gulf of Maine (a feeding ground), a long-term study has monitored individually identified humpback whales on an almost daily basis from spring through autumn for over 20 yr (Clapham *et al.* 1993). Despite this high effort, there are no records of attacks on humpbacks, and very few of the presumed predator itself. Similarly, no killer whales were sighted in 16 winters of study in the major humpback habitats in the West Indies (D. Mattila and P. Clapham, unpublished data). Elsewhere, there are no more than a handful of records of killer whale attacks, only one of which may have resulted in the death of a whale (Flórez-González *et al.* 1994). Were predation a significant source of humpback whale mortality on either breeding or feeding grounds, one would expect to observe predation attempts with at least occasional frequency; on the contrary, such events are extremely rare in virtually all locations where this species has been studied. In many locations the "predator" itself is rarely, or never, observed.

The details of scar acquisition are particularly pertinent in evaluating where humpback whales are most vulnerable to being attacked. It is significant that, in the Gulf of Maine, all but one of the many individuals observed with killer whale scars acquired them prior to our first observation of the animal concerned. That is, only one individual humpback was observed without marks one summer but displayed marks the following year. As I have suggested elsewhere (Clapham 2000), this constitutes compelling evidence that killer whale attacks occur primarily on humpback calves during the calves' first migration from tropical waters to the feeding grounds. A similar suggestion has been made for other humpback populations by Chittleborough (1953) and Dolphin (1987). These data represent a potentially serious problem for Corkeron and Connor's hypothesis, since a strategy which seeks to avoid predation will hardly be adaptive if it involves migration through areas of high predation risk.

That neonatal mortality (whatever the cause) is highest during migration to the feeding grounds is supported by the results of a recent calf mortality study (Gabriele *et al.* 1999). The authors compiled records of mature female humpbacks sighted in Hawaii with a newborn calf in winter, and then later in the same year in Alaska (either with or without the calf). Using these data, calf mortality between breeding and feeding areas was estimated at 17.9%. In contrast, on the Gulf of Maine humpback whale feeding grounds there were no records of mothers losing their calves between successive sightings in a single summer during the past twenty years (Clapham and Mayo 1990; D. Mattila and J. Robbins, unpublished data). Once again it is important to note that the frequency of lethal attacks (whether on migration or elsewhere) is unknown; most of the animals we have recorded exhibit only light scarring suggestive of relatively trivial encounters, although obviously we observe only the survivors.

One can, of course, counter that migration would remain a preferred strategy so long as the mortality from predation was significantly lower than it would be for whales overwintering and calving in high latitudes. As noted above, however, there is little evidence that humpback whales are anything more than a very occasional target of killer whales anywhere. That humpback calves are occasionally killed by killer whales cannot seriously be disputed; but a phenomenon which occurs now and then should not be confused with one recurring so regularly that it becomes an evolutionary force. Typically, taxa suffering high rates of predation exhibit adaptive traits such as a social structure designed in part to thwart predators through increased group size or other behavioral factors (Gosling and Petrie 1981). As humpback whales exhibit no such structure, the role played by predation in shaping the social ecology of this species

appears to be minimal. Of course, avoidance itself could also be considered an adaptive trait.

The selective pressures which caused the adoption by mysticetes of a life history strategy as dramatic as migration and fasting remain unclear. However, I believe that Corkeron and Connor's dismissal of energy factors is premature. While the argument that overwintering in warm low-latitude waters is less costly energywise than remaining in high latitudes when prey are scarce (Brodie 1975, 1977; Kshatriya and Blake 1988) has been characterized as untenable (Lavigne *et al.* 1990, Corkeron and Connor 1999; see also Kanwisher and Sundnes 1966), neither view stands on a firm foundation of data. Specifically, precise values are unavailable for several of the key variables used in the relevant energy equations, and values at the extremes of a plausible range can readily be employed to support opposing conclusions.

I would speculate that the selective force underlying mysticete migration can be found in a tenet given only cursory treatment by Corkeron and Connor (1999, p. 1232): that, for whale calves, energy conserved in warm water during the first months of life is energy that can be devoted to growth and development. If such calves gain a developmental advantage over those born in cold water, this may translate into larger size in adulthood, which in turn may result in higher reproductive success (RS). Such correlations between offspring development and increased RS exist in terrestrial taxa (Trivers and Willard 1973, Clutton-Brock *et al.* 1982). Higher RS can result from either (for larger females) enhanced ability to bear offspring that survive to recruitment, or (for larger males) increased competitive ability within the mating system. If this connection exists in humpback whales, it would have represented a powerful selective force for the evolution of migration. However, I acknowledge that convincing explanations for the evolution of migration await far better data than we currently possess.

As a final note, it is important to emphasize what I believe is the key point in this debate: that increased RS is ultimately what drives the evolution of any behavior, and that RS involves *individuals*, not populations. Accordingly, future efforts to explain mysticete migration should focus not only on variation within and among species (as suggested by Corkeron and Connor) but also, explicitly, on the costs and benefits to individual animals of different sexual and maturational classes. Juvenile animals usually have very different energy and life history requirements than adults (typically, growth and development *versus* reproduction); similarly, the energy needs of a pregnant female are quite different from those of a lactating or resting animal (Lockyer 1981, 1986). Accordingly, it is vain to suppose that identical migratory strategies will be employed by all individuals, and any migration model that does not account for these fundamental life history differences is probably doomed to failure.

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#### PREDATION PAST AND PRESENT:

#### KILLER WHALES AND BALEEN WHALE MIGRATION

We fully agree with Clapham's (2000) "key point," that any theory of whale migration must focus on the costs and benefits to individuals and life history differences among age and sex classes. We see our critical focus on the benefits of migration to newborn infants as an example of this approach. Unfortunately, Clapham seems to have misunderstood our characterization of alternative hypotheses and underestimates the potential of killer whale predation to explain baleen whale migration. In response, we first address our presentation of the energetics model, then consider Clapham's challenges to the killer whale predation model.