



Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males?

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Accepted 25 October 2013; published online 7 December 2013

Abstract

Humpback whales congregate annually in low-latitude winter breeding and calving grounds. While on these grounds, females with a dependent calf ('maternal females') are sometimes closely attended by one or more male escorts. Using data collected from a shore-based observation platform in the Hawaiian Islands, we tested the hypothesis that the spatial distribution of maternal females is driven primarily by avoidance of males. As predicted, we found that (1) pods containing a calf occurred in significantly shallower water than pods that did not contain a calf, (2) unescorted maternal females occurred in significantly shallower water than escorted maternal females, (3) the number of males escorting a female decreased significantly with decreasing water depth, and (4) the swimming speed of maternal females increased as a function of male presence, with escorted females travelling significantly more rapidly than unescorted females and a significant positive correlation between swimming speed and number of escorts. We suggest that maternal females incur increased energetic costs when escorted by males and consequently position themselves in shallow waters to reduce the likelihood of unwanted male attention.

Keywords

humpback whale, depth, speed, habitat use, avoidance of males, harassment.

1. Introduction

Worldwide, the winter breeding grounds of humpback whales (*Megaptera novaeangliae*) tend to be found in relatively shallow waters, for example,

on nearshore or offshore banks or areas abutting island regions (Clapham & Mead, 1999). Within these locations there appears to be spatial segregation such that pods containing a calf ('calf pods') tend to be found in shallower waters than pods without a calf ('non-calf pods') (e.g., Herman & Antinoja, 1977; Smultea, 1994; Ersts & Rosenbaum, 2003). Here, based on extensive data collected from a shore-based location within the Hawaiian breeding grounds, we investigate whether this segregation is driven by female avoidance of males.

Three main hypotheses have been proposed to explain the predominance of calf pods in shallow waters: a preference for calm, sheltered waters, avoidance of predators, and avoidance of male harassment (Smultea, 1994; Ersts & Rosenbaum, 2003). The 'sheltered waters' hypothesis can be rejected for Hawai'i because although calf density is high in the sheltered waters between the islands of Maui, Moloka'i, Lana'i and Kaho'olawe it is also high in the open, unsheltered and frequently rough waters of Penguin Bank which extends approximately 44 km southwest of the coastline of Moloka'i (Herman & Antinoja, 1977; Mobley et al., 1999). Likewise, although predation pressure in high latitudes may have been an important selection pressure driving pregnant females to migrate to low-latitude breeding grounds for calving (Corkeron & Connor, 1999), it is unlikely to be the key determinant of spatial segregation within these breeding grounds. In Hawai'i, for example, orcas (*Orcinus orca*) are seldom seen despite considerable observation effort (Baird et al., 2006; cf., Steiger et al., 2008) and observations elsewhere demonstrate that orcas in pursuit of marine mammals are undeterred by shallow water (Guinet & Bouvier, 1995). The only reported predatory attacks on humpback whales in Hawai'i have been by tiger sharks (*Galeocerdo cuvier*) that have generally targeted individuals already moribund for reasons such as entanglement in fishing gear, illness or (in the case of calves) probable abandonment by the mother (Mazzuca et al., 1998). Moreover, the ranging patterns of tiger sharks through both deep and shallow waters in Hawai'i (Holland et al., 1999; Meyer et al., 2009) offer no support for the suggestion that shallow waters provide refuge from this species. Thus, the available evidence suggests that the 'predator avoidance' hypothesis may be rejected as an explanation for the spatial segregation of humpbacks within Hawai'i. A more plausible hypothesis is that maternal females (i.e., females accompanied by a dependent calf) occupy shallower waters in an attempt to minimise harassment by males seeking mating opportunities (Smultea,

1994). Females with or without a calf are often closely attended ('escorted') by one or more males while on the breeding grounds (Herman & Antinaja, 1977). Associations between males and females are short-lived, generally lasting for a few hours at most (Mobley & Herman, 1985). Thus, male escorts are widely assumed to be prospecting for potential mating opportunities (Mobley & Herman, 1985; Clapham, 1996). Although females without a dependent calf are more likely than maternal females to ovulate, post-partum ovulation sometimes occurs (Chittleborough, 1958). Consequently, males may be attracted to maternal females as potential mates and the harassment of unreceptive females may ensue.

Despite the suggestion that avoidance of male harassment may influence maternal female distribution (Smultea, 1994), the distribution of calf pods as a function of male presence has not been widely investigated. Ersts & Rosenbaum (2003) reported that in Antongil Bay, Madagascar, female humpbacks with calves were found in shallower waters and closer to shore than other group types, but the differences between unescorted and escorted mother-calf pairs did not quite reach statistical significance. Using opportunistic data collected from whale-watch vessels in Ecuadorian waters, Félix & Botero-Acosta (2011) found that maternal females accompanied by a single escort tended to occur in deeper waters than unescorted maternal females, but these authors did not systematically investigate depth differences amongst escorted maternal female pods as a function of the number of escorts. The overall sex ratio of individuals in *non*-calf pods is heavily skewed towards males, given that such pods include singers (all male), non-singing singletons (predominantly male), same-sex dyads (predominantly male) and pods containing a single female with multiple males (Craig et al., 2002; Herman et al., 2011; Pack et al., 2012). Thus, if maternal females (i.e., those in calf pods) seek to avoid males, one possible tactic would be to occupy areas in which there is a low probability of encountering non-calf pods.

Maternal females should only avoid males if the costs of being escorted outweigh the benefits. Cartwright & Sullivan (2009) reported that association with multiple escorts increased the energetic expenditure of female-calf pairs in Hawai'i, reducing the time spent resting and increasing the time spent travelling. Energetic expenditure assumes particular importance for maternal female humpbacks because (1) the energetic costs of lactation in mysticetes are much higher than in most other mammals (Lockyer, 1981), and (2) as a consequence of fasting on the breeding grounds female humpbacks must metabolise stored energy reserves in order to sustain themselves and produce

sufficient milk for their offspring (Chittleborough, 1965; Dawbin, 1966). Thus, the challenges to a female's energy budget are evident, and minimising additional energetic expenditure should confer substantial fitness benefits. A maternal female must meet both the direct costs of her own swimming and the indirect costs of her calf's swimming: as maternal milk is the sole food source of calves on the breeding grounds (Chittleborough, 1958; Clapham & Mayo, 1987), a female must provision her calf with sufficient milk to offset its energetic expenditure on locomotion. Direct empirical data on the total costs of transport in large cetacean species are sparse, but Rodriguez de la Gala-Hernandez et al. (2008) showed that when swimming, gray whale (*Eschrichtius robustus*) calves were less efficient and had to expend more effort than adults. Given that humpbacks are similar to gray whales in terms of both adult and calf body size (Rice & Wolman, 1971; Clapham & Mead, 1999), it seems apparent that a maternal female humpback should seek to minimise expenditure on swimming not only because of the direct costs to herself, but also because her calf will face higher energetic costs of transport than those incurred by adults.

In the present study, we examined data collected across three breeding seasons from a shore-based observation platform in the Hawaiian Islands to test the hypothesis that the distribution of maternal females is governed primarily by avoidance of males. We investigated the spatial distribution of pods to determine whether there was variation in water depth as a function of pod composition with respect to calf presence, male presence and number of escorts. We then examined the swimming speed of calf pods to determine whether there was variation as a function of male presence, including in our analysis a consideration of the number of escorts. If maternal females occupy shallow waters to avoid males and if the energetic costs of being escorted are reflected in swimming speed we would predict that (1) calf pods will be found in shallower water than non-calf pods; (2) unescorted maternal females will be found in shallower water than escorted maternal females; (3) the number of males escorting a female will decrease progressively with decreasing water depth; and (4) the swimming speed of maternal females will increase as a function of male presence.

2. Material and methods

We conducted land-based observations from an elevated (56.46 m) site ('Pu'u Pilau'), located at 156°38'3"W, 20°49'49"N, approximately 3 km

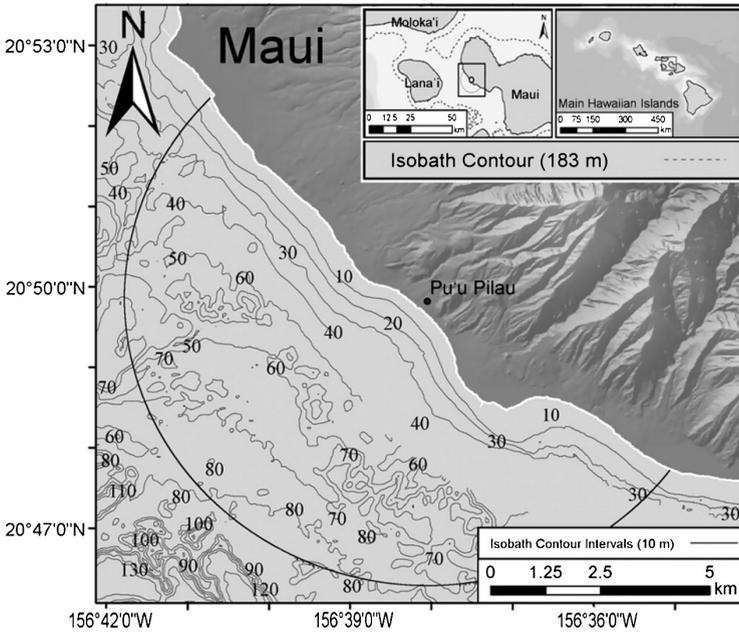


Figure 1. Map of the study area. The semi-circle indicates the area within a 6.5 km radius of the theodolite site at Pu'u Pilau.

NNW of Olowalu, Maui, Hawai'i, USA (Figure 1). Since humpback whales are not territorial and are very mobile while in Hawaiian waters, as reflected in the rarity of resightings of individuals on more than one occasion within the same area and by data obtained from tagged individuals (Mate et al., 1998; Craig et al., 2001), sampling from a fixed location enables data to be collected on a large number of different individuals without the impediment of pseudoreplication. A scan sampling procedure (Altmann, 1974) was used to record the distribution and composition of all whale pods within a 6.5 km radius of the observation site. Each scan sample lasted for 15 min to increase the probability that any pod in the sampling area would be at the surface at some time during the sample, but each pod was counted only once. Scan samples were collected between 09:15 and 17:00 each day, weather permitting, between January and April of 1996, 1997 and 1998. Observer effort was consistent across all samples. Scan samples were separated by at least 3 h so that they could be treated as independent (Smultea, 1994; Frankel & Clark, 2002). Using a Sokkia DT5 theodolite (accurate to within 5'' of arc), we obtained time-stamped spatial position 'fixes' for all pods observed

during each scan. The range and bearing of each pod were derived from the angles of declination and azimuth of the theodolite fix (e.g., see Tyack, 1981; Smultea, 1994; Frankel & Clark, 2002). Pod compositions were determined by an experienced observer via the 30-power optics of the theodolite spotting scope and pods were observed during multiple surfacings to confirm that pod compositions were accurate. Only samples collected when the Beaufort Sea State was 3 or less were included in the analysis to preclude the possibility of high sea states affecting the detectability of whales. Within the 6.5 km radius it was possible to reliably determine pod compositions, including the presence or absence of a calf (e.g., see Mobley & Herman, 1985; Craig et al., 2002). The term ‘non-calf pod’ was applied to lone adults as well as to pods consisting of two or more adults. In 1998 individual pods were position fixed multiple times (mean = 2.8, SD = 1.3). Time-stamps associated with these fixes allowed for the calculation of swimming speeds (e.g., see Sumich, 1983; Rodriguez de la Gala-Hernandez et al., 2008).

A Geographic Information System (GIS) model of the study area was constructed using ArcGIS 9.3 (Environmental Systems Research Institute, 2008) and all pod sightings were plotted to create a data layer that was superimposed over the model. Coastline data from the Hawai’i State GIS Program (<http://hawaii.gov/dbedt/gis/>) were incorporated as a vector layer and depth data from the Main Hawaiian Islands Multibeam Bathymetry Synthesis website (<http://www.soest.hawaii.edu/hmrg/multibeam/index.php>) were incorporated as a 50 m bathymetric grid. The Spatial Analyst tool ‘Extract’ — ‘Extract Values to Points’ was used to derive the depth of each pod and the Analysis tool ‘Overlay’ — ‘Spatial Join’ was used to determine the distance from each pod to the closest point of shoreline. Both derived continuous variables were appended to each positional record.

Data were exported to SAS databases (SAS Institute, 2002) and all statistical analyses were conducted in SAS. The data were not normally distributed so we computed medians and inter-quartile ranges prior to conducting non-parametric statistical tests. There was a strong positive correlation between depth and distance from shore for whale locations within our study area (Spearman rank correlation: $r_s = 0.854$, $N = 823$, $p < 0.0001$) so in line with Smultea (1994) we selected depth as our dependent variable because high humpback densities on offshore shallow banks in Hawai’i and other breeding areas (Herman & Antinaja, 1977; Whitehead & Moore, 1982; Mobley et al., 1999) suggest that depth is more ecologically important than

distance from shore. Two-tailed Wilcoxon rank sum tests were used for all two-way comparisons of depth and speed. All correlational analyses were conducted using Spearman rank correlation. As previous studies have found seasonal and diurnal trends in distribution (Smultea, 1994; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011), we controlled for temporal variation by using non-parametric partial correlational analyses.

3. Results

3.1. Depth

Table 1 summarises the depths at which all pod types occurred. Calf pods were found in shallower water (median = 53.54 m) than non-calf pods (median = 62.51 m) (Wilcoxon rank sum test: $S = 96950.0$, $N_1 = 297$, $N_2 = 526$, $p < 0.0001$). Moreover, unescorted calf pods were found in shallower water (median = 49.58 m) than escorted calf pods (median = 55.35 m) (Wilcoxon rank sum test: $S = 14812.0$, $N_1 = 110$, $N_2 = 187$, $p = 0.0273$). There was a significant positive correlation between the number of escorts and depth both overall (Figure 2; Spearman rank correlation: $r_s = 0.157$, $N = 297$, $p = 0.0067$) and when scan sample date and time were partialled out (Spearman partial rank correlation: $r_s = 0.150$, $N = 297$, $p = 0.0099$). Thus, all predictions relating to depth were fulfilled.

3.2. Swimming speed

Overall, the median swimming speed of calf pods (2.34 km/h) was significantly slower than the median swimming speed of non-calf pods (3.45 km/h) (Table 2; Wilcoxon rank sum test: $S = 26347.0$, $N_1 = 168$, $N_2 = 179$, $p = 0.0020$). When only calf pods were considered, the median swimming

Table 1.
Median water depth for each humpback whale pod type.

Pod type	Water depth (m)		N
	Median	Inter-quartile range	
All non-calf pods	62.51	18.00	526
All calf pods	53.54	31.50	297
Escorted calf pods	55.35	31.84	187
Unescorted calf pods	49.58	32.59	110

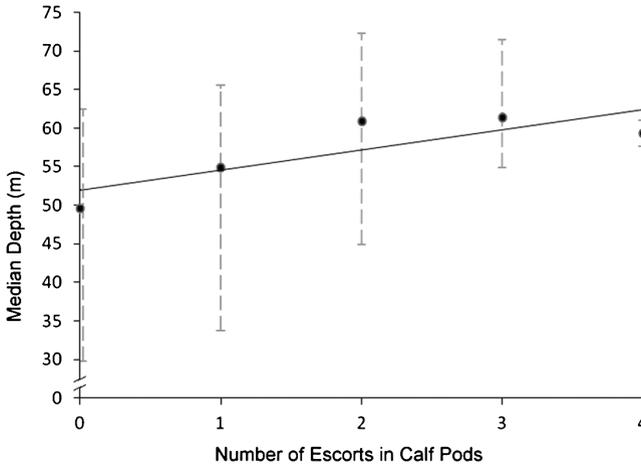


Figure 2. Median depth occupied by calf pods as a function of the number of escorts. The overall trend is illustrated by the line of best fit to the medians. Error bars represent inter-quartile ranges.

speed of unescorted pods (1.56 km/h) was significantly slower than the median swimming speed of escorted pods (2.72 km/h) (Wilcoxon rank sum test: $S = 3765.0$, $N_1 = 56$, $N_2 = 112$, $p = 0.0011$). There was a significant positive correlation between swimming speed and the number of escorts in calf pods both overall (Figure 3; Spearman rank correlation: $r_s = 0.305$, $N = 168$, $p < 0.0001$) and when the potential effects of depth were controlled for statistically (Spearman partial rank correlation: $r_s = 0.307$, $N = 132$, $p = 0.0004$; sample size reduced because full bathymetric data were not available in all cases). Thus, as predicted, the swimming speed of maternal females increased as a function of male presence.

Table 2.

Median swimming speed for each humpback whale pod type.

Pod type	Swimming speed (km/h)		<i>N</i>
	Median	Inter-quartile range	
All non-calf pods	3.45	3.94	179
All calf pods	2.34	2.78	168
Escorted calf pods	2.72	2.74	112
Unescorted calf pods	1.56	1.93	56

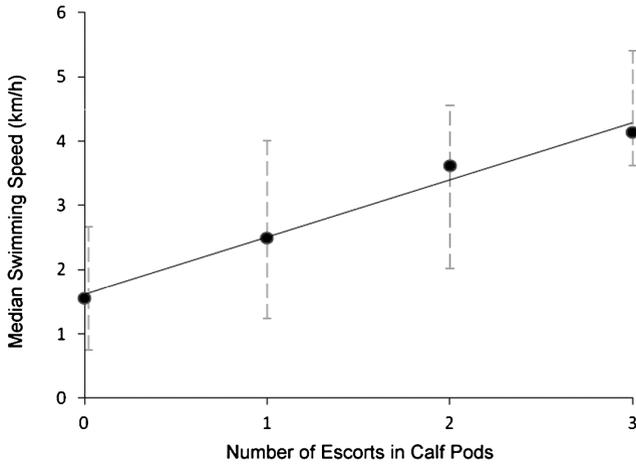


Figure 3. Median swimming speeds of calf pods as a function of the number of escorts. The overall trend is illustrated by the line of best fit to the medians. Error bars represent interquartile ranges.

Additional analyses explored trends in swimming speed as a function of depth. We focused on single-escort maternal pods because this was the most numerous maternal pod type and provided a sample size large enough to permit a more detailed correlational analysis. After computing the arithmetic average of the depths associated with the first and last position fix of each pod for which both full depth data and speed were available, we found a significant positive correlation between average depth and swimming speed (Spearman rank correlation: $r_s = 0.231$, $N = 73$, $p = 0.0493$). Thus, the swimming speed of single-escort maternal pods became progressively slower as depth decreased. However, the swimming speed of unescorted maternal females did not vary significantly with depth (Spearman rank correlation: $r_s = -0.181$, $N = 45$, $p = 0.234$).

4. Discussion

Overall, the data supported the hypothesis that the distribution of maternal females is governed primarily by avoidance of males. In line with previous studies (e.g., Smultea, 1994), we found that calf pods occupied shallower water than non-calf pods. Given the previously-noted preponderance of males in non-calf pods, this implies that maternal females favoured areas in which the probability of encountering males was low. We also found that unescorted

maternal females occupied shallower water than escorted maternal females and, importantly, that the number of males escorting a female decreased progressively with decreasing water depth. The swimming speed of calf pods increased as a function of male presence, suggesting that escorted maternal females bore increased energetic costs. Not only was speed of travel significantly faster for escorted than unescorted calf pods, the positive correlation between speed of travel and number of escorts suggests that the energetic costs of being escorted increase with the number of males in pursuit. As noted previously, a maternal female faces not only the direct costs of her own locomotion but also the indirect costs arising from the inefficient locomotion of her calf. Thus, collectively, these data suggest that maternal females seek refuge from costly associations with males by preferentially occupying relatively shallow waters.

4.1. Do females avoid all escorts or intentionally seek a single escort?

Examining the behaviours of female-calf pairs in Hawai'i, Cartwright & Sullivan (2009) found that association with multiple males reduced the time spent resting and increased the time spent travelling. However, they did not detect a difference between unescorted female-calf pairs and those accompanied by a single escort. This led them to speculate that Mesnick's (1997) 'bodyguard' hypothesis may be applicable to humpback whales. Mesnick reviewed evidence demonstrating that in several primate species, females with dependent offspring may associate with one male in order to reduce harassment from other males. However, the relevance of this hypothesis to humpback whales is debatable. Our speed data suggest that for maternal females, associating with a single escort imposes greater energetic costs than remaining unescorted. It would therefore be more adaptive for maternal females to evade all escorts rather than seek a single escort. Our distributional data are consistent with this suggestion, indicating that maternal females preferentially occupy shallower waters in which males are less likely to be found. Moreover, if maternal females actively sought a 'bodyguard' we would expect that observations of maternal females approaching single males would be relatively common. The available evidence, however, suggests that such observations are remarkably rare (Tyack, 1981; Tyack & Whitehead, 1983; Medrano et al., 1994; Darling et al., 2006; Smith et al., 2008). For example, Smith et al. (2008) reported that single male humpbacks frequently approached maternal females but maternal females did not approach single

males. Thus, the formation of mother-calf-escort pods owed more to the behaviour of males than the behaviour of females. Also, single escorts typically swim behind rather than ahead of a maternal female and her calf (Glockner & Venus, 1983; Baker & Herman, 1984). It is far from certain, moreover, that a single escort would prevent other males from approaching. In fact, Spitz et al. (2002) showed that single escorts associating with maternal females tend to be smaller on average than principal escorts (who physically defend their position of closest proximity to the female in competitive pods populated by multiple escorts). Finally, associations between females and their escorts are transient; there is a distinct lack of the repeated associations between individuals that are typical of primates (Tyack & Whitehead, 1983; Mobley & Herman, 1985). These varying lines of evidence converge to support the conventional suggestion that the association between a maternal female and a single escort is due to the male prospecting for potential mating opportunities (Mobley & Herman, 1985; Clapham, 1996; Smith et al., 2008) and not to the female seeking a 'bodyguard'.

4.2. Costs of association with males

In many species, harassment by males may increase the risk of injury to a female or her offspring (Mesnick & Le Boeuf, 1991; Hiruki et al., 1993; Réale et al., 1996; Chilvers et al., 2005; Le Galliard et al., 2005). There is currently no direct evidence of such injurious harassment in humpbacks but there is some anecdotal evidence suggesting that male pursuit may increase the risk of mother-calf separation. Pack et al. (2002) observed a maternal female being separated temporarily from her calf during an attempted copulation by one of three escorts. The female then actively retrieved her calf with the escorts in close pursuit. Cartwright & Sullivan (2009) described brief separations of mothers and calves on six occasions when an escort was present. Premature separation of a calf from its mother on the breeding grounds would have clear fitness consequences as the calf could not survive without access to its mother's milk. Elwen & Best (2004a) found that strandings of southern right whale (*Eubalaena australis*) calves were more common in areas with a high density of non-maternal whales than in areas occupied primarily by maternal females, and raised the possibility that in this species harassment by other whales may affect calf survival.

While the evidence of fitness costs involving injury or mother-calf separation in humpbacks is limited, our data on swimming speeds suggest that

being escorted by even a single male affects the energetic expenditure of females and their calves. The absence of feeding on the breeding grounds (Chittleborough, 1965; Dawbin, 1966) and the high energetic demands of mysticete lactation (Lockyer, 1981) place particular pressure on the energy budget of maternal females. The high physical costs of reproduction in female humpbacks were demonstrated by data from commercial whaling: females captured in late lactation yielded only 50% of the oil that was obtained from females in early pregnancy caught at the same location (Dawbin, 1966). As lactating female humpbacks must subsist on stored energy reserves during their residency on the breeding grounds, any increased energetic expenditure associated with male presence cannot be mitigated by increased foraging. For both a female and her calf there are clear advantages to minimising unnecessary energetic costs. As Elwen & Best (2004a) noted for southern right whales, reducing post-partum energetic costs would enable calves to invest more heavily in growth and facilitate a more efficient transfer of energy between maternal blubber and calf mass. This would potentially increase the calf's chance of surviving the migration from the breeding grounds to the feeding grounds, or perhaps even permit the female to leave the breeding grounds and begin feeding somewhat earlier. Given the apparent energetic costs of being escorted, the best strategy for a maternal female seeking to conserve energy appears to be the preferential occupation of shallower waters. Aside from the finding that unescorted maternal females occurred in shallower waters than escorted maternal females, our finding of a significant relationship between water depth and number of escorts suggests that the probability of male presence declines progressively with decreasing water depth. Moreover, the positive correlation between depth and speed of travel for maternal females accompanied by a single escort suggests that even escorted females are able to reduce the energetic expenditure associated with an escort if they enter shallower waters. By positioning themselves in shallow waters it seems that females with dependent calves are able to mitigate the costs of unwanted male attention, and perhaps also protect their offspring from the possibility of accidental harm.

4.3. Why does shallow water deter male escorts?

Our data also suggest that in relatively shallow waters the costs to males of escorting maternal females exceed the benefits. Elwen & Best (2004b) proposed that courting whales have reduced manoeuvrability in shallower

waters. Our finding that the swimming speed of single-escort pods declines with decreasing depth is consistent with this proposition. However, escorted maternal females in other humpback breeding areas are commonly found in considerably shallower depths (ca. 20 m) than those reported here for unescorted maternal females (ca. 50 m) (Félix & Botero-Acosta, 2011; Be-tancourt et al., in press). Thus, there is no compelling evidence that male humpbacks in Hawai'i are deterred from pursuing maternal females into shallower waters because of constraints on manoeuvrability. A more probable explanation is that maternal females are less likely to ovulate and thus have lower reproductive potential than females without a calf (Chittleborough, 1958; Craig et al., 2002). Since non-calf pods are typically found in deeper waters than calf pods, the probability of encountering females with the highest reproductive potential will be reduced in the shallower waters occupied preferentially by maternal females. Moreover, a male in shallower waters may compromise his ability to adopt alternative mating tactics: both singing and escorting may contribute to reproductive success (Cerchio et al., 2005; Herman et al., 2013) and males commonly occupy deeper waters when singing (Frankel et al., 1995).

4.4. Habitat use and male harassment

Our findings are consistent with literature showing that females of other taxa counter costly male harassment by changing their patterns of habitat use. For example, female Trinidadian guppies (*Poecilia reticulata*) experience costly harassment by courting males and alter their habitat use as a consequence (Darden & Croft, 2008), as do female seed-eating true bugs (*Neacoryphus bicrucis*) (McLain & Pratt, 1999). Differences in habitat use as a function of female reproductive state have been found in other species of marine mammal, with female-offspring pairs occupying areas where antagonistic interactions involving males are less likely (Kovacs et al., 1990; Martin & da Silva, 2004; Weir et al., 2008; Fury et al., 2013). This differential habitat use has been linked to the need for females with dependent young to reduce harassment by courting males, though in each case other explanations could not be discounted. For example, Kovacs et al. (1990) considered that one potential reason for maternal female segregation at harbour seal (*Phoca vitulina*) haul-out sites was the reduced potential for interference from sexually active males. However, the evidence did not allow this

to be favoured over alternative possibilities such as a preference for calmer sea conditions. Likewise, Martin & da Silva (2004) suggested female avoidance of male harassment as a potential explanation for sexual segregation in botos (*Inia geoffrensis*), along with the differing nutritional needs of females with calves relative to mature males and possibly also the need to shelter from strong currents. However, little is known about courtship behaviour or associations between males and females in this species and the authors considered these alternative explanations to be equally likely. Weir et al. (2008) found that dusky dolphin (*Lagenorhynchus obscurus*) nursery groups, consisting of multiple female-calf pairs, had a significant preference for shallow waters, whereas other group types had no such preference. The data supported their hypotheses that nursery groups occupy these waters to reduce the probability of encountering both tour boats and harassment by males. However, the authors also noted some additional factors that may influence maternal dusky dolphins' preference for shallow waters in this area, including predation risk and foraging opportunities. Fury et al. (2013) documented spatial segregation in the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), reporting that female groups were found more commonly in shallower estuary channels than mixed-sex groups. They noted several factors that may drive this segregation including predator avoidance, differing nutritional requirements and refuge from male harassment. Overall, they concluded that the most probable explanations were avoidance of aggressive males and/or access to suitable prey.

Avoidance of male harassment, then, is one of several explanations that have been proposed to account for differential habitat use by male and female marine mammals. However, in the case of humpback whales we are able to definitively exclude nutritional requirements as a potential explanation because neither calves nor adults seek prey on the breeding grounds. Moreover, the available evidence suggests that predator avoidance and access to sheltered water are not key drivers of the fine-scale distribution of maternal female humpbacks. The avoidance of tour boats, as suggested for dusky dolphins, has not been examined here as a potential explanation. However, the fact that vessels in our study area occur predominantly in shoreline regions (Cartwright et al., 2012) renders this an unlikely explanation for our distributional data. Overall, the most plausible explanation is that maternal females are seeking to reduce the probability of male harassment.

4.5. Conclusion

We have previously argued that energetic constraints are an important influence on the migratory behaviour of humpback whales, resulting in sex differences in migration and differential migratory timing as a function of reproductive status (Craig & Herman, 1997; Craig et al., 2003). We now extend our argument to suggest that energetic constraints may also ultimately affect the spatial distribution of humpback whales on the breeding grounds because they lead maternal females to avoid the costs of male harassment by seeking waters that are sufficiently shallow to deter male escorts. Future studies that include extended focal observations of behaviour and fine-scale movements may help to elucidate both the detailed behavioural responses of maternal females to approach by males and the reasons why males rarely pursue maternal females into shallower waters.

Acknowledgements

We are grateful to the many people who assisted in data collection, particularly Becca Cowan, Mark Deakos, David Glickman, Katie Hadfield, Kitty Hudson, Molly Hurst, Krista O'Mally, Carrie Southgate, Scott Spitz and Kathy Zagsebski. This work was supported through contributions from members of The Dolphin Institute (TDI), TDI participants, Earthwatch volunteers, LeBurta Atherton, The Homeland Foundation, the Robles Foundation, the Seto Foundation, the LeBurta Atherton Foundation, Sokkia Corporation and Becky Goodman. We thank Tom Kieckhefer and A. William Archibald for data collection software and Maui County for access to the Pu'u Pilau shore station. Finally, we thank Bruce Schulte and the anonymous reviewers for insightful comments that contributed to the development of this manuscript.

References

- Altmann, J. (1974). Observational study of behavior: sampling methods. — Behaviour 49: 227-267.
- Baird, R.W., McSweeney, D.J., Bane, C., Barlow, J., Salden, D.R., Antoine, L.K., LeDuc, R.G. & Webster, D.L. (2006). Killer whales in Hawaiian waters: information on population identity and feeding habits. — Pac. Sci. 60: 523-530.
- Baker, C.S. & Herman, L.M. (1984). Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. — Can. J. Zool. 62: 1922-1937.

- Betancourt, L., Herrera-Moreno, A. & Beddall, K. (in press). Spatial distribution of humpback whales (*Megaptera novaeangliae*) in Samana Bay, Dominican Republic. — *J. Cetacean Res. Manage.*
- Cartwright, R., Gillespie, B., LaBonte, K., Mangold, T., Venema, A., Eden, K. & Sullivan, M. (2012). Between a rock and a hard place: habitat selection in female-calf humpback whale (*Megaptera novaeangliae*) pairs on the Hawaiian breeding grounds. — *PLoS One* 7: e38004, DOI:10.1371/journal.pone.0038004.
- Cartwright, R. & Sullivan, M. (2009). Associations with multiple male groups increase the energy expenditure of humpback whale (*Megaptera novaeangliae*) female and calf pairs on the breeding grounds. — *Behaviour* 146: 1573-1600.
- Cerchio, S., Jacobsen, J.K., Cholewiak, D.M., Falcone, E.A. & Merriwether, D.A. (2005). Paternity in humpback whales, *Megaptera novaeangliae*: assessing polygyny and skew in male reproductive success. — *Anim. Behav.* 70: 267-277.
- Chilvers, L., Robertson, B.C., Wilkinson, L.S., Duignan, P.J. & Gemmill, N.J. (2005). Male harassment of female New Zealand sea lions, *Phocartos hookeri*: mortality, injury, and harassment avoidance. — *Can. J. Zool.* 83: 642-648.
- Chittleborough, R.G. (1958). The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). — *Aust. J. Mar. Freshwat. Res.* 9: 1-18.
- Chittleborough, R.G. (1965). Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). — *Aust. J. Mar. Freshwat. Res.* 16: 33-128.
- Clapham, P.J. (1996). The social and reproductive biology of humpback whales: an ecological perspective. — *Mammal Rev.* 26: 27-49.
- Clapham, P.J. & Mayo, C.A. (1987). Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979-1985. — *Can. J. Zool.* 65: 2853-2863.
- Clapham, P.J. & Mead, J.G. (1999). *Megaptera novaeangliae*. — *Mammal. Species* 604: 1-9.
- Corkeron, P.J. & Connor, R.C. (1999). Why do baleen whales migrate? — *Mar. Mammal Sci.* 15: 1228-1245.
- Craig, A.S. & Herman, L.M. (1997). Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. — *Can. J. Zool.* 75: 1923-1933.
- Craig, A.S., Herman, L.M., Gabriele, C.M. & Pack, A.A. (2003). Migratory timing of humpback whales (*Megaptera novaeangliae*) in the central North Pacific varies with age, sex and reproductive status. — *Behaviour* 140: 981-1001.
- Craig, A.S., Herman, L.M. & Pack, A.A. (2001). Estimating residence times of humpback whales in Hawaii. — Report to the Hawaiian Islands National Marine Sanctuary. National Oceanic and Atmospheric Administration, Washington, DC.
- Craig, A.S., Herman, L.M. & Pack, A.A. (2002). Male mate choice and male-male competition coexist in the humpback whale (*Megaptera novaeangliae*). — *Can. J. Zool.* 80: 745-755.
- Darden, S.K. & Croft, D.P. (2008). Male harassment drives females to alter habitat use and leads to segregation of the sexes. — *Biol. Lett.* 4: 449-451.

- Darling, J.D., Jones, M.E. & Nicklin, C.P. (2006). Humpback whale songs: do they organize males during the breeding season? — Behaviour 143: 1051-1101.
- Dawbin, W.H. (1966). The seasonal migratory cycle of humpback whales. — In: Whales, dolphins, and porpoises (Norris, K.S., ed.). University of California Press, Berkeley, CA, p. 145-170.
- Elwen, S.H. & Best, P.B. (2004a). Female southern right whales, *Eubalaena australis*: are there reproductive benefits associated with their distribution off South Africa? — Mar. Ecol. Prog. Ser. 269: 289-295.
- Elwen, S.H. & Best, P.B. (2004b). Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa 1: broad scale patterns. — Mar. Mammal Sci. 20: 567-582.
- Environmental Systems Research Institute (2008). ArcGIS Release 9.3. — Environmental Systems Research Institute, Redlands, CA.
- Ersts, P.J. & Rosenbaum, H.C. (2003). Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. — J. Zool. (Lond.) 260: 337-345.
- Félix, F. & Botero-Acosta, N. (2011). Distribution and behaviour of humpback whale mother-calf pairs during the breeding season off Ecuador. — Mar. Ecol. Prog. Ser. 426: 277-287.
- Frankel, A.S. & Clark, C.W. (2002). ATOC and other factors affecting the distribution and abundance of humpback whales (*Megaptera novaeangliae*) off the north shore of Kauai. — Mar. Mammal Sci. 18: 644-662.
- Frankel, A.S., Clark, C.W., Herman, L.M. & Gabriele, C.M. (1995). Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai'i, determined using acoustic and visual techniques. — Can. J. Zool. 73: 1134-1146.
- Fury, C.A., Ruckstuhl, K.E. & Harrison, P.L. (2013). Spatial and social sexual segregation patterns in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). — PLoS One 8: e52987, DOI:10.1371/journal.pone.0052987.
- Glockner, D.A. & Venus, S.C. (1983). Identification, growth rates and behavior of humpback whale (*Megaptera novaeangliae*) cows and calves in the waters off Maui, Hawaii, 1977–1979. — In: Communication and behavior of whales (Payne, R.S., ed.). Westview Press, Boulder, CO, p. 223-258.
- Guinet, C. & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. — Can. J. Zool. 73: 27-33.
- Herman, L.M. & Antinaja, R.C. (1977). Humpback whales in the Hawaiian breeding waters: population and pod characteristics. — Sci. Rep. Whales Res. Inst. 29: 59-85.
- Herman, L.M., Pack, A.A., Rose, K., Craig, A., Herman, E.Y.K., Hakala, S. & Milette, A. (2011). Resightings of humpback whales in Hawaiian waters over spans of 10–32 years: site fidelity, sex ratios, calving rates, female demographics, and the dynamics of social and behavioral roles of individuals. — Mar. Mammal Sci. 2: 736-768.
- Herman, L.M., Pack, A.A., Spitz, S.S., Herman, E.Y.K., Rose, K., Hakala, S. & Deakos, M.H. (2013). Humpback whale song: who sings? — Behav. Ecol. Sociobiol. 67: 1653-1663.

- Hiruki, L.M., Stirling, I., Gilmartin, W.G., Johanos, T.C. & Becker, B.L. (1993). Significance of wounding to female reproductive success in Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island. — *Can. J. Zool.* 71: 469-474.
- Holland, K.N., Wetherbee, B.M., Lowe, C.G. & Meyer, C.G. (1999). Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. — *Mar. Biol.* 134: 665-673.
- Kovacs, K.M., Jonas, K.M. & Welke, S.E. (1990). Sex and age segregation by *Phoca vitulina concolor* at haul-out sites during the breeding season in the Passamaquoddy Bay region, New Brunswick. — *Mar. Mammal Sci.* 6: 204-214.
- Le Galliard, J.F., Fitze, P.S., Ferriere, R. & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. — *Proc. Natl Acad. Sci. USA* 102: 18231-18236.
- Lockyer, C. (1981). Growth and energy budgets of large baleen whales from the Southern Hemisphere. — In: *Mammals in the seas*, Vol. 3. Food and Agricultural Organization of the United Nations, Rome, p. 379-487.
- Martin, A.R. & da Silva, V.M.F. (2004). River dolphins and flooded forest: seasonal habitat use and sexual segregation of botos (*Inia geoffrensis*) in an extreme cetacean environment. — *J. Zool. (Lond.)* 263: 295-305.
- Mate, B.R., Gisiner, R. & Mobley, J. (1998). Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. — *Can. J. Zool.* 76: 863-868.
- Mazzuca, L., Atkinson, S. & Nitta, E. (1998). Deaths and entanglements of humpback whales, *Megaptera novaeangliae*, in the main Hawaiian Islands, 1972-1996. — *Pac. Sci.* 52: 1-13.
- McLain, D.K. & Pratt, A.E. (1999). The cost of sexual coercion and heterospecific sexual harassment on the fecundity of a host-specific, seed-eating insect (*Neacoryphus bicrucis*). — *Behav. Ecol. Sociobiol.* 46: 164-170.
- Medrano, L., Salinas, M., Salas, I., Ladron de Guevara, P., Aguayo, A., Jacobsen, J. & Baker, C.S. (1994). Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering grounds of the Mexican Pacific Ocean. — *Can. J. Zool.* 72: 1771-1774.
- Mesnick, S.L. (1997). Sexual coercion, female mate choice and the bodyguard hypothesis: implications for the evolution of animal mating systems. — In: *Feminism and evolutionary biology: boundaries, intersections, and frontiers* (Gowaty, P., ed.). Chapman & Hall, New York, NY, p. 207-260.
- Mesnick, S.L. & Le Boeuf, B.J. (1991). Sexual behaviour of male northern elephant seals: II. Female responses to potentially injurious encounters. — *Behaviour* 117: 262-280.
- Meyer, C.G., Clark, T.B., Papastamatiou, Y.P., Whitney, N.M. & Holland, K.N. (2009). Long-term movements of tiger sharks (*Galeocerdo cuvier*) in Hawaii. — *Mar. Ecol. Prog. Ser.* 381: 223-235.
- Mobley, J.R., Bauer, G.B. & Herman, L.M. (1999). Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. — *Aquat. Mamm.* 25: 63-72.
- Mobley, J.R. & Herman, L.M. (1985). Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) in the Hawaiian wintering grounds. — *Can. J. Zool.* 63: 762-772.

- Pack, A.A., Herman, L.M., Craig, A.S., Spitz, S.S. & Deakos, M.H. (2002). Penis extrusions by humpback whales (*Megaptera novaeangliae*). — Aquat. Mamm. 28: 131-146.
- Pack, A.A., Herman, L.M., Spitz, S.S., Craig, A.S., Hakala, S., Deakos, M., Herman, E.Y.K., Millette, A.J., Carroll, E., Levitt, S. & Lowe, C. (2012). Size-assortative pairing and discrimination of potential mates by humpback whales in the Hawaiian breeding grounds. — Anim. Behav. 84: 983-993.
- Réale, D., Boussès, P. & Chapuis, J.L. (1996). Female-biased mortality induced by male sexual harassment in a feral sheep population. — Can. J. Zool. 74: 1812-1818.
- Rice, D.W. & Wolman, A.A. (1971). Life history and ecology of the gray whale (*Eschrichtius robustus*). — Am. Soc. Mammal. Spec. Publ. 3, 142 pp.
- Rodriguez de la Gala-Hernandez, S., Heckel, G. & Sumich, J.L. (2008). Comparative swimming effort of migrating gray whales (*Eschrichtius robustus*) and calf cost of transport along Costa Azul, Baja California, Mexico. — Can. J. Zool. 86: 307-313.
- SAS Institute (2002). Statistical analysis software system. — SAS Institute, Cary, NC.
- Smith, J.N., Goldizen, A.W., Dunlop, R.A. & Noad, M.J. (2008). Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. — Anim. Behav. 76: 467-477.
- Smultea, M.A. (1994). Segregation by humpback whale (*Megaptera novaeangliae*) cows with calves in coastal habitat near the island of Hawaii. — Can. J. Zool. 72: 805-811.
- Spitz, S.S., Herman, L.M., Pack, A.A. & Deakos, M.H. (2002). The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. — Can. J. Zool. 80: 1938-1947.
- Steiger, G.H., Calambokidis, J., Straley, J.M., Herman, L.M., Cerchio, S., Salden, D.R., Urbán-R, J., Jacobsen, J.K., von Ziegesar, O., Balcomb, K.C., Gabriele, C.M., Dahlheim, M.E., Uchida, S., Ford, J.K.B., de Guevara-P, P.L., Yamaguchi, M. & Barlow, J. (2008). Geographic variation in killer whale attacks on humpback whales in the North Pacific: implications for predation pressure. — Endanger. Species Res. 4: 247-256.
- Sumich, J.L. (1983). Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. — Can. J. Zool. 61: 647-652.
- Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. — Behav. Ecol. Sociobiol. 8: 105-116.
- Tyack, P. & Whitehead, H. (1983). Male competition in large groups of wintering humpback whales. — Behaviour 83: 132-154.
- Weir, J.S., Duprey, N.M.T. & Wursig, B. (2008). Dusky dolphin (*Lagenorhynchus obscurus*) subgroup distribution: are shallow waters a refuge for nursery groups? — Can. J. Zool. 86: 1225-1234.
- Whitehead, H. & Moore, M.J. (1982). Distribution and movements of West Indian humpback whales in winter. — Can. J. Zool. 60: 2203-2211.