SOCIAL FORAGING OF THE SOUTHEAST ALASKAN HUMPBACK WHALE, *Megaptera novaeangliae*

by

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Abstract

Relative to other baleen whale populations, the humpback whales *Megaptera novaeangliae* inhabiting Southeast Alaska are noteworthy in that they form large, enduring groups when foraging on schools of Pacific herring *Clupea harengus pallasi.* These groups use a variety of unusual feeding tactics when attacking prey including the production of loud feeding calls, the release of bubbles, and the waving of their large pectoral flippers. Past observations of these groups have been largely anecdotal so little is known about their social behavior or the function of their feeding tactics. In particular, it is unclear if these pods are based on cooperative interactions or if they represent groups of individuals who are competing for prey that occurs in dense aggregations. In addition, little is known about the underlying social structure of these pods and whether they are composed of kin. The objective of this study was to employ field and laboratory techniques to gain insight into the function of the unusual feeding tactics, and to describe the basic social structure of these pods.

In order to test the prediction that bubbles, feeding calls, and flipper movements represent prey manipulation tactics, herring schools were brought into the laboratory and subjected to various simulated humpback whale feeding behaviors. I found that these simulated behaviors produced strong avoidance responses from the herring schools, suggesting that humpback whales use these tactics to manipulate the behavior of their prey. Seven years of field observations revealed that humpbacks with enduring social bonds (i.e., high coefficients of association) specialized on herring and represented a small proportion of the entire whale population. Calves born to these "core members" were never observed to return and feed with their mothers in subsequent years, suggesting that these groups are not composed of close kin. This was verified by analysis of haplotype variation in the mitochondrial genome and microsatellite variation in the nuclear genome. Individuals within these pods appear to invest in by-product benefits, with the enduring bonds between whales in Chatham Strait (cf. krill feeders in Frederick Sound) possibly representing combinations of individuals performing compatible tasks (i.e., bubble blower, herder, vocalizer).

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General Introduction

> Be wary then,
> best safety lies in fear....
>
> Shakespeare, Hamlet

Relative to most mammals, baleen whales tend to exhibit relatively low levels of sociality. Their asocial tendencies are exemplified by the humpback whale *Megaptera novaeangliae*, which is generally characterized by small, unstable groups (Baker 1985, Weinrich 1991, Clapham 1993, 2000). While on most feeding grounds, humpback associations tend to be relatively short in duration, typically lasting only a few minutes to a few hours (Whitehead 1983, Baker 1985, Weinrich 1991, Clapham 1993). Foraging group size is relatively small, with most individuals feeding alone or in groups of two to three individuals (Baker 1985, Weinrich 1991, Clapham 1993). Relative to other populations of humpback whales, those inhabiting Southeast Alaska have been reported to form large, enduring groups when foraging on schools of Pacific herring *Clupea harengus pallasi* (Baker 1985, D' Vincent et al. 1985). These groups are also noteworthy in that they use a variety of unusual feeding tactics when attacking prey, including the production of loud feeding calls, the release of bubble nets, and the waving of their large pectoral flippers. The extensive use of sound is particularly unusual, since humpbacks were thought to be largely silent while on the feeding grounds. Past observations of these groups have been largely anecdotal, so little is known about their social behavior or the function of their unusual feeding tactics.

A number of observers have suggested that the close spatial proximity and repeated lunge formation of these Alaskan pods provide evidence of cooperation (Baker and Herman 1984, Baker 1985, D' Vincent et al. 1985, D' Vincent et al. 1989). Furthermore, it has been suggested that the use of bubbles represents a sophisticated type of communal tool use (D' Vincent et al. 1989), and that the broadcasting of feeding calls is part of a set of cooperative prey-herding tactics. These hypotheses, however, remain untested.

In contrast to a cooperative model, group feeding has also been viewed as non-mutualistic aggregations of individuals engaged in scramble competition for dense prey patches (B. Dolphin in Giddings 1984). The extensive flipper movements observed as the whales rise to the surface have been interpreted as "pushing and shoving", implying interference competition (Watkins and Schevill 1979). The vocalizations broadcast during attacks on herring schools may also be associated with dominance interactions (Baker 1985). Finally, the extensive use of bubbles during foraging may be indicative of agonistic interactions, given that air release is used extensively during male-male competition on the breeding grounds (Baker and Herman 1984).

Previous studies have suggested that humpbacks feeding in large groups in SE Alaska may have enduring bonds which could represent family ties (Baker 1985). Matrilineal kinship groups could form within a feeding group if fidelity to a feeding region is established when a calf first travels to the feeding grounds with its mother (Baker 1985). Support for matrilineal fidelity has been demonstrated at a regional level in the North Pacific, where the Alaskan and Californian populations are characterized by an absence of overlapping mtDNA haplotypes (Baker et al. 1990, 1994). These genetic analyses corroborate photo-identification studies which have demonstrated that humpbacks breeding in Hawaii segregate into relatively discrete and geographically isolated feeding herds in the North Pacific (Straley 1994). However, it remains unclear whether humpbacks show matrilineally directed site fidelity at smaller geographic scales in Alaska.

A logical first step toward understanding Alaskan humpback foraging groups is to determine the function of their unusual foraging tactics, i.e., bubbles, feeding calls, and flipper movements. If these tactics produce predictable responses from herring schools, it would suggest that they are used by group members for prey manipulation, as opposed to being primarily associated with agonistic interactions. The first three chapters of this thesis examine the effects of these tactics on captive herring schools in the laboratory and in open-water net pens. For each of these experiments, *a priori* predictions were made as to the expected changes in school behavior if whales were using these tactics to increase their capture success. These predictions were then tested by exposing the fish to bubbles, feeding calls, and a large moveable model of a humpback pectoral fin.

In Chapter 1, I determined if herring could be physically contained within the boundaries of an artificial bubble net, and if a school was willing to cross through a bubble curtain when frightened by a predatory stimulus. I also investigated whether the crossing tendency of a herring school is influenced by the relative numbers of fish on each side of the bubble curtain. In Chapter 2, playbacks of humpback feeding calls were used to ascertain if herring could detect these sounds, and if they would respond by reducing inter-individual distance and moving away from the sound source. In Chapter 3, a large moveable model of a humpback flipper was used to test if these fins function to frighten or herd prey toward the whale's mouth. In Chapters 2 and 3, I also discuss the "rare enemy effect" (Charnov 1976, Dawkins 1982) which provides one possible mechanism that could account for the humpback's ability to exploit herring schools with these conspicuous feeding tactics.

Chapters 4 and 5 of this dissertation describe results of field studies of humpback feeding groups in Southeast Alaska. A much clearer picture of underwater foraging activity was required in order to understand the function of the different foraging tactics, and to extrapolate the findings obtained in the laboratory to the wild. For example, if feeding calls are intended to produce an avoidance response from herring and force the fish to the surface, then they should be broadcast from a position below the school. Consequently, the objective of Chapter 4 was to employ a vertical profiling sonar to describe the spatial relationships between fish schools, bubbles, whale dive depths and bottom topography. In this chapter, I also endeavored to quantify some of the temporal aspects of this behavioral interaction such as whale attack speed, herring flight speed, and the rise rate of bubbles in order to construct the first integrated model of humpback whale bubble-net foraging. In Chapter 5, I used photo-identification to characterize the social structure of herring-feeding humpback groups in Frederick Sound and Chatham Strait, Alaska. Tissue was then collected from individuals both within these groups and from the larger humpback population in Southeast Alaska to determine if those individuals exhibiting high coefficients of association (CoA's) were close kin. The results of this study are used to provide an overview of the social structure of Alaskan social pods and to provide insight into the extent to which the interactions between individuals are based on cooperation or competition.

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Chapter 1

The Behavior of Pacific Herring Schools In Response to Artifical Humpback Whale Bubbles*

*Also appears in:

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Abstract

There are numerous reports of humpback whales and other marine predators deploying bubbles during foraging activities. However, the effects of bubbles on schooling prey organisms remain poorly understood. We conducted a series of laboratory experiments to gain insight into the effect of bubbles on the Pacific herring *Clupea harengus pallasi*, a principal prey species of the humpback whale *Megaptera novaeangliae*. The fish were found to exhibit a strong avoidance of bubbles, and could be contained within a circular bubble net. The herring schools were also reluctant to swim through a curtain of bubbles even when frightened. However, herring were much more willing to cross through a bubble curtain or net if there was a relatively larger aggregation of fish on the opposite side. Individuals and small groups of herring also waited less time before crossing than did larger groups. These experiments suggest that herring are strongly frightened by bubbles, and can readily be manipulated or contained within bubble nets by their predators.

Introduction

The release of bubbles during foraging activity has been noted in a number of marine predators including the killer whale *Orcinus orca* (Simila and Ugarte 1993), spotted dolphin *Stenella frontalis* (Fertl and Würsig 1995), grey whale *Eschrichtius robustus* (Volker Deecke, pers. comm.), fin whale *Balaenoptera physalus* (Samuel S. Sadove, pers. comm.), Bryde's whale *Balaenoptera edeni* (Hiroko Wada, pers. comm.), river otter *Lutra canadensis* (F. Sharpe unpub. data), humpback whale *Megaptera novaeangliae* (Ingebrigtsen 1929; Jurasz and Jurasz 1979; Hain et al. 1982, Baker 1985; D' Vincent et al. 1985; Baraff et al. 1991; Weinrich et al. 1992) and several species of alcids (Sharpe 1994). Compared to other predators, the humpback whale is unusual in that it deploys bubbles in a much more elaborate manner, and utilizes bubbles while foraging on a variety of prey species including schooling fishes and euphausiids.

Humpback whales are known to produce a variety of bubble structures, often in conjunction with other unusual feeding behaviors such as the broadcasting of low frequency sounds, group hunting, and the flashing of their very large pectoral flippers at prey (Brodie 1977; Baker 1985; D' Vincent et al. 1985; Sharpe pers. obs.). Ingebrigtsen (1929) first documented the release of air by humpbacks when he noted the species capturing krill in circular bubble nets. Jurasz and Jurasz (1979) made extensive observations in Southeast Alaska, where they described the use of bubble nets on both krill and schooling fishes. In the North Atlantic, Hain et al. (1982) described humpbacks utilizing a number of bubble structures including nets, curtains, and clouds. In addition, there are a number of reports of foraging techniques, including flick feeding and lob tailing, where bubbles are injected into the water column by a rapid moment of the flukes (Jurasz and Jurasz 1979; Hain et al. 1982; Weinrich et al. 1992), which may also constitute a use of bubbles to manipulate prey organisms.

There has been considerable speculation as to how bubbles assist in capturing prey. Most observers have noted that predators use bubbles to frighten or herd prey, although it is not known specifically if it is the acoustic, visual, or mechanical characteristics of the bubbles, or a combination of these attributes, that elicits a response from fish. Ingebrigtsen (1929) suggested that bubbles were visually detected by krill and were used to frighten the crustaceans into the center of bubble nets. Jurasz and Jurasz (1979) noted that bubbles could be used to contain prey spatially and serve as a barrier against which to herd them. Hain et al. (1982) suggested that bubbles may aid in the detection of prey or serve to mask the approaching whale. Weinrich et al. (1992)

speculated that the bubble cloud produced by a lob tailing whale may mark a spot of high prey concentration for the subsequent lunge. Experiments in the laboratory found that herring could avoid a curtain of air bubbles in the dark, suggesting tha the fish were not relying on vision to detect the air curtain (Blaxter and Batty 1985). Laboratory experiments by Akiyama et al. (1992) found that jack mackerel *Trachurus japonicus* also avoid bubble curtains during both light and dark conditions. In one of the few attempts to replicate humpback whale bubble structures in the laboratory, Kieckhefer (1991) found that small bubbles could disorient euphausiids and drive them to the surface. The effectiveness of bubbles in containing the movement of fish schools has also been demonstrated by their use in small scale bait fishing operations (Smith 1961). In this commercial application, a bubble curtain is used to trap fish within the upper portion of a fjord during high tide, thus permitting easier capture.

Although previous studies have been instructive, there have been no attempts to bring schooling fish into the laboratory to test their response to bubble structures similar to those produced by humpback whales. We conducted a series of laboratory experiments with the objective of gaining insight into the effect of bubbles on fish schooling activity. These experiments examined if Pacific herring *Clupea harangus pallasi* could be physically contained within the boundaries of a bubble net, and if a herring school was willing to cross through a bubble curtain when frightened by a predatory stimulus. We also conducted a third experiment when we found that the crossing tendency of a herring school appeared to be influenced by the relative numbers of fish on each side of the bubble curtain. In particular, we noted that small schools tended to escape from the bubble net more frequently than large schools. In our study, we tested the following predictions: 1) a herring school will spend more time in the confines of a bubble net relative to an equivalent space in a no-bubble control, 2) herring will avoid crossing a bubble net even when exposed to a predatory stimulus, and 3) a school will cross through a bubble curtain more frequently, and will wait less time before initiating a crossing, the larger the school is on the opposite side of the net.

Materials and methods

This study was conducted at the West Coast University Marine Biological Station, Bamfield, B.C., during the spring of 1993 and 1994. Experiments were conducted indoors in a large (200,000 l) circular aquarium measuring 2.8 m in depth and 27 m in circumference. A smaller outdoor circular tank (1.7 m depth x 3.1 m circumference) was used for the group-size crossing experiments. Lighting for the indoor tank was provided by four 200 watt flood lamps and from indirect light entering through a 1 x 0.6 m hole in the ceiling. Bubble structures were produced by turning a control valve which allowed 50 PSI compressed air through 5 cm PVC tubing perforated with 0.3 mm holes. The perforated PVC was anchored to the tank floor by securing it to two additional PVC pipes packed with gravel. The bubble curtain produced in this way resembled those produced by humpback whales, in terms of both over all circumference and individual bubble diameter (Hain et al. 1982; pers. obs.).

The herring used in the experiments were live-captured in Bamfield Inlet, Barkley Sound on 2 June 1993 and 20 May 1994 with a 60 m hand seine. The fish were taken from a stock of prespawning 2 year olds averaging 14 cm in total length and weighing 22 g. Care was taken to minimize stress to the fish by quickly transferring them to the Station where they were placed in a dark, outdoor circular (1.7 x 3.1 m) holding tank. Any fish exhibiting more than 15% scale loss or abnormal schooling behavior were removed from the experiment.

Experiment 1: Bubble net crossing

This objective of this experiment was to test whether a herring school encircled by a bubble net would have its movements restricted compared to a control school without bubbles. A total of 18 trials were conducted, 10 during the spring of 1993 and 8 during the spring of 1994. The bubble net was produced by placing a 6.5 m diameter ring of perforated PVC tubing on the center of the aquarium floor, approximating the size of nets produced by humpback whales in the wild. The tubing was drilled with 22 holes spaced about 0.3 m apart. When the air valve was turned on, water was gradually displaced from the tube, with the hole closest to the high pressure line being the first to produce a bubble column. As water continued to be displaced from the tube, each of the holes produced a bubble column in a clockwise succession, resulting in a circular bubble curtain (comprised of coalescing columns) that took approximately 7 s to fully close. Each bubble column was composed of a dense, cone-shaped air jet with individual bubbles ranging in size from a few mm to 15 cm in diameter. A floating breakwater constructed of transparent plastic was floated in the center of tank, producing a smooth pool of water (5.5 m diameter) which permitted videotaping through the surface turbulence created by the bubbles. Fish behavior was recorded with a video camera located 5 m above the water's surface. Analysis of the video was conducted with a VHS freeze frame player.

On the evening prior to each experiment, a school of 50 fish was placed into the large tank and permitted to acclimate overnight. The bubble treatment commenced the following morning by videotaping the school of 50 fish when it made a crossing through the center of the tank. If 25 or more members of the school crossed inside the ring of PVC tubing, the air valve was turned on. If it at least one individual was trapped within the confines of the bubble net, the net remained on until all the fish escaped. If no fish escaped, the air was turned off after 60 s. If the entire school escaped the bubble net before it closed, the air was immediately turned off and a five minute waiting period ensued prior to the next trial. A similar procedure was conducted for the controls, except that the air was not turned on. Each of 18 schools received both the control and bubble treatments, in random order. The crossing durations (i.e., the time it took 50% of the school to cross from the inside of the PVC ring to the outside) in the control and treatment trials were then compared with a Wilcoxon signed-rank test. Crossing frequencies were compared for schools of different size (Kruskal-Wallis test).

Experiment 2: Fright stimulus and crossing tendency

The purpose of this experiment was to determine whether a herring school could be induced to swim through a curtain of bubbles if frightened. The experimental apparatus consisted of a perforated PVC pipe laid down along the centreline of the large aquarium. The pipe was drilled with 26 holes spaced 34 cm apart. A floating breakwater was placed above the PVC pipe, providing an undisturbed section of water on one side of the curtain for videotaping. The procedure for acclimating the fish and recording their behavior was the same as in Experiment 1.

Each treatment began by turning on the bubble curtain to trap the school on one side of aquarium (chosen at random). The bubble curtain remained on for 60 s during which time the school was exposed to a fright stimulus consisting of 5 thrusts with a plunge pole (a 15 cm diameter rubber plunger on the end of a 3 m PVC pole). Thrusts of 1.5 m were delivered at 10 s intervals from a stationary point and directed toward the school. Crossing events were tallied each time an individual fish, or the entire school, crossed the tank centerline in either direction. A school was considered to have crossed when 50% or more of the individuals swam over the centerline. The same procedure was conducted during the controls, with the exception that the bubble curtain was turned off. A total of 10 schools were tested, with each of the schools receiving both the control and experimental treatment. The numbers of crossings in the controls and treatments were then compared with a paired-t test.

Experiment 3: Crossing tendency and group size

The purpose of this experiment was to examine the effect of group size on crossing tendency. This was done by varying the number of fish on each side of a bubble curtain to determine if a smaller group exhibited a greater tendency to cross over to the larger school. This experiment was conducted in the outdoor circular tank outfitted with a perforated PVC pipe laid down the centerline. The pipe was drilled with 11 holes placed 15 cm apart. Each trial utilized a group of 8 fish which was permitted to acclimate to the tank for a minimum of 3 h prior to testing.

The experimental procedure involved varying the number of fish on each side of the bubble curtain so that all five possible combinations of group sizes were tested (8-0, 7-1, 6-2, 5-3, and 4-4) for each school of fish. In order to minimize any bias in crossing due to the features of the tank, each combination of fish was tested twice, with the numbers on each side of the bubble curtain reversed (i.e., 8-0, 0-8; 7-1, 1-7; etc.). This resulted in a total of ten crossing tests for each batch of fish. The order in which each of the 10 combinations of herring group sizes were tested was randomized. At the start of each trial, the fish were split into two appropriately sized groups by turning on the bubble curtain as the school passed over the centerline. The time until the first fish crossed through the bubble curtain (from either direction) was recorded. If there were no crossings, the air was shut off after 60 s. A five minute waiting period was implemented before the next trial was conducted. This process was continued until all 10 combinations were tested. A total of 32 different batches of fish were tested in this fashion. The time waited prior to crossing for each group size was then compared using a Kruskal-Wallis and Chi-square test.

Results

Experiment 1: Bubble net crossing

Fish schools encircled by the bubble net spent a mean of 52.8 s in the center of the tank, while controls spent a mean of 3.9 s there (Table 1.1). Fish were significantly more likely to remain in the center portion of the tank when encircled by a bubble curtain (Wilcoxon signed-rank test, $p>.0002$). This clearly indicates that a circular curtain of bubbles can spatially contain the movement of a herring school. We compared the frequency of outward crossings (escapes) for trials with (a) 1 to 24, (b) 25 to 40, and (c) 41 to 50 herring initially captured in the bubble net. Crossing frequency differed significantly between these three groups (Kruskal-Wallis, P value = 0.0048). Indeed, on the five occasions when the entire school was captured in the bubble net, no escape crossings occurred. However, when smaller groups were captured in the net, the proportion of individuals escaping during the 60 s trial was much higher (means of 73.2% and 12.8% for group sizes 1-24 and 25-40, respectively). And on several occasions, small groups of fish were noted to swim into the bubble net (through the closing gap) in order to join a larger group of herring on the inside of the net.

Experiment 2: Fright stimulus and crossing tendency

A mean number of 5.8 individual fish (SD = 12.9) crossed the bubble curtain during the treatments (Table 1.2A). In contrast, the mean number of individual crossings during the no bubble controls was 178.6 (SD = 48.6). Fish were significantly less likely to cross the centerline of the tank (paired t-test, p>.0001) when the air curtain was turned on. Similarly, whole school crossing events were significantly less common (paired t-test; p>.0001) during the bubble treatments (X=0.1, SD = 0.31) compared to the no bubble controls (X=3.3, SD =3.3; Table 1.2B).

Experiment 3: Crossing tendency and school size

As was the case in Experiment 1, there was a correlation between group size and crossing tendency, with smaller groups more frequently swimming across the bubble curtain to join the larger group (Table 1.3). For example, in the 1-7 trials, the solitary individual initiated the crossing on 88% of the trials. In the 8-0 trials, the school exhibited a strong tendency to remain on one side of the tank, with no crossing occurring in 70% of the trials. Smaller groups also waited less time before crossing (Figure 1.1, Kurskal-Wallis, P < .0001).

Discussion

Taken as a whole, these experiments reveal that herring take strong evasive action to avoid bubbles and are reluctant to swim through a curtain of bubbles, even when frightened. Bubble nets are capable of spatially containing an aggregation of herring, even in regions of the tank they normally avoid (i.e., the center). The tendency of individuals to cross through a bubble curtain is strongly mediated by relative group size, with individuals or small groups of fish more likely to cross if there is a larger group on the other side. In addition, individuals and small groups wait less time before crossing than larger groups. This study also found that a herring school would swim into a closing bubble net if a larger group of fish occurred on the inside.

These findings confirm field observations that humpback whales use bubbles to manipulate prey behavior by constraining the movement of fish schools. The strong avoidance responses of herring noted in the laboratory suggests that whales may use bubbles to herd fish into more exploitable spatial arrangements (such as tight aggregations) or force the school upward in the water column, thus trapping them against the surface.

That fish will cross through a bubble curtain to join a larger group (a minority departure rule) has previously been reported (without any supporting data) by Radakov (1973), and is analogous to the findings of other studies. For example, Hager and Helfman (1991) found that minnows in the presence of predators chose larger shoal sizes, made their choices more quickly, and exhibited a heightened ability to discriminate shoal size. Itazawa et al. (1978) noted that fish in smaller groups are more nervous and have higher respiratory rates. In the wild, the size of herring schools are known to fluctuate widely over a 24-hour period (Carson 1984; Robinson 1991). Consequently, the size of the school may be an important factor in determining how the fish respond to an enclosing bubble net deployed by humpbacks. The observation in this study of fish entering a closing bubble net suggests that a bubble net may have a capture area greater than its actual diameter, if fish outside the net are enticed into it by a larger group on the inside.

Given the general reluctance of herring to cross through bubble curtains, it was rather puzzling to find in Experiment 3 that fish in the 0-8,8-0 trials crossed fairly regularly to the side with no fish. Schools of eight waited a relatively long time to cross ($\overline{X}$=22.0 s) and perhaps became somewhat habituated to bubbles and therefore more willing to do so. In addition, it was frequently a single fish that crossed over after becoming separated from the main school. The increased vulnerability of a solitary individual to predators (see below) may favor actions that increase the likelihood of a lone fish promptly relocating school mates.

Most studies that have examined the interactions between predators and fish schools have studied predators that focus their attacks on solitary individuals. These studies have demonstrated that individuals separated from a group are more likely to be captured by a predator (Magurran and Pitcher 1987; Godin and Smith 1988; Parrish et al. 1989) and that the success of aquatic piscivores decreases when prey group size increases (Neill and Cullen 1974; Milinski 1979; Tremblay and FitzGerald 1979; Poole and Dunstone 1975). Such feeders (fish, seabirds, and pinnipeds) may be the dominant predator type encountered by herring and other bait fishes; thus, their best strategy will usually be to close ranks whenever threatened. It is interesting to note, however, that these schooling behaviors appear to be less effective, or even detrimental, in response to bulk-feeding predators such as baleen whales. When the air was first turned on during each of the trials in this study, any fish located near or above the rising bubble plumes reacted with a strong flight response directly away from the bubbles. In the wild, fish may perceive rising bubbles as an approaching predator, and thus execute an inappropriate response to the bulk-feeding humpbacks below.

It is not known if it is the acoustic, mechanical, or visual characteristics of rising bubbles that are most frightening to herring and other schooling fishes. It is likely, however, that the effectiveness of these three stimuli varies under different environmental conditions. As a fish swims it generates a wake of counter-rotating vortices (Pitcher and Parrish 1993). Schoolmates appear able to detect these vortices using otoliths and lateral line organs up to one fish length away, and can use them to synchronize schooling activities (Gray and Denton 1991). The strong mechanical disturbance created by rising bubbles (Fan and Tsuchiya 1990) may be disruptive to the school's flow regime, thus making effective avoidance maneuvers more difficult. This appears similar to Strand and Hamner's (1991) finding that krill *Euphausia superba* were reluctant to school in turbulent water, apparently due to the confusing rheotactic (mis)information compared to the normal turbulence produced when swimming. In one of the few other attempts to replicate humpback whale bubble structures in the laboratory, Kieckhefer (1991) found that small bubbles could disorient euphausiids and even drive them to the surface due to micro-bubbles trapped underneath their carapaces or adhering to their feeding appendages.

Our experiment found some evidence that herring may also be responding to the acoustic and visual components of rising bubbles. When the bubble net or curtain was first turned on, fish up to several meters away (well beyond the range of mechanical influence of the bubbles) would respond with pronounced startle or avoidance maneuvers. Playbacks of bubble sounds were found to produce a moderate avoidance response from herring, further suggesting that the acoustic component of a bubble structure may be used to manipulate fish behavior by wild humpbacks (F. Sharpe, unpubl. data). Observations of humpbacks deploying bubble nets at night (L. Dawson, pers. comm.) further implicate acoustic or mechanical influences. However, the possibility that herring are responding to the visual component of bubbles at night cannot be ruled out, as bioluminescent organisms may make bubble nets highly visible. Further field investigations are required to better understand how varying environmental conditions influence the manner in which fish schools respond to bubbles. However, this study provides strong evidence that the deployment of air can be a highly effective tool for humpback whales and other predators of schooling fishes.

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Trial	Caught (of 50)	Proportion Caught	Escaped	Proportion Retained	$T_{treatment}$	$T_{control}$
1	17	0.34	1	0.94	60	3
2	20	0.40	20	0.0	28	6
3	25	0.50	0	1.0	60	7
4	31	0.62	0	1.0	60	2
5	32	0.64	5	0.84	60	4
6	35	0.70	0	1.0	60	4
7	38	0.76	17	0.55	60	3
8	50	1.0	0	1.0	60	8
9	50	1.0	0	1.0	60	5
10	50	1.0	0	1.0	60	6
11	36	0.72	4	0.89	60	2
12	28	0.56	3	0.90	60	3
13	50	1.0	0	1.0	60	4
14	16	0.32	16	0.0	14	1
15	50	1.0	0	1.0	60	7
16	22	0.44	22	0.0	9	2
17	10	0.2	4	0.4	60	3
18	26	0.52	0	1.0	60	1
$\bar{X}$					52.8	3.9
SD					16.8	2.1

Table 1.1. Initial capture and retention success of the artificial bubble net (Exper. 1). Proportion caught represents the proportion of the herring from the school of 50 individuals that were initially trapped inside the bubble net. Proportion retained represents the proportion of the school remaining in the bubble net after 60 s. $T_{treatment}$ represents the time the bubble net remained turned on. (Note that if the entire school escaped, the bubbles were turned off before the 60 s trial time had elapsed.). $T_{control}$ is the time required for 50% of the fish to leave the equivalent space when no bubbles were present.

Treatment	N	$\bar{X}$	SD	P (2-tailed)
A. Individual fish				
bubbles	10	5.8	12.9	
no bubbles	10	178.6	48.6	.0001
B. Whole schools				
bubbles	10	0.1	0.31	
no bubbles	10	3.3	0.82	.0001

Table 1.2. The influence of bubbles on the tendency of herring to cross the centreline of a large aquarium (Exper 2). A. Individual fish crossings. B. Whole school crossings.

Group size combinations	No. of events crossing to greater	Time to cross to greater (s)	No. of events crossing to smaller	Time to cross to smaller (s)	No. of events without crossings	P
0-8, 8-0	-	-	19	22.0*	45	
1-7, 7-1	56 (88%)	7.4	6	16.5	2	>.001
2-6, 6-2	44 (69%)	12.3	16	16.1	4	>.001
3-5, 5-3	41 (64%)	11.4	19	14.0	4	>.001
4-4, 4-4	52 (81%) *	11.8 *	-	-	12	

* with a group size combination of 4-4, there is, of course, no larger or smaller group.

Table 1.3. The influence of relative group size on the willingness and speed with which herring cross a bubble curtain (Exper 3). Columns 2 and 3 show the number of times that an individual crossed from the smaller to the larger group, and the mean time required to do so, respectively. The numbers in parentheses in column 2 represent the percentage of events (out of 64) where the fish crossed from the side of the net with fewer to side of the net with more fish. Columns 4 and 5 present the data for crossings of individuals from the larger to the smaller group. The penultimate column shows the number of occasions (out of a total of 64 trials on 32 schools) in which no crossings occurred. The p-value is from a X^2-test of the hypothesis that the direction of first crossing is independent of the relative numbers of fish on the two sides of the bubble curtain.

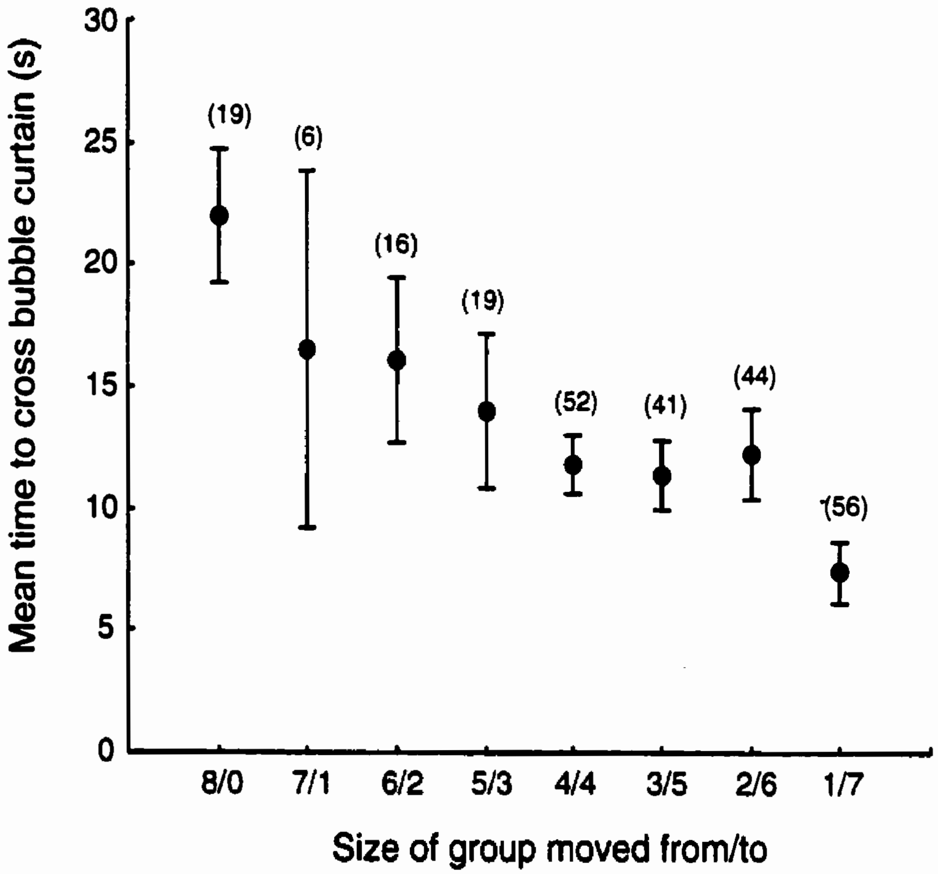

Figure 1.1 The mean time required for an individual herring to cross the bubble net, plotted against the size of its school, relative to that on the other side of the net (Exper. 3).
For example, if there were initially 7 fish on one side and 1 on the other, it took an average of 16.5 s for one of the fish from the school to cross the net, and this happened infrequently (n=6); much more often (n=56), and more quickly (mean = 7.4 sec), the lone individual crossed to join the group. Every group size combination was tested 64 times, twice for each of 32 herring schools.

Chapter 2

Does the humpback whale use feeding calls to manipulate fish schools?

Abstract

Alaskan humpback whales *Megaptera novaeangliae* produce loud trumpet-like calls underwater when feeding on schools of Pacific herring *Clupea harengus pallasi*. It has been theorized that these sounds are associated with 1) agonism, 2) group coordination, or 3) the manipulation of herring schools. In this study, the prey manipulation hypothesis was tested by conducting playbacks of humpback feeding calls to herring schools in the wild, in net pens, and in a large onshore tank facility. Specifically, I tested the predictions that herring can detect the feeding calls, and in the open water environments show an avoidance response. I also predicted that the feeding calls would result in compaction of the herring schools. Support for the prey manipulation hypothesis was found, as herring in each of the different settings modified their behavior in response to the calls. The herring in the open water environments (net pens and wild) showed a significant tendency to flee away from the source of the playback and to decrease inter-individual distance. In the wild, a clumping and fleeing response would be advantageous for the whales, as this would drive the prey upwards where it could be encircled in a bubble net and trapped against the surface. Herring are known to possess acute hearing, suggesting that they may be particularly vulnerable to such acoustic exploitation. The ability to manipulate prey with sound represents an unusual hunting tactic, and may represent an example of the rare enemy effect.

Introduction

Relative to many other aquatic predators, very little is known about the manner in which baleen whales interact with their prey. Baleen whales possess enormous mouths and feed by engulfing large amounts of prey-laden water into an expandable throat pouch (Nemoto 1970, Pivorunas 1979). Closing its mouth, the whale filters the water back out through baleen plates, thus retaining the prey which are then swallowed. In order to maximize ingestion rates, most baleen whales specialize on locally abundant species such as schooling fish, squid, and crustaceans.

Although considerable research has been conducted on the anti-predator benefits of schooling, nearly all previous studies have looked at interactions with smaller predators such as fish, seabirds, pinnipeds, and odontocetes. Collectively, these smaller predators are referred to as raptorial feeders, which forage quite differently than baleen whales. Instead of engulfing prey, raptorial feeders capture prey by seizing a single individual, or a few individuals per attack. When confronted by a raptorial predator, a basic response of fish schools is to flee directly away (Edmunds 1974, Howland 1974, Keenleyside 1955, Weihs and Webb 1984, Sih 1987) and "close ranks", which reduces the distance between individuals (Breder 1951, Ruppell and Gosswein 1972, Andorfer 1980, Pitcher and Wyche 1983, Magurran et al. 1985, Pitcher and Parrish 1993). In this study, I examine whether baleen whales engage in tactics to elicit these fright responses from fish schools, thereby making them easier to herd toward the surface and engulf with their large mouths.

Among the great whales, the humpback *Megaptera novaeangliae* is noteworthy in that its engulfment feeding occurs in conjunction with a variety of other unusual foraging behaviors. These include the formation of large social groups (Baker 1985), the deployment of bubble structures (Jurasz and Jurasz 1979, Hain et al. 1982, Sharpe and Dill 1997), and movements of their large pectoral flippers while lunging through prey aggregations (Sharpe, pers. obser.). Some of the most complex foraging behaviors have been observed in Southeast Alaska where pods of up to 20 individuals simultaneously attack schools of Pacific herring *Clupea harengus pallasi* (Greenough 1981, Giddings 1984, Baker 1985, D' Vincent et al. 1985). A striking feature of these pods are the loud, trumpet-like feeding calls which are produced as they approach and engulf herring schools (Jurasz and Jurasz 1979, Baker 1985, D' Vincent et al. 1985). These calls consist of a series of repetitive narrow bandwidth tones (called phrases) which are typically constant in amplitude (**Fig 2.1**). Although most calls tend to be uniform in frequency, they may also possess subtle oscillations, and terminate with a pronounced rise or fall in frequency

(D' Vincent et al. 1985). These calls typically have most of the energy concentrated in the fundamental frequency, which ranges from 350 to 1200 Hz. The calls may also possess multiple harmonics, which can range in frequency up to 8 kHz (Baker 1985, D' Vincent et al. 1985). Each time a pod feeds, they typically produce from 5 to 30 of these phrases, with each phrase lasting about 3 s (Cerchio and Dahlheim, in press). Sonar studies (Chapter 4) have suggested that the whales forage by diving down near the bottom and broadcasting these sounds from a position below the herring schools. The calls continue as the whales rush the school from underneath and force the herring up toward the surface. During this herding and vocalizing, the whales force the rising school into a vertical cylinder of bubbles, which serves to contain the school as the whales engulf the fish at the surface (Sharpe and Dill 1997). One whale typically produces most of the vocalizations, although additional individuals often begin chorusing (on the last few phrases) as the group rushes to the surface (Baker 1985).

These feeding calls are of interest, as most predators typically avoid displaying conspicuous behaviors that signal their presence or position to potential prey (Bradbury and Vehrencamp 1998). It has been suggested by Baker (1985) that these sounds are associated either with 1) agonistic interactions, 2) group coordination, or 3) manipulation of herring schools to facilitate capture by the whales. In this study, playbacks were conducted to herring schools in order to test Baker's prey manipulation hypothesis, which posits that humpbacks use these sounds to herd and coalesce herring schools. The playbacks were performed on schools in different environments including the laboratory, open water net pens, and the wild. I predicted that the herring would detect these calls, and in the net pen and wild (where sound reflection was not a confounding factor) respond by closing ranks and moving away from the sound source. The results were used to evaluate how the feeding calls might function in the wild, by exploiting the anti-predator behavior of their prey. I also discuss the rare enemy effect (Dawkins 1982), which provides one possible mechanism that could account for the humpback's ability to exploit herring schools in this fashion.

Methods

The playbacks were conducted in two basic settings: a large laboratory tank and the open water environments of net penned and wild herring schools. The feeding calls used in these playbacks were recorded in Southeast Alaska from free-ranging pods foraging on herring schools.

Playbacks in the laboratory

The laboratory tests were conducted at the West Coast University Marine Biological Station (WCUMBS), Bamfield, B.C., Canada, during the months of April-June of 1993 and 1994. The experiments were carried out indoors in a 200,000 l circular concrete tank measuring 2.1 m in depth and 27 m in circumference. Lighting was provided by 4-200 W flood lamps, and from diffuse natural light entering through a 0.7 x 1.5 m opening in the roof of the building in which the tank was housed.

Herring were captured with a 60 m hand seine in a nearby inlet. The fish were prespawning 2-year olds with a mean total body length of 14 cm and mean weight of 22 g. Care was taken to minimize stress by quickly transferring the fish to the research station where they were placed in a covered, 4 m^3 circular holding tank. Any fish exhibiting more than 15% scale loss or abnormal schooling behavior were removed from the holding tank. Prior to each experiment, a school of 50 fish was placed in the experimental tank and allowed to acclimate overnight. The fish typically maintained a single, fairly compact school that avoided the central portion of the tank and swam around the perimeter.

The playback system consisted of an Aquavox underwater speaker, a 100 w amplifier, and a Sony TKD cassette tape deck. Sound pressure levels of the feeding calls ranged from 130 to 135 dB re 1μPa-m. The speaker was placed 10 cm above the bottom along the northeast wall of the tank. The playback experiments began by turning on the speaker when the school passed directly in front of it. Each playback trial lasted 60 s. School responses were recorded with a video camera mounted on the rooftop and directed down through the opening in the roof, 4.5 m above the center of the tank. Two playbacks were performed: one of whale feeding calls, the other a blank tape control. The order of the treatment and control playbacks was randomized, with each school (n=9) receiving a single treatment and control.

Five measures of school behavior were adopted from Schwarz and Greer (1984). These measures were recorded from the video tape for each 60 s trial. (1) Swimming speed was measured as the time it took the school to travel 6.5 m, or 1/4 of the tank's circumference; (2) A direction change was counted each time 25 or more of the fish in the school turned more than 150° after having traveled along a straight path for at least 1 m; (3) The frequency of school splits was measured by counting the number of times two or more fish departed the school for more than 3 seconds; (4) Time in the center of the tank was measured as the number of seconds that 25 or more members of the school were located inside a 7.5 m diameter ring placed in the center of the tank; (5) School circumference was obtained by measuring the distance around the convex perimeter of the school. Given that the herring may have had difficulty in localizing the sound source in the laboratory (due to reflection off the tank walls), I limited my interpretation of these laboratory results to whether the herring could detect the sounds. However, the next series of playbacks in open water net pens eliminated the problem of sound reflection, thus permitting a more comprehensive analysis of the fishes' flight response and change in spacing among individuals.

Playbacks in open net pens

Playbacks were conducted at Port Gamble, Washington, USA, during October and November of 1999. The herring were part of a live commercial bait fish operation, and were housed in 10 rectangular net pens 16 x 8 x 5.5 m deep at mean low water. Individual herring averaged 18.5 cm in length and had been captured during the previous two months with seine nets.

Playbacks were conducted at night when background noise levels were much reduced. In addition the fish were closer to the surface and could be more easily observed without daytime surface glare. Lighting was produced by a 200 W flood lamp situated on a 4.5 m pole in the middle of the net pens, and a portable 100 W flood lamp affixed 1.3 m above each pen. The playback system consisted of a CD player (Panasonic SL-S360) and 100 watt amplifier (Alesis RA) connected to an underwater speaker (135 watt Clark Synthesis Tactile Sound Transducer; frequency response; 20 to 20,000 Hz). Sound pressure level of the feeding calls was estimated at 145 to 150 dB re 1uPa-m. The speaker was placed at a depth of 2 m inside the net pen, 10 cm from netting. A hydrophone (Offshore Acoustics) was placed in the water and connected to a DAT player (Sony TCD-D7) and headset to monitor sound levels.

Eight experimental groups of herring were used. Since the herring were part of a commercial operation, I could not closely control the size of each school. However, it was estimated that each pen contained from 10,000 to 20,000 individuals. The fish tended to space themselves uniformly within each pen, thus producing a single large aggregation that swam clockwise or counterclockwise about its own axis. Between playback trials, the herring normally swam past the playback speaker at 1-3 body lengths per second. Using the portable flood lamp to illuminate the water, a circular test area approximately 3.5 m in diameter was established in front of the speaker. The light's beam was positioned so that it would obliquely illuminate the fish, but was not sufficiently strong to cause an avoidance response. In this way, it was possible to monitor fish behavior to a depth of about 4 m.

Each school received a total of eight different playbacks. Two of the playbacks (400 & 800 Hz) were feeding calls while a third consisted of "social sounds" (300 to 2000 Hz), which are routinely produced by groups of foraging humpbacks in between feeding bouts. Three pure tones were used (200, 450, and 800 Hz) and a white noise sample with a frequency bandwidth from 15 to 11,000 Hz. Both the tones and white noise were obtained from sample sounds included with Canary Software version 1.2©. A single control sound was used consisting of blank DAT tape. The order in which the sounds were played was randomized for each school. Relative to the shore-based tank, the fish tended to return to pre-stimulus condition much more rapidly, so a shorter playback period (10 s) was used.

Five measures of school behavior were recorded. The first was the angle at which the fish took flight from the speaker. Since the fish in the pre-stimulus condition swam past the speaker at right angles to its broadcast direction, this measure was estimated as the modal change in swimming direction (degrees) in response to playback. The second measure was the aggregate increase in fish speed in response to the playback. The third was an alarm response index adapted from Schwarz and Greer (1984) to describe the change in polarization: 0 = no response; 1 = avoidance (slight polarization); 2 = alarm (mild polarization); 3 = startle (strong polarization). The fourth measure was the percentage of fish that departed the 3.5 circular test zone at the end of the 10 s playback. I also noted if the spacing between individuals increased, decreased, or remained unchanged following the playback.

Wild playbacks

Playbacks were conducted around the floating docks of the WCUMBS in July, 1999. These were conducted at night when the fish were close to the surface and could be observed with the dock's overhead flood lamps. A rectangular patch of open water (3 x 2.5 x 3-4 m depth) situated between the docks served as the test area. Observations were made from a walkway that extended from shore to the floating dock 2.5 m above the water surface. The speaker was placed at a depth of 1.5 m, just outside the illuminated test area. Similar to the net pens, a 10 s playback duration was used. However, since the presence of wild schools around the docks was unpredictable and ephemeral, it was not possible to use the larger set of playback treatments employed in the net pen. Consequently, the playback methods followed the same procedure as the laboratory tests, where only randomly presented feeding calls and blank tape controls were used.

A playback was initiated when a herring school swam past and occupied at least 90% of the test area. A waiting period of at least 5 minutes was established between successive playbacks, permitting new individuals to drift or swim into the area, so that each playback was likely conducted on a different group of fish. Similar to the net pen experiments, I measured changes in speed, and the percent of the school departing the test area, as well as noting changes in school density. However, instead of measuring the flight angle away from the speaker, I recorded the number of times the school changed direction (at least 50% of the fish in the test area turned 150°). Playbacks were carried out on 7 schools of herring, each containing approximately 300 individuals estimated to be approx. 24 cm in length. For these playbacks, an Oceanears speaker and amplifier system were connected to a Macintosh Powerbook 180. The feeding call sounds were played directly from Canary software© files producing sound pressure levels estimated at 125 to 135 dB re 1uPa-m.

Results

Playbacks in the laboratory

Laboratory playbacks were conducted on nine different schools of herring. The results of each of the behavior measures are listed in **Table 2.1**. Significant changes in school behavior were noted in the directional changes, splits, and school circumference, all of which increased **(Table 2.1)**. Although there was a tendency of the fish to increase both their swimming speed and time in the center of the tank, neither of these measures were found to be significant. Given that 3 of the 5 responses were significantly different, I concluded that herring are able to detect the feeding call sounds.

Playbacks in open net pens

All quantitative measures of herring behavior were highly correlated for all pairwise combinations ($P \leq .0001$, r^2 ranged from .76 to .91) indicating that Principal Components Analysis would be suitable for the analysis of school responses. PC1 explained 83% of the variation in behavior **(Table 2.2)** and all response variables had similar loadings (range = 0.49-0.50). All other axes accounted for ≤ 8 % of the variation in the herring's escape response and will not be considered further.

Each of the treatment pairs were contrasted using a sequential Bonferroni procedure. Other than the blank tape control, the herring responded to all the sounds, with the 200 Hz test tone producing a significantly greater response than all other treatments **(Table 2.3, Figure 2.2)**. In general, the responses to all of the treatments were similar, and tended to differ only in magnitude. Similar to the finding of Schwarz and Greer (1984), the fish did not approach the speaker during any of the playbacks;

instead they avoided the sounds by fleeing away from the speaker, increasing swimming speed, increasing polarization, decreasing inter-interindividual distance, and departing a portion of the test area.

Wild playbacks

All three of the behavioral measures were significantly different between the playback treatments and the controls (**Table 2.4**). In response to all the feeding call playbacks, the fish increased their speed, increased directional changes, decreased their inter-individual distance and moved partially out of the test zone.

Discussion

The results from each of the playback experiments demonstrated that herring can readily detect humpback whale feeding calls, Both the wild and net pen playbacks elicited strong and predictable directional movement away from the speaker, and also resulted in an increase in school density. These findings corroborate earlier studies of net-penned herring (Schwarz and Greer 1984) which showed that herring clump and move away from synthesized sounds of similar frequency to humpback calls. Taken together, the findings of Schwarz and Greer (1984) and those of the present study support Baker's (1985) hypothesis that the function of the humpback whale's feeding calls is to herd and coalesce herring schools.

Compared to the blank tape controls, all of the sound treatments in the net pens produced significant behavioral responses, demonstrating that herring detect and react to a variety of different sounds. This corroborates earlier studies (Enger 1967, Olsen 1969, 1976) which found that the Atlantic herring, *C. h. harengus* , a subspecies with the Pacific herring, can detect sounds over a frequency range between 30 and 10,000 Hz. Despite this broad range, certain sound characteristics produce stronger negative responses from herring. In general, sounds that are loud, low frequency, pulsed and broadband are most effective at modifying herring behavior (Enger 1967, Olsen 1969, 1976, Schwarz and Greer 1984). Some of these features are evident in the feeding calls, suggesting they are suitable for prey manipulation. For example, Thompson et al. (1986) found that Southeast Alaskan humpbacks produce social sounds with source levels of 177-188 dB re 1μPa-m. Although the source level of feeding calls has not been measured, it has been my field experience that they can consistently be detected at greater distances than social sounds, suggesting that they possess source levels that are equivalent to, or higher than social sounds. Given the diversity of humpback call types (**Fig. 2.1**) ranging from nearly pure tones to those with extensive harmonics and/or strong frequency modulation, it may be sufficient for humpbacks to simply produce loud sounds within a general frequency range to get the desired response from the school. Another feature of the humpback's calls consistent with a manipulative function is their relatively low fundamental frequency. Nearly all calls possess a fundamental between 390 and 950 Hz which overlaps with the herring's region of maximal hearing sensitivity (500 Hz and below; Blaxter and Holiday 1958, Hering 1968, Olsen 1969, 1976, Baker 1985). The discrepancy between the frequency of the feeding call and the herring's maximal hearing sensitivity may be associated with tradeoffs for other vocal functions (i.e., singing, social sounds). Many of the calls exhibit slight frequency oscillations, which may effectively increase the fundamental's bandwidth and impart a pulsed quality to the calls, further enhancing their effectiveness.

Among the sound treatments used in the net pen, only the 200 Hz test tone produced significantly greater responses compared to the other sounds. That the 200 Hz test tone produced the strongest response is consistent with earlier findings, that lower frequency signals are more effective at producing negative responses from herring (Blaxter and Holiday 1958, Hering 1968, Olsen 1969, 1976). The strong response to the test tones may also be associated with their relatively rapid rise in amplitude, which has previously been shown by Schwarz and Greer (1984) to elicit stronger responses than sounds with slower rise times. That the feeding calls consistently produce stronger responses than social sounds (flight angle, speed, and departure from the test area), and that they possess a different structure from both social sounds and songs, further suggests that they are specifically produced by the whale for prey manipulation. It has been previously recognized that feeding calls possess a distinct tonal (D'Vincent et al. 1985), or trumpet-like quality (Baker 1985), and that concentrating the sound energy in a particular frequency may be the most effective tactic for modifying prey behavior. During the final rush on the school, individual phrases tend to become longer in duration (D' Vincent et al. 1985) and additional whales initiate calling (Baker 1985), suggesting that maintaining an uninterrupted source of acoustic energy is more important than pulsing the call.

That feeding calls are used for prey manipulation is also supported by field observations of herring-feeding humpback groups. Sonar studies (Chapter 4) found evidence that humpbacks feed by diving down near the bottom, and broadcast the calls from a position below the herring schools. The whales then rush the school from underneath while continuing to vocalize, and force the school up into a bubble net and against the surface. Herring are known to have good sound localization capabilities

(Blaxter and Holiday 1958, Hering 1968, Olsen 1969, 1976, Schwarz and Greer 1984) suggesting that they can readily localize the feeding calls when the whales broadcast these sounds from below. This strategic position may prevent schools from diving toward the bottom, which is a well documented escape response in herring (Wardle 1993, Olsen 1970, Nottestad 1998). The feeding calls may also help keep the school contained, as clumping is a common response of fish to predators (Pitcher and Parrish 1993). In addition, the call may induce the fish to engage in selfish cover-seeking behaviors, whereby individuals attempt to reach the center of a school (Hamilton 1971, Pitcher and Wyche 1983, Grover and Olla 1983). This clumping tendency would clearly be beneficial to the humpbacks as it would increase the density of prey in front of their mouths during engulfment.

In combination with other information on feeding humpbacks, my results do not support Baker's (1985) other possibilities that the feeding calls are associated with agonism or coordination with other whales. Agonism has been well documented on the humpback's breeding grounds and involves aggressive physical contact (Darling 1983). Such behaviors are rarely observed in social foraging groups in Alaska, which are distinguished by predictable dive orders (unpub. data) and stable positions in the lunge formation relative to the other members of the pod (D' Vincent et al. 1985). Evidence against an agonistic function for the feeding call has also been provided by Mobley et al. (1988) who found that playbacks of feeding calls to humpbacks on the Hawaiian breeding grounds elicited a non-aggressive approach, apparently from amorous males. Feeding call playbacks were also instrumental in eliciting a prolonged approach response from a whale ("Humphrey") trapped in the upper reaches of the Sacramento River (Mobley et al. 1988). There is also little support for Baker's coordination hypothesis. Occasionally, the feeding calls are omitted during the lunge, indicating that it is possible for a group of whales to deploy a bubble net and synchronously lunge without producing vocalizations.

When Baker (1985) first recorded these calls, he recognized the unusual context in which they occurred, and posited that they might function to elicit a stereotyped flight response from the herring. The fleeing and clumping responses found in this study were similar to those reported by many previous studies of fish behavior. These responses are believed to confer an advantage against raptorial predators such as fish, seabirds, pinnipeds, and odontocetes, which attack by seizing a single, or at most a few, individuals in their mouth. A compact school is believed to confer safety to individuals by enhancing information transfer (via the lateral line or visually) and thus facilitating escape maneuvers. It has also been suggested that closing ranks reduces the size of the school's vulnerable margins (Hamilton 1971) and increases the confusion effect, making it more difficult for a raptorial predator to single out and attack an individual prey (Milinski 1977, Krakauer 1995). What is of interest, however, is that these responses appear to be maladaptive against gulp-feeding baleen whales which benefit by increasing the density of prey as they attack.

If humpback whales are using sounds to elicit flight and clumping responses from the fish, this raises the question why the herring simply don't ignore these sounds or develop other countermeasures to render them ineffective. One mechanism by which predators are able to exploit the stereotyped flight responses of their prey was proposed by Charnov (1976). Dubbed "the rare enemy effect" by Dawkins (1982), this suggests that a prey species will develop the strongest anti-predator adaptations to those predators which cause the greatest mortality. Consequently, predators that are rarely encountered may be able to evolve specialized tactics that take advantage of a prey's stereotyped responses (Dawkins 1982). Selection may even favor enhanced conspicuousness of these traits in order to maximize their effectiveness (Jablonski 1999).

Humpbacks may not be the only marine animal that uses sound during prey capture. It has been speculated that the burst pulse sounds produced by sperm whales *Physeter macrocephalus* and killer whales *Orcinus orca* are used to stun or kill fish (Norris and Mohl 1983). The sounds produced by pistol shrimp, *Alphaeus californiensis* may also be used for acoustic debilitation of their prey (MacGinitie and MacGinitie 1968). Fin whales are also known to produce impulsive sounds coincident with the opening of their mouth to engulf prey (Watkins 1981, Watkins and Wartzok 1985). It has been proposed by Brodie (1993) that these sounds, produced by realignment of the tips of the mandibles, may serve to startle and retain prey within the whale's throat pouch. Acoustic properties of the aquatic medium, namely rapid sound transmission and low signal attenuation, may make it uniquely suited for sonic hunting techniques. It has also been pointed out by Major et al. (1986) that only in marine systems do large, coordinated groups of predators capture large aggregations of small prey. This unusual type of predator-prey interaction, so characteristic of humpback whales in Alaska, may favor the development of sonic hunting tactics which facilitate the herding and coalescing of prey.

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School Behavior	n	Control		Treatment		P value, 2-tailed
		$\bar{X}$	SD	$\bar{X}$	SD	
Speed (s per 1/4 tank)	9	0.6	0.1	0.7	0.2	.08
Direction changes	9	0.8	0.7	3.4	2.3	.016
Splits	9	0.1	0.3	2.7	1.9	.012
Time in center	9	4.0	3.6	8.0	5.3	.16
Circumference	9	5.3	1.1	10.2	3.7	.002

Table 2.1. Behavioral responses of herring in the indoor tank to feeding calls and blank tape controls.

	PC1	**PC2**	**PC3**	**PC4**
Proportion of Variation	0.83	.08	0.05	0.03
Flight Trajectory	0.49	-.61	0.16	0.59
Speed Increase	0.49	0.40	0.73	-.19
Alarm Index	0.49	0.57	-.56	0.32
% Depart Test Zone	0.50	-.36	-.33	-.70

Table 2.2. Proportion of variation explained by each principal component for the four response variables.

Treatment	**n**	**Flight Angle**		**Speed Increase (s)**		**Alarm Index**		**% Depart**		**Num. Trials Clump**
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	
460 Hz Feed Call	8	78.1	24.4	4.3	1.6	1.5	0.5	65.5	31.5	8/8
800 Hz Feed Call	8	73.7	32.2	3.5	1.3	1.3	0.5	60.0	29.8	8/8
Social Sounds	8	66.1	25.0	2.7	1.4	1.1	0.3	47.7	23.9	6/8
200 Hz Test Tone	8	88.1	3.7	6.5	1.3	2.8	0.3	87.5	20.3	8/8
460 Hz Test Tone	8	80.6	11.7	5.3	1.3	1.7	0.8	67.5	30.1	8/8
800 Hz Test Tone	8	63.5	21.3	3.1	0.9	1.1	0.3	58.7	29.1	8/8
White Noise	8	69.3	16.5	2.6	0.9	1.2	0.4	42.1	18.3	7/8
Blank Tape	8	3.1	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0/0

Table 2.3. Behavior of net penned herring in response to treatment and control sounds. The last column (Number of Trials Clumped) represents the number of times the fish were observed to decrease inter-individual distance.

School Behavior		**Control**		**Treatment**		**P Value**
	n	**$\bar{X}$**	**SD**	**$\bar{X}$**	**SD**	**2-tailed**
Speed increase	7	1.1	0.3	1.8	0.6	.02
Direction changes	7	0.1	0.3	1.1	0.6	.002
% school depart test area	7	19.2	9.7	76.4	27.0	.002
# Trials spacing decrease	7	0		7		

Table 2.4. Behavioral responses of wild herring to playbacks of humpback feeding calls and blank tape controls.

Figure 2.1. Sonogram of two vocalizing humpback whales recorded in SE Alaska on 17 July 1997. Individual A has a fundamental frequency at .435 kHz, where most of the sound energy is concentrated. Individual B has a fundamental frequency at .950 kHz, with much of the sound energy dispersed among the first four harmonics. Sonogram was generated using Canary Software (frame length 1024 pts., FFT size 2048 pts., filter bandwidth 88.24, 50% overlap).

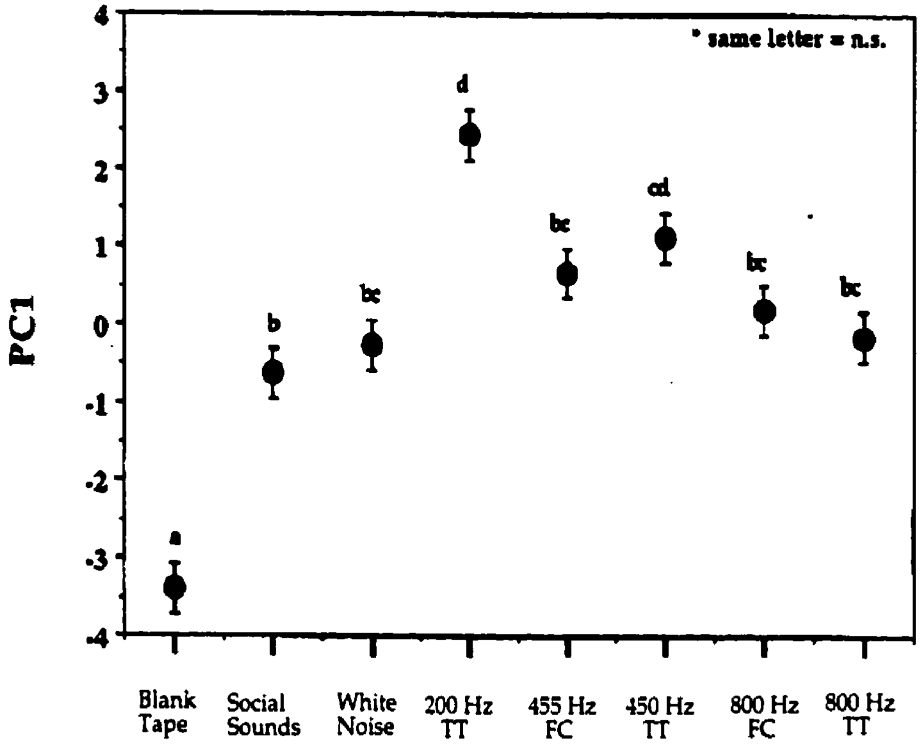

Figure 2.2. Principal Component Analysis scores of net penned herring in response to treatment and control playbacks.

Chapter 3

Does the humpback use its large flippers to exploit prey escape behavior?

Abstract

Among the mysticetes, the humpback whale *Megaptera novaeangliae* is noteworthy in possessing unusually long and brightly colored pectoral flippers. During foraging activities, these appendages are often waved or flashed as the whales lunge through and engulf aggregations of prey. Despite many descriptions of this feeding activity, relatively little is known about how these flipper movements affect prey behavior. One of the more intriguing hypotheses is that humpbacks use the white undersides of the flippers to frighten or herd prey toward their mouth. I conducted a laboratory test of this hypothesis with the use of an artificial flipper which was rotated or "blazed" at captive herring schools. I tested and found support for the prediction that individual fish within a school respond to this stimulus by fleeing directly away from the long axis of the flipper. Furthermore, the school's approach angle toward the flipper did not significantly affect the angle at which the school fled from it. I use the results of this study to evaluate how the flippers may assist in capturing prey in the wild. I also discuss the results in the context of the rare enemy effect, which provides one possible mechanism that could account for the humpback's ability to exploit herring schools in this fashion.

Introduction

Compared to the other baleen whales, the humpback whale *Megaptera novaeangliae* is unusual both in terms of its morphology and its foraging behaviors. Among the species' most distinctive features are its enormous pectoral flippers, which can extend up to one third of the whale's body length (up to 4.5 m in adult animals) (Scammon 1874, Tomlin 1957, Leatherwood and Reeves 1983, Fish and Battle 1995). All worldwide populations of humpbacks possess white coloration on most or all of their flippers' ventral surfaces (Pieter Folkens personal communication). In addition, most individuals possess white over much of the dorsal surface (Mason Weinrich, Pieter Folkens personal communication), although in the North Pacific, only about 25% of the population have white on these (Herman and Antionja 1977). When the flippers are exposed to downwelling surface light, the white "amelanotic" patches on the flippers can brilliantly reflect light (Brodie 1977, **Fig. 3.1a**).

While feeding, humpbacks often make extensive, deliberate movements of the pectoral flippers and other parts of the body. A number of different feeding tactics have been described including pectoral fin sculling (D' Vincent et al.1989), flick feeding (Jurasz and Jurasz 1979), lob-tailing (Weinrich et al. 1992), circular swimming/thrashing (Hain et al. 1982), blaze feeding (Brodie 1977), cooperative lunge feeding (Baker 1985, D'Vincent et al. 1985) and vertical rise and subsidence (Hays et al. 1985). These flipper and body movements are often used in combination with other distinctive feeding tactics including the deployment of bubble structures (Jurasz and Jurasz 1979, Hain et al. 1982, Sharpe and Dill 1997), the production of loud sounds (Baker 1985, D' Vincent et al. 1985), and the formation of large foraging groups (Baker 1985, D' Vincent et al. 1985).

One of the more interesting theories concerning the effects of the flippers on prey was proposed by Howell (1930), who suggested they may help direct schools of fish into the whale's capacious mouth. Brodie (1977) elaborated on this idea after he observed individual humpbacks approaching fish schools with their flippers spread and positioned slightly forward. He suggested that schooling prey may perceive the white portions of the flippers as two brilliant white bars, separated by the darker head. Brodie (1977) postulated that fish near the base of the flippers escape inward toward the dark gap, resulting in a denser concentration of prey near the whale's mouth. In Southeast Alaska, humpback whales make extensive use of their pectoral flippers when socially foraging on schools of Pacific herring *Clupea harengus pallasi* (pers. obser.). While lunging through fish schools trapped against the surface, individuals in these pods frequently have their flippers projecting forward at approximately 45° to their body. In addition, the flippers are often waved vigorously back and forth, a motion which can expose or flash their white undersides (**Fig 3.1b**).

Another feeding technique using the flippers has been described by Ingebrigtsen (1929) and Hain et al. (1982) in the North Atlantic. They noted humpbacks swimming in a broad circle while thrashing or "roiling" the surface with their flippers and flukes. The whales subsequently dove and then surfaced in the center of the foaming ring with mouths agape. Aerial observations of bubble feeding humpbacks by Hain et al. (1982) have also revealed that as solitary humpbacks release air, they roll onto their sides so that the flippers are oriented in a vertical plane. They suggested that the flippers may act in unison with the bubbles to herd and/or entrap the prey. It has further been suggested by Weinrich et al. (1992) that humpbacks may manipulate prey by splashing their pectoral fins or other appendages on the surface. These percussive behaviors may directly stun and/or disorient prey, or inject bubbles into the water (Weinrich et al. 1992).

Despite the considerable speculation about the role of flippers during foraging, no attempts have been made to test any of these ideas. The objective of this study was to examine the role of the humpback's flippers during foraging by testing how herring schools respond to a large flipper-like object. Specifically I wished to test if the extensive flipper movements of foraging humpbacks serve to frighten or herd prey toward their mouths. This was done in a laboratory setting with the use of an artificial pectoral flipper, which could be rotated or "blazed" (Brodie 1977) at herring schools. I predicted that the fish would flee directly away from the long axis of the flipper since in the wild, this flight trajectory would result in fish concentrating in front of the whale's mouth. In order to determine how generalized this flight response is in herring, I tested the school's behavior at four different approach angles. I use the results to evaluate how the flippers may assist in capturing prey. I also discuss the rare enemy effect, which provides one possible mechanism that could account for the humpback's ability to exploit herring schools in this manner.

Methods

This study was conducted at the West Coast Universities Marine Biological Station, Bamfield, BC, during the spring of 1994. Experiments were conducted indoors in a 200,000 l circular tank measuring 2.8 m in depth and 27 m in circumference. Lighting was provided by four 200-watt flood lamps and from diffuse natural light entering through a 1 x 2 m opening in the roof of the building.

An artificial humpback pectoral flipper was constructed from a 1.8 x 0.4 m aluminum plate (**Figure 3.2a,b**). To imitate the color pattern of the majority of North Pacific humpbacks the flipper was painted black on one side (dorsal) and white on the other. It was suspended 25 cm above the tank floor on each end by a small stand which matched the color of the tank wall. Two transparent marionette lines made of 50 lb-test fishing line were attached to the flipper. When pulled, they rotated the flipper on its long axis which exposed its white underside at the school.

Herring used in this experiment were live-captured with a 60 m hand seine in Bamfield Inlet, Barkley Sound, BC from a stock of prespawning 2-year-olds averaging 14 cm in total length and 22 g in weight. Care was taken to minimize stress to the fish by rapidally transferring them (within 20 min.) to the research station in 15 l pails. The fish were then placed in an opaque-covered, 4 m^3 circular holding tank. Any fish exhibiting more than 15% scale loss or abnormal schooling behavior were discarded. The remaining fish were also used in two other experiments which tested the effects of humpback sounds and bubbles on schooling behavior (cf. Sharpe and Dill 1997; Chapter 1).

Prior to each experiment, 50 fish were placed in the large test tank and allowed to acclimate overnight. During this time the flipper was maintained in a horizontal position with the darker dorsal side oriented upwards, which the school responded to by swimming beneath it. The fish typically swam in a single, fairly compact school that traveled around the perimeter of the tank. At the end of the approx. 14 h acclimation period the fish generally exhibited no response to the flipper in the neutral position other than a slight elongation of the school whenever it passed underneath.

Each trial began when 25 or more individuals of the school entered a 2 x 2 m zone in front of the flipper. When the group was centered over the test zone, the flipper was rotated with a firm pull on one of the lines, thereby flashing the white underside of the flipper at the fish. The school's response was recorded by videotaping through the hole in the roof of the building with Sony 8 mm video camera. This was later analyzed with a freeze-frame video player (30 frames/s) by laying a transparency printed with a coordinate system and a protractor over the monitor screen (**Fig 3.3**). The positions of the 25 central fish in the school were plotted at 0.5 s and 0.75 s after the flipper was flashed. A line drawn between the two positions provided the flight trajectory of each individual fish. relative to the flipper's long axis.

The response of the fish to the suddenly blazed flipper was tested at four different approach angles (70°, 90°, 135°, and 180°). These approach angles were measuered from the coordinate system (**Fig 3.3**) with the 0° line occuring at right angles to the flipper. The various approach angles were obtained by adjusting the position of the flipper relative to the tank wall **(Fig 3.2c)**. Six different herring schools were tested, with each school being subject to one blazing event at each of the four different angles. The order of the four trials per school was randomized. It was predicted that a school approaching from any of the four directions would change its heading so that its flight angle would be directly away from the long axis of the flipper (i.e., along the zero path). Each approach angle thus generated a different predicted change in direction of travel (i.e., 70°/70°, 90°/90°, 135°/135° and 180°/180). The Watson-Williams test (Batschelet 1981) was used to test observed angles against these expectations.

Results

Regardless of approach angle, the fish in the school responded by changing their orientation, so that their flight path was more-or-less perpendicular to the long axis of the flipper **(Fig. 3.4)**. This change between the approach and flight trajectories was highly significant, related to the approach angles, in the predicted fashion (Watson-Williams Test, F=511, P<.05, **Table 3.1**). In no instances were any fish observed to move toward the flipper.

Fish near the ends of the flipper tended to move outwards (i.e., they deviated from the right angle flight path) suggesting that the most effective portion of a humpback's flipper for herding prey is the central portion of the blade.

Discussion

This experiment revealed that herring exhibit a consistent flight response away from the long axis of an artificial flipper, regardless of their initial approach direction. That prey respond by taking flight directly away from a threat has previously been observed in several other species of fish (Keenleyside 1955, Edmunds 1974, Howland 1974, Weihs and Webb 1984). The finding lends credence to Howell's (1930) and Brodie's (1977) assertion that the flippers assist in herding prey toward the mouth. These findings also suggest that socially foraging Alaskan humpbacks are using their flippers to modify prey flight behavior by lunging through herring school with their flippers oriented forward of their bodies at approximately 45°. Any prey that initially takes flight from the approaching flippers with a 90° fast start response will have a higher probability of fleeing into the path of the approaching whale.

By effectively serving as extensions of the mouth, the flippers may increase the volume of water from which the whale is able to sweep prey. Natural selection may have favored the elongation of the flippers so that they were the first stimulus to intrude in visual field of individuals within the school. The fact that any black on the ventral surface is typically confined to the insertion point near the base of the flipper (personal communication Scott Spitz) supports Brodie's (1977) hypotheses that the darker mouth may function as a deceptive refuge. In addition, by having the distal portions of the flipper white, it permits the humpback to extend the bright patches farthest from its body, presumably providing the greatest visual "leverage" for manipulating prey.

The complex side-to-side flipper movement observed in Alaskan humpbacks (personal observations) may also interfere with the school's ability to perform synchronized escape maneuvers. Moving the flippers out-of-phase may produce separate subgroups within the school, each fleeing along different trajectories. The overlapping flight paths may interfere with those of adjacent subgroups, preventing them from responding to the looming mouth as a cohesive, synchronized group. It has been shown that when neighboring subschools attempt to merge, they create zones of confusion where individuals are temporarily misaligned and apparently become more vulnerable to predation (Pitcher and Wyche 1983). The stimulus created by the moving flippers may be analogous to certain fish predators attacking in groups, where the multiple threats tend to break down school structure (Major 1978, Pitcher & Parrish 1993, Parrish 1993).

The limited ability of light to travel through water may also hamper the ability of individuals in the school to detect a refuge at the edge of the flashing pectoral flippers. This may delay the prey from promptly establishing a safe flight trajectory, or may simply force the prey to move directly away from the perceived threat, though not necessarily out of danger. Since humpback whales often forage in groups a further advantage of a larger capture area may be analogous to a phenomenon known as the ricochet effect for spider groups (Uetz 1986, 1988). With colonial spiders it has been shown that insects deflected from web to web become increasingly susceptible to capture by one of the spiders in the group (Rypstra 1989). Similarly, herring who are forced into a series of startle-responses may quickly fatigue and be engulfed more easily by the encroaching whales.

Even if the fish initially avoid being consumed by fleeing directly away from the onrushing mouths, they frequently fall victim to the whales by being herded against the water's surface. It has been demonstrated (Chapter 4, Sharpe and Dill 1995) that southeast Alaskan humpbacks frequently herd herring up to the surface from a depth of 30 m or more. Much of this upward herding is conducted inside a vertical cylinder of bubbles, which appears to prevent horizontal escape movements of the school. In addition to the physical presence of the whales' bodies the flippers very likely contribute to the threatening stimuli that drives the prey upwards. The flippers may also be useful for blocking interstices between the whales in the group, thus preventing the school from escaping downward within the confines of the net.

In addition to flight direction, it has been shown that the proper timing of the flight maneuver is essential (Dill 1974, Major 1978, Webb 1986, Howland 1974, Katzir and Cambi 1993); fish increase their flight initiation distance in response to larger, faster moving predators (Dill 1974, Hurley and Hartline 1974, Helfman 1989). It has been suggested by Jablonski (1999) that predators such as painted redstarts *Myioborus pictus* may use conspicuous coloration to send false information to their prey, thus appearing larger or closer then they really are. If the humpback's flippers operate in a similar fashion, they may cause the fish to expend their fast-start response prematurely, and thus be in a sub-optimal spatial arrangement to perform a second evasive maneuver before being engulfed.

Compared to baleen whales, most marine predators (i.e., seabirds, fish, pinnipeds, and odontocetes) secure prey with a very different capture mode. Instead of a large mouth, these "raptorial" predators have relatively small jaws or bills that are used for grasping single, or at most a few individuals per attack. In contrast baleen whales feed by using their enormous gape and expandable gular pouch to engulf large amouts of prey-laden water. A large mouth is thought to be advantageous because it increases the distance that the prey must traverse per unit time in order to escape (Webb and De Buffrénil 1990). By targeting relatively small prey (with decreased relative manouverability and acceleration abilities) a rorqual further reduces the probability that prey can escape from its attack trajectory (Webb and Keyes 1981).

A number of studies have demonstrated that when two or more predator species exploit a single prey type, the effect on the prey may be more complicated than a simple summation of each predator's impact (Soluk and Collins 1988, Martin et al. 1989). For example, the simultaneous presence of two different predator types can result in increased vulnerability to the prey since the defences against one predator put it at greater risk of being captured by the other. More complex interactions involving multiple predators have been proposed by Charnov (1976) and Dawkins (1982) who suggested that a prey species will develop the strongest anti-predator adaptations to those predators which exert the greatest mortality. Known as the "rare enemy effect", it proposes that predators that are infrequently encountered may be able to evolve specialized tactics that take advantage of a prey's stereotyped responses (Dawkins 1982). Selection may even favor enhanced conspicuousness of these traits in order to maximize their effect on the prey (Jablonski 1999).

Although the rare enemy effect provides an intriguing mechanism for the evolution of conspicuous hunting tactics, there have been few attempts to test this idea. To date, only Jablonski (1999) has performed a direct test by examining the responses of a prey organism to different predator models. His work focused on the painted redstart which belongs to a canopy-foraging guild most of whose member species attack invertebrate prey by gleaning them from the substrate. Most insects within this community have evolved the evasive tactic of taking flight directly away from such predators (Edmunds 1974). In contrast to the substrate gleaners, the redstart constantly feeds with half-spread wings and a broadly spread and half-raised tail which exposes distinct bright patches on the tail and wings (Robinson and Holmes 1982). In a series of field experiments using redstart models, Jablonski (1999) was able to demonstrate that the frequency of escape responses increased when the model had its wings and tail spread. Jablonski (1999) further noted that the redstart is relatively "rare" given that it is the only flush-pursuer among the nearly two-dozen species of insectivorous birds that inhabit the oak-pine woodlands of the southwestern United States. Consequently, he was able to demonstrate that the redstart met the conditions of a rare enemy which forages by exploiting stereotyped prey escape behavior. It is interesting to note that the flush/pursuit foraging tactic of redstarts bears an uncanny resemblance to the flipper movement foraging of humpback whales. Both species feed by waving or flashing their appendages at prey, and both have large white patches on their ventral surface, rendering them highly conspicuous. Further studies on the relative mortality rates caused by humpbacks and raptorial predators are required to determine if the humpback whale is sufficiently uncommon to constitute a rare predator.

There is evidence that other marine predators also use bold coloration patterns to assist in prey capture. Bottlenose dolphins *Tursiops truncatus*, dusky dolphins *Lagenorhyncus obscurus*, and killer whales *Orcinus orca* have been observed to expose white patches on the flanks or abdomen to herd and concentrate prey (Wursig et al. 1990; Kathleen Dudzinski, personal communication). It has been shown by Wilson et al. (1987) that the bold stripes on the sides of African penguins *Spheniscus demersus*, and in several species of dolphins can aid in the depolarization of fish schools. In the lab, Kieckhefer (1991) found that krill *Euphausia pacifica* were attracted to their own bioluminescence reflected off a white sheet of paper, suggesting that in some contexts amelanotic patches may serve as an attractant to prey. Brodie (1977) also suggested that white patches on the pectoral fins of minke whales may be used to herd prey in a fashion similar to humpbacks.

In addition to their use in foraging, many other theories have been advanced concerning the adaptive value of the humpback's long flippers. These include rubbing and clasping (Scammon 1874, Howell 1930), shallow water navigation (Tomlin 1957, Perkins and Whitehead 1977), percussive signaling (Tomlin 1957, Tyack 1981) visual signaling (Madsen and Herman 1980), intraspecific competition (Baker 1985), feeding competition (Watkins and Schevill 1979), locomotion and maneuvering (Edel and Winn 1978, Fish and Battle 1995), predator defense (D'Vincent et al. 1989), and temperature regulation (Scholander and Schevill 1955, Kanwisher and Sundnes 1966, Tomlin 1957). It is noteworthy, however, that only the feeding and perhaps the visual signaling hypotheses can account for the white on only the undersides of the flippers. The findings of this study suggest the light coloration and movements of the humpback's flippers are used to manipulate prey, as opposed to being used in interference competition as proposed by Watkins and Schevill (1979). This implies that cooperation, as opposed to competition, may underlie the interactions between individuals in social pods. It should also be noted that both within and between populations, humpbacks exhibit extensive variation in pigmentation on the ventral surface of their bodies, ranging from nearly all black to all white. However, the white on the ventral surface of the flippers varies little, suggesting that these amelanotic patches play an important role in modifying the behavior of prey organisms.

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Approach Angle	Predicted Δ in Angle	Mean Observed Δ in Angle	Standard Deviation of Δ Angle
70	70	74.4	16.7
90	90	89.1	20.5
135	135	126.6	14.7
180	180	172.8	8.6

Table 3.1. Predicted and observed flight trajectory for each of the four approach angles. The change in angle differed significantly between each of the four approach directions (Watson-Williams Test, F=511, P<.05). All angles are given in degrees.

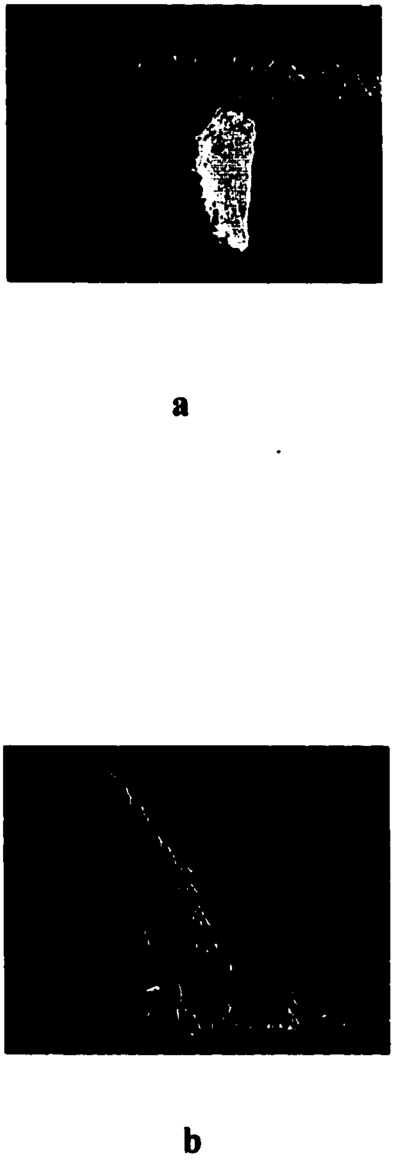

Figure 3.1a) Humpback whale flipper exhibiting ability to reflect downwelling surface light. **b)** Extended pectoral flipper of a whale lunging through the surface

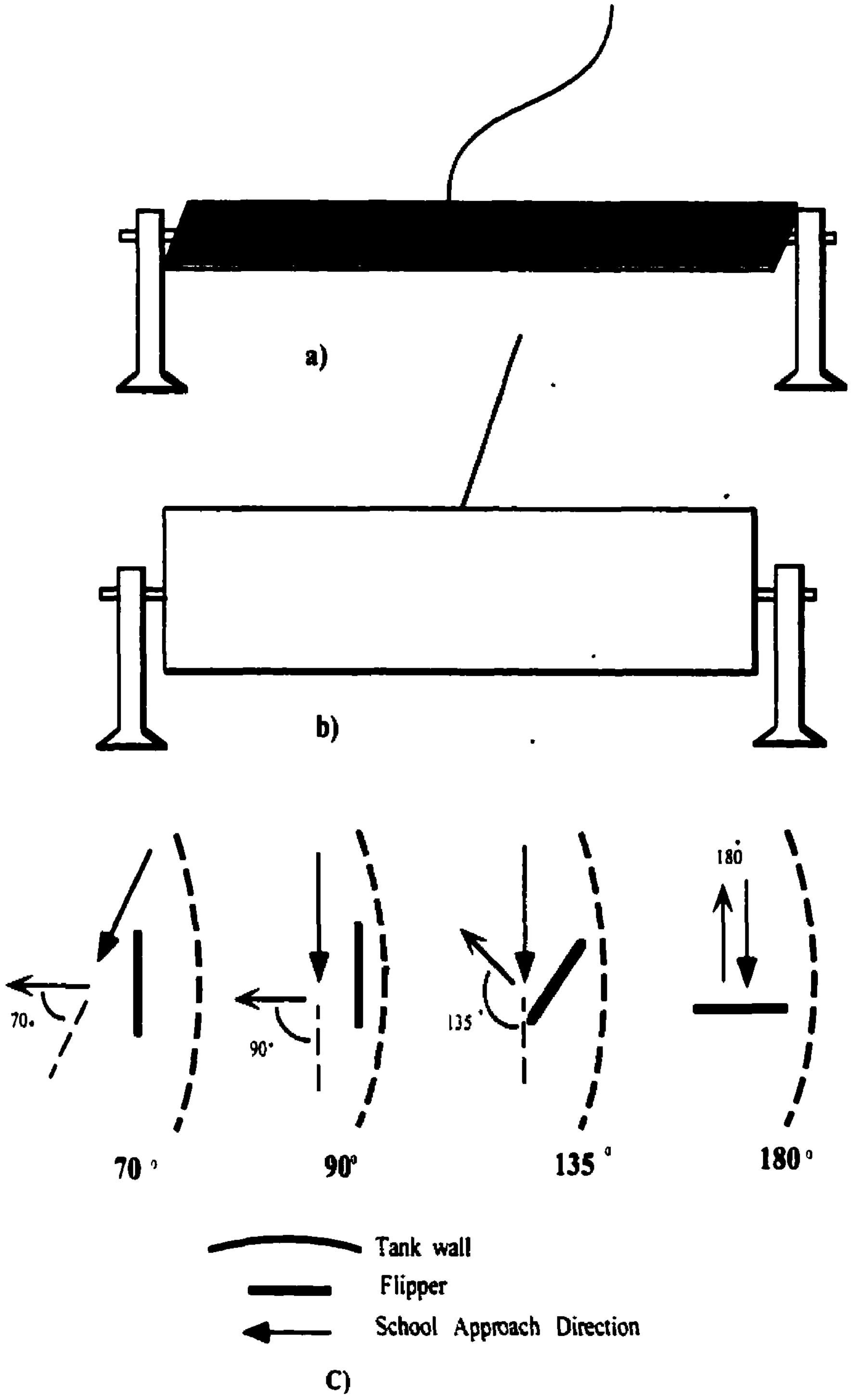

Figure 3.2. Flipper board in a) neutral, and b) blazed position. c) Flipper orientation relative to the tank wall is shown for each of the four school approach angles.

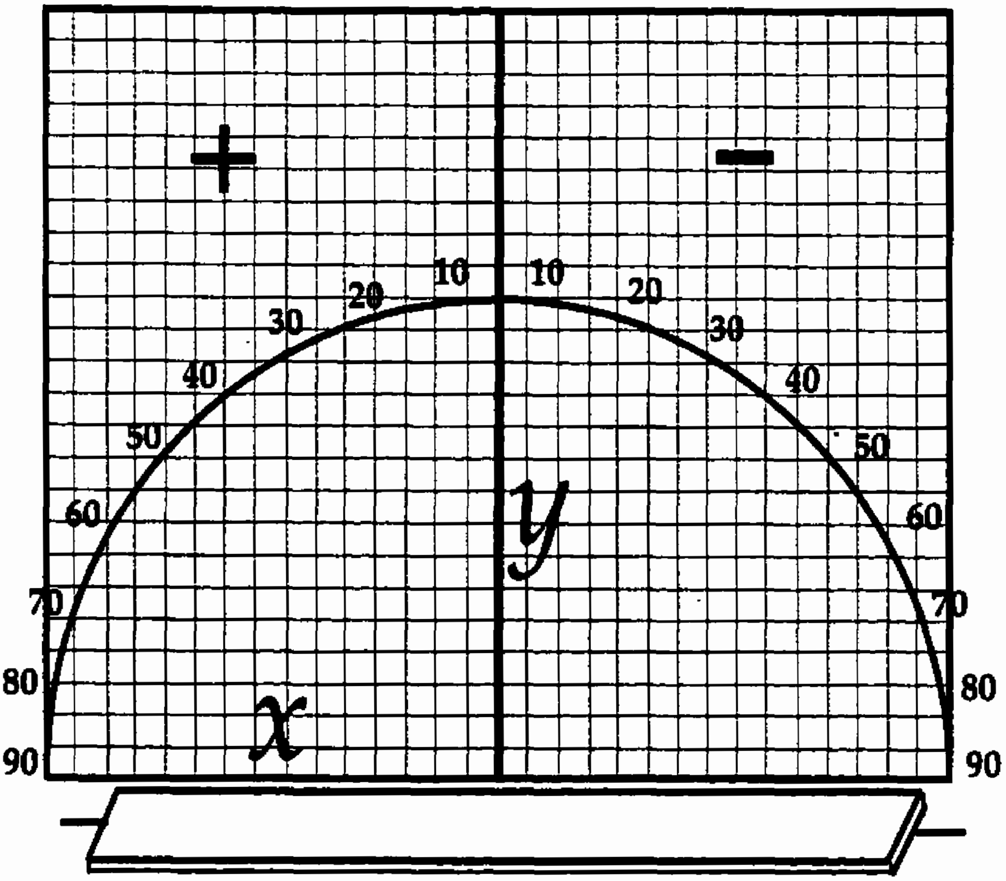

Figure 3.3. Coordinate system used to plot fish approach and flight trajectories.

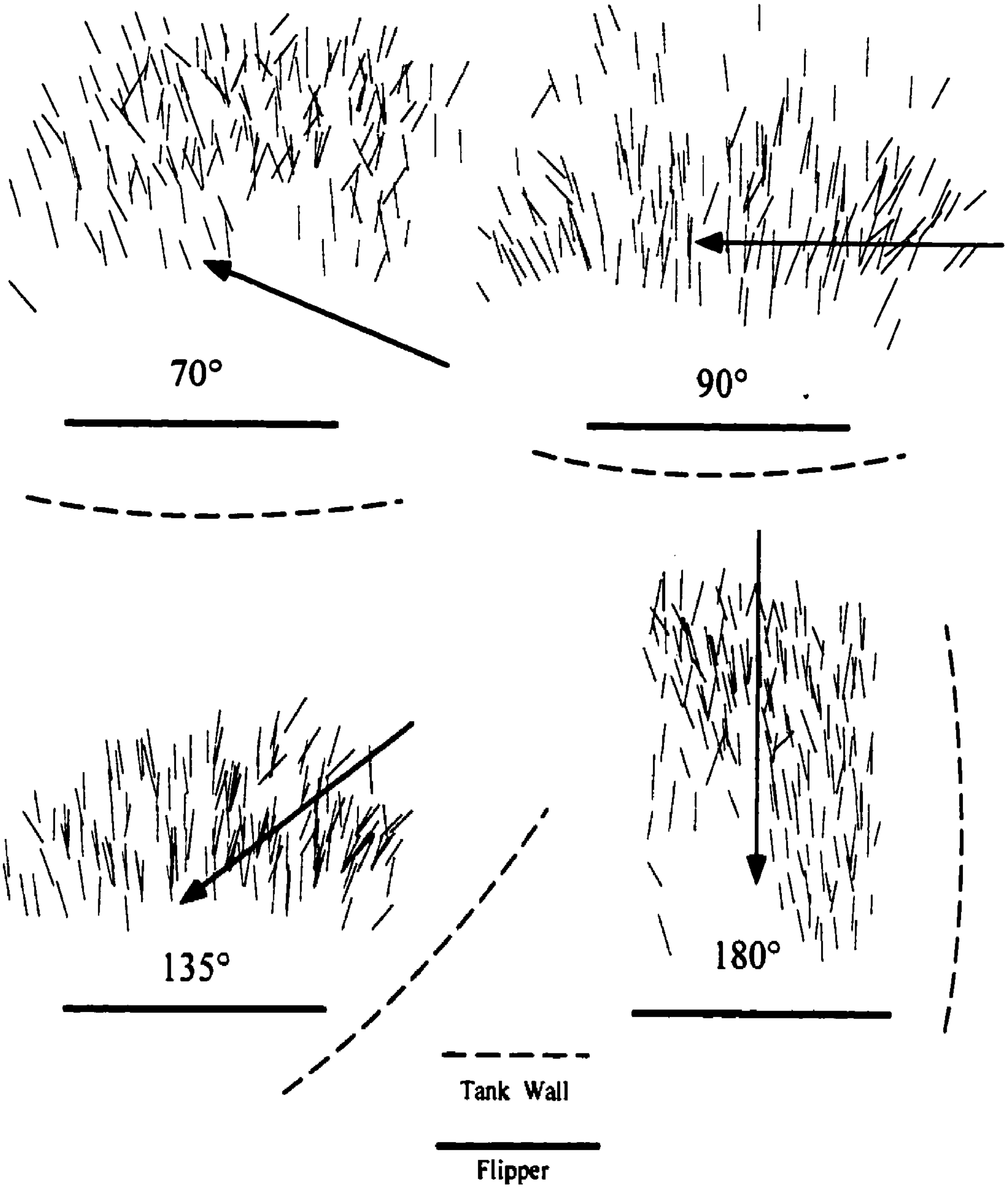

Figure 3.4. Approach angle (arrow) and all individual flight trajectories (thin lines) of the fish for each of the four different approaches to the flipper.

Chapter 4

The Underwater Behavior of Socially Foraging Humpback Whales in SE Alaska

Abstract

The humpback whales *Megaptera novaeangliae* of Southeast Alaska are unique in that they engage in elaborate social foraging behaviors when attacking schools of Pacific herring *Clupea harengus pallasi.* This involves the formation of large pods which capture the herring by encircling them in large bubble nets and broadcasting loud feeding calls. Our understanding of this unusual foraging tactic is limited, however, as past studies have employed only opportunistic surface observations. The goal of this study was to use sonar to investigate the underwater events where most of the complex interactions between whales, bubble structures, feeding calls, and fish schools occur. The sonar revealed that the depth of bubble nets increased (across pods) by 0.21 m for every 1 m increment in fish depth, indicating that the whales adjust the depth of the net to account for the escape speeds of the fish, which move much faster than the bubbles. This feeding event appears to be carefully timed with the whales forcing the prey upwards so that they arrive at the surface simultaneously with the encircling net of bubbles. Individuals within a group appear to perform two basic tasks: prey herding and bubble blowing.

An air release device was used to test a number of predictions about the characteristics of rising bubbles (speed, size, sorting) to determine if the observed depth limit of the net (approx. 20 m) was associated with some physical aspect of rising bubbles. The results of these deployments suggest that a humpback is confronted with an important tradeoff between net depth and the formation of gaps in the cylinder's walls due to differential rise rates of the larger, faster spherical cap bubbles and smaller, slower effervescence. Observations on the escape speeds of schooling herring were also conducted. These results are integrated with the sonar data and bubble release experiments to provide the first comprehensive picture of the underwater foraging of the Alaskan humpback whale.

Introduction

The release of bubbles by air breathing predators can be a potent tool for manipulating prey organisms in the marine environment. Rising air creates a strong visual, acoustic, and mechanical barrier (Fan and Tsuchiya 1990) which can be used to frighten prey organisms (Ingebrigtsen 1929, Jurasz and Jurasz 1979, D' Vincent et al. 1989, Sharpe and Dill 1997). Laboratory studies have shown that schooling fish can readily be trapped within a bubble net, and are reluctant to swim through an air curtain, even when confronted by a predatory stimulus (Blaxter and Batty 1985, Akiyama et al. 1992, Sharpe and Dill 1997). A wide diversity of species have been observed releasing bubbles in the wild, including cetaceans (Simila and Ugarte 1993, Fertl and Würsig 1995), pinnipeds (Davis et al. 1999), seabirds (Sharpe 1994) and mustelids (pers. obser.).

Some of the most intriguing forms of bubble use are found in the humpback whale *Megaptera novaeangliae*. This species deploys bubbles in a variety of social contexts including mating and foraging. On their subtropical winter breeding grounds, bubbles are used by rival males as agonistic intrasexual signals (Forestell and Herman 1979, Baker 1985). On the temperate summer feeding grounds, the species uses bubbles to assist in the capture of prey, which include schooling fishes and swarming crustaceans (Jurasz and Jurasz 1979, Hain et al. 1982, D'Vincent et al. 1985). Different methods are used to release these bubbles, with the most common being the release of air from the blowhole, and occasionally the mouth. The flukes and flippers also appear to be used to entrain bubbles into the water when they are forcefully slapped on the surface (Weinrich et al. 1992). Ingebrigtsen (1929) first documented the release of air by humpbacks when he noted the species capturing krill in circular bubble nets. Jurasz and Jurasz (1979) conducted vessel studies in Southeast Alaska, where they described the use of bubble nets on both krill and schooling fishes. In the North Atlantic, Hain et al. (1982) made observations from both boats and aircraft to describe the shape, diameter, and deployment direction of various bubble structures including nets, curtains, and clouds.

Air release by humpbacks is noteworthy in that the use of bubbles varies within and between populations (Jurasz and Jurasz 1979, Hain et al. 1982, Weinrich et al. 1992). The most elaborate forms of bubble foraging are exhibited by the humpback whales inhabiting the waters of Southeast Alaska (Jurasz and Jurasz 1979, Greenough 1981, Giddings 1984, Baker 1985, D' Vincent et al. 1985). Here groups of up to 20 individuals will release a large bubble net and then surface through its center to engulf schools of Pacific herring *Clupea harengus pallasi*. Although there is considerable variation in how a bubble net is constructed, an observer at the surface can distinguish three parts: an approach curtain (which may extend up to 40 m in length), a cylinder, and several large clouds (**Fig 4.1**). SE Alaskan humpbacks use these bubbles in conjunction with other unusual feeding tactics including the broadcasting of loud, trumpet-like calls (Chapter 2) and the flashing of their large pectoral flippers at prey (Brodie 1977, Baker 1985, D' Vincent et al. 1985, pers. obs., Chapter 3).

Although past observations have provided useful surface descriptions of bubble foraging in humpbacks, little is known about subsurface events where most of the complex interactions between whales, bubble structures, feeding calls, and fish schools occur. It is not known how deep the whales dive, or at what depth they encounter the fish schools and deploy the bubble net. It is also not known how the whales get the fish to the surface and how they are able to time their arrival with the closing bubble net. In fact, it is still unclear whether the interactions between whales in these groups are based on interactions that are cooperative (Baker 1985, D'Vincent et al. 1985, D'Vincent et al. 1989), competitive (B. Dolphin in Giddings 1984), or a combination of both conflicting and converging interests.

To obtain a more comprehensive understanding of this unusual foraging behavior a 160 kHz sonar was used to sample underwater events in the vicinity of bubble-feeding humpbacks. The second phase of the study was initiated when sonar data revealed that humpbacks rarely deployed bubble nets below a certain depth. The characteristics of rising bubbles (speed, size, and sorting) were measured with a bubble release device in order to test if this depth limitation was associated with some physical property of rising bubbles. Finally, observations were made on the flight speed of herring in the laboratory to construct a comprehensive picture of underwater events associated with group foraging in humpback whales.

Methods

Sonar Sampling

Studies were conducted in the waters of Chatham Strait, Southeast Alaska during the months of July to September from 1994 to 1996. Sonar profiles were obtained from either a 7-m or 15-m research vessel outfitted with a Lowrance X-16 computer sonar with a paper recorder. A 20° transducer mounted 0.5 m below the vessel's waterline was aimed vertically into the water column. Sonar data were obtained by following a group of feeding humpback whales allowing simultaneous monitoring of prey conditions and bottom topography. Hi8 and digital video cameras were used to synchronize feeding activity with the sonar recordings, and provide a chronometer for analysis of the sonar tape. When the whales lunged, the research vessel was maneuvered in their direction, and slowed to a speed of 1.5 knots, to sample the site where the bubble net had been deployed. An attempt was made to motor the vessel directly over the center of the net, which was visible as an effervescing ring of rising bubbles. Even when individual bubbles could no longer be observed rising to the surface, the site where the net was deployed was visible as a luminous green patch. This patch was created by the infusion of micro-bubbles into the water column and could readily be observed on the sonar. To determine if these persistent micro-bubbles could provide an adequate measure of the net's actual depth, I positioned the stationary research vessel over a number of bubble nets to observe the rate at which the bottom of the micro-bubble signature rose toward the surface. It was noted that the depth and strength of the micro-bubbles remained relatively constant for several minutes before gradually fading away. Therefore, it was deemed appropriate to use the micro bubbles as a measure of actual net depth if the site could be sampled within 120 s after the whales lunged. Lunge sites that took longer than 120 s to reach with the research vessel were not included in the analysis. In many cases, the prey species (herring) could be determined by noting fish leaping at the surface before the whales lunged, or by examining scales and stunned fish after the whales departed the site.

Data were transcribed from the sonar tapes while concurrently viewing the Hi8 videotapes. Depth of underwater targets was obtained from the calibration lines on the sonar tape. At each lunge site, an attempt was made to obtain two depth measures of the bubble net (approach curtain and cylinder), three depth measures of the fish school (top, mid, and underside), and bottom depth under each of these features. The reason for obtaining independent bottom depth measures under both schools and nets was because these features were often located several meters apart (on the horizontal axis), which if located over a sloping bottom gave different depth values. While motoring between lunge sites, I also recorded the depth of any herring schools which were situated more than 100 m from a feeding site and appeared to be undisturbed by the whales. Whenever possible, I attempted to record whales on the sonar. However, it was disruptive and hazardous to the researcher and whales to attempt to position a vessel directly above a forming bubble net, so humpbacks were only recorded opportunistically.

Two methods were used to analyze sonar data, the first based on mean values calculated for each pod, and the second based on successive diving events of individual pods. In the first analysis, the null hypothesis was investigated that the depth at which different pods ($\underline{N} = 31$) deployed bubble nets was independent of herring school and bottom depth. The mean value of each variable was calculated for only those events in which all data had been recovered from the sonar readings.

In the second analysis, simple regression was used to investigate the null hypothesis that the depth at which successive bubble nets were deployed by individual pods was independent of fish school depth. Mid-school depth (transformed) was used as the predictor variable, because this was best correlated to bubble-net depth across pods. To determine whether the observed differences in net depth-school depth relationships could be explained by differences in sample size (i.e., the number of bubble nets recorded) or depth of fish schools (mean, maximum and range) among pods, the pods were divided into two groups, based on whether or not a significant positive correlation was detected, and compared with respect to the above-mentioned variables. $\underline{T}$ tests were used for the comparisons as variances were homogeneous (Levene test, $\underline{P} > 0.10$) in all cases.

Bubble Deployment Trials

Previous surface observations of feeding humpbacks suggested that the bubble net generally consists of two basic types of bubbles (Jurasz and Jurasz 1979, per. obs.), including large (cantaloupe-sized) spherical cap leaders (SCL) which range in size volumn 100-500 ml, and smaller pea-sized effervescence of 2-30 ml. Spherical cap leaders typically arrive at the surface before the effervescence, but it was unclear whether these two bubble types originate from a single release event or represent different events. SCL may be more important for entrapping prey since they typically surrounded the school during the surface lunge (Jurasz and Jurasz 1979; per. obs.).

To investigate the characteristics of rising bubbles, an air release device was constructed, consisting of a transparent plastic tube (1.15 m in length and 10 cm in diameter). This device could release specific amounts of air at different depths in the water column **(Fig. 4.2)**. A 5-cm valve was attached to one end, while the opposite end remained open. The device was hung vertically in the water by a line attached to the end with the valve. A 24 kg weight was attached to the lower, open end, permitting the device to sink when full of air. By pulling on a second line attached to the valve handle, the air in the device could be released.

Both deep and shallow water bubble deployments were conducted. The deep water releases were carried out by lowering the device to four different depths (7.5, 15, 22.5 and 30 m). Three different volumes of ambient air (2.2, 4.5, and 9 l) were deployed 15 times at each of the 4 depths, resulting in a total of 180 experimental releases. On each of the releases, an observer on the vessel recorded the time it took bubbles to arrive at the surface, the size of the bubbles (SCL or effervescence), the total time each size class could be observed percolating at the surface, and the duration of any gaps that formed between successive pulses of bubbles. In order to gain a better understanding of the behavior of different sized bubbles in the immediate vicinity of the release site, shallow water deployments were conducted at 1 m intervals in the top 7 m of the water column. Four volumes were used (1.1, 2.2 , 4.5 , and 9 l) with each being deployed 10 times for a total of 280 deployments.

Herring Flight Speeds

Social foraging pods appear to feed on a wide variety of fish size classes. However, observations of prey being engulfed at the surface and opportunistic collections of stunned fish suggest that the humpbacks most frequently exploit adult herring approximately 15 to 24 cm in length. This is supported by fisheries catch data (Skud 1963, Reid 1971, Blankenbeckler and Larson 1987, Carson 1984) indicating that the majority of herring commercially harvested in the study area are 4 to 6 year old adults measuring 18 to 22 cm. In order to obtain information on the swimming speeds of herring in this size range, I videotaped schools of captive herring in a large circular tank (200,000 l) at the Bamfield Marine Station. I conducted flight response tests on 5 schools of herring, each consisting of ten 20 cm individuals. A 10-m measuring bar, marked at 1-m intervals, was placed on the bottom of the tank at right angles to the wall. As the school swam past the intersection of the tank wall and the bar, a fright stimulus was created by banging the end of a 4-m metal pole onto the floor of the tank. The flight response of those individuals that traveled parallel to the measuring bar was recorded with a digital video camera.

Results

Analysis of bubble-net depth across pods

The five independent variables pertaining to depth of prey and of the sea floor were strongly correlated with one another (**Table 4.1**) indicating that their inclusion in a multivariate model would not be appropriate. The correlation of depth of fish and of the sea floor (**Fig. 4.3**) is noteworthy as it indicates that herring can be predictably found within 5-10 m of the bottom. This suggests that the herring recorded by sonar in the vicinity of bubble nets had not started progressing towards the surface in response to the whales' foraging. This hypothesis is also supported by the fact that the depth at which these focal fish schools were recorded was virtually identical to that of other ambient fish schools recorded in the absence of bubble nets (**Table 4.2**).

The mid-depth of fish schools was the variable best correlated to bubble-net depth across pods (see **Table 4.1**), accounting for 61% of the variability in bubble-net depth, and indicating that whale pods deployed bubble nets at greater depths with increasing depth of fish schools ($F_{1,29} = 45.46$; $P < 0.0001$). To remedy normality and linearity assumptions, I subjected the independent variable to a logarithmic transformation, which slightly increased the predictive power of the model to 66% (**Fig. 4.4**; $F_{1,29} = 55.21$, $P < 0.0001$). Bubble nets were generally deployed shallower than (i.e., above) the middle of the school (**Fig. 4.5**), suggesting that other mechanisms (i.e., whales below the prey) force the fish to the surface and "direct" them into the net. Interestingly, the five pods which did not fit this pattern were foraging on some of the shallower herring schools (mean depth of mid-school between 10-20 m), suggesting that humpback whales may employ different foraging strategies depending on the depth of their prey.

Analysis of bubble-net depth within pods

There was a large amount of variability among pods in the relationship between bubble net depth and school depth; of the 29 analyses conducted, seven indicated a significant and positive relationship between bubble-net depth and fish-school depth, while the remaining 22 indicated no significant relationship (**Table 4.3**). Obtaining more than six significant correlations out of a possible 29, at a level of 0.05, is unlikely to happen by chance alone ($x^2 = 4.267$, $DF = 1$, $P = 0.039$). Furthermore, the mean correlation coefficient (r) of 0.187 was significantly greater than 0 ($t=2.785$, $P = 0.009$), which also indicates a significant bias towards positive correlations. These analyses thus indicate that pods tended to adjust their bubble-netting behavior during successive dives in relation to variations in prey depth.

Significant regressions between bubble-net depth and mid-school depth were not based on a greater number of observations ($t = 1.685$, $DF = 27$, $P = 0.104$) than non-significant regressions, nor did the pods belonging to these two categories (i.e., significant versus non-significant regressions) differ with respect to the mean ($t = 0.957$, $DF = 27$, $P = 0.347$), maximum ($t = 0.600$, $DF = 27$, $P = 0.580$) or range ($t = 0.539$, $DF = 27$, $P = 0.594$) of depths at which their prey occurred.

Bubble Rise Characteristics

The bubble release tests revealed that a single deployment of air produces both spherical cap leaders and effervescence. When air is first released, it forms an undifferentiated bubble swarm that moves relatively rapidly (**Fig. 4.6**). After rising two meters from the release point, this turbulent swarm begins sorting into different bubble size classes and a more structured cloud is formed. The sorting of leaders and effervescence continues until they become two largely separate clouds after rising approximately 6 m. The turbulent, almost explosive nature of the initial release results in approximately half of the air being "rendered" into the effervescence which rises at the relatively slow rate of approximately 0.38m/s. The remainder of the air develops into the larger SCL (100-500 ml) which move at nearly twice the speed of the effervescence **(Fig. 4.7)**.

Spherical cap leaders deployed below 25 m are not completely rendered into effervescence. Although it was noted that there was a visible decrease in the size of leaders arriving at the surface from the deeper deployments, this shrinkage appeared to be offset to some extent by expansion of the bubble due to the decrease in pressure at shallower depths. Consequently, all of the experimental deployments (including the deepest, lowest volume releases) resulted in SCL's reaching the surface. Therefore, it is concluded that the breakdown of spherical cap leaders into effervescence is not a principal factor limiting the depth at which humpbacks deploy bubble nets. Although no attempt was made to capture and measure the size of individual bubbles, the lower volume releases (and hence smaller SCL's) had considerably slower rise rates for the first several meters above the deployment site. Eventually, however, all SCL leaders tended to converge on a common rise rate around 0.68 m/s. Thus it appears that the larger, fast moving SCL's shed effervescence at a proportionally higher rate, but after about 10 m their speed and size reduces to a point where they become relatively stable, and can rise for considerable distances. There is a positive correlation between depth of deployment and spatio-temporal separation or gap formation between the effervescence and leaders **(Fig 4.8)**. However, this separation can be reduced to a considerable extent by increasing the volume of air released. Finally, it was also found that the rise rate of the leaders was increased by increasing the volume of air released **(Fig. 4.7)**.

Herring Flight Speeds

Since I was interested in comparing the velocity of rising bubbles to maximum herring swimming speeds, I retained the 5 highest measures recorded in the laboratory resulting in a mean flight speed of 3.3 m/s (range: 3.0 to 4.1).

Humpback Feeding Behavior

A feeding event is initiated when the whales dive below the surface as a compact group. On many sonar images it is possible to see that the surface microbubble layer is disrupted at a steep angle **(Fig. 4.9a)**, suggesting that the whales descend steeply toward the bottom (**Fig. 4.9b**). Once at depth, the whales tend to travel close to the bottom (**Fig. 4.10**) and below the mean depth of herring schools (**Fig. 4.11**). The relatively deep position of the whales was also evident from the data obtained during the vertical attacks on the prey (**Fig. 4.12**) and from a single complete feeding event obtained on sonar (**Fig. 4.13**). This tendency to hunt the schools from below appears to strategically position the whales so they can readily herd the schools toward the surface. When frightened, herring and other species of schooling fish are known to dive to the bottom and become motionless (Schwarz and Greer 1984, Wardle 1993, Nottestad and Axelsen 1999); attacking from below presumably prevents the fish from seeking refuge on or near the seabed. This relatively deep position may also facilitate detection of herring schools by silhouetting them against down-welling surface light. As the herders move under the targeted prey patch they turn up from the bottom and ascend rapidly and directly toward the prey. A mean ascent rate of 2.8 m/s was obtained from 5 measures of rising whales, with a maximum of 3.4 m/s.

In contrast to the deep diving herders, it appears that at least one individual remains at a shallower depth to deploy the bubble net. Although I rarely imaged the bubble blower due to my sampling method the depth of this individual can be inferred from the lower end of the curtain or cylinder where the air was released. It was found that humpbacks deployed the cylinder at a mean depth of 17.1 m, which was considerably shallower than the mean mid-depth of herring schools (24.7 m) and mean maximum depth at which herders (27.4 m) were first imaged during their rush to the surface.

The results of the deployment studies revealed that the rise rate of spherical cap bubbles (approximately 0.65 to 1.0 m/s) is much slower than the rate at which the whales force the prey to the surface (approx. 3 m/s). Thus it appears that the whales rapidly drive the prey into a pre-constructed net, so as to synchronize their arrival at the surface with the leading edge of the bubble cylinder. However, when foraging on relatively shallow schools (between 10 and 20 m) the mean depth of the bubble net often extends below the mean mid-depth of the herring school. This suggests that when possible, the pod prefers to wrap the entire school in the bubble net, rather than force the herring up through the bottom of the cylinder.

That the whales attempt to synchronize the arrival of the cylinder at the surface with that of the fishes may provide one explanation for the increasing distance between prey and bubble nets when herring schools are situated deeper in the water column (**Fig. 4.4**). If bubble nets are initiated too deep, herring rising through the water column could escape above the bubble net before it reached the surface. Because fleeing herring can move much more rapidly than rising bubbles, an increase in fish depth should thus be accompanied by a smaller increase in bubble-net deployment depth. Specifically, we expect the proportional increase in depth of bubble-nets relative to fish schools to reflect the relative speeds of these entities. The slope of the relationship depicted in **Figure 4.4** indicates that the distance between bubble nets and fish schools increased (across pods) by 0.79 m for every 1 m increment in fish depth, implying that the depth at which different pods deployed bubble nets increased by only 0.21 m (1 m - 0.79 m) for every meter increase in prey depth. This figure can also readily be obtained from the relationship between non-transformed values of mid-school depth and bubble-net depth data depicted on **Fig. 4.5**, the slope of which is 0.21. Therefore, according to this hypothesis, one would predict that fleeing herring rise through the water column at a speed approximately 4.8 (1 / 0.21) times the rate of rising bubbles. This relationship compared well to the lab measurements of herring flight velocity, which found that the fish ascend through the water at approximately 4.7 times the speed of rising spherical cap bubbles (3.3 m/s /0.7 m/s). Given the different rise rates of bubbles and prey, it appears that the humpbacks must start their rush toward the surface while the leading edge of the bubble cylinder is still some distance below the surface (e.g., approx. 4 m below the surface for a net deployed at 18 m).

Discussion

The results of this study suggest that a humpback whale is confronted with an important tradeoff when deciding at what depth to begin constructing a bubble net. By increasing deployment depth, they produce a longer conduit or cylinder within which prey can be guided to the surface. However, the deeper a net is deployed, the more it is prone to develop gaps in the walls of the cylinder due to the separation of the different bubble size classes. It is not known how much air a whale can hold in its lungs and respiratory passages when it dives, although it is certainly possible that this could place an important constraint on net construction, thus limiting approach curtain length, and/or the depth of the cylinder and the thickness of its walls. Consequently, a whale may not be able to overcome gap formation simply by releasing more air, which could account for the depth limitations of bubble nets I observed in this study.

Given the large amount of air that comprises the walls of the cylinder, it is certainly possible that my experimental releases were of considerably lower volume than that actually deployed by humpbacks. By deploying large volumes of air, humpbacks may be constructing cylinders whose ascent is dominated by the rapidly moving swarm phase. In this case, the leaders' rise rate of 0.7 m/s used in the model may underestimate the actual rise rate of the cylinder. Some evidence for an underestimation comes from the sonar trace in **Figure 4.13**, where an average rise rate of 0.86 m/s was obtained for the ascent of the spherical cap leaders. The cylinder appears to serve as a conduit within which the prey is forced upwards and as a vessel to contain horizontal escape movements as the whales lunge through the prey trapped against the surface (Chapter 1). It is interesting to note, however, that during most encounters, the prey is initially moved some distance upwards without the aid of a net.

Unlike our experimental apparatus which was stationary, a whale is moving forward as it deploys the bubbles. Instead of a single burst, the whale produces a sheet of rising leaders, which greatly increases each bubble's potential interaction with neighboring bubbles. It has been shown by Otake et al. (1977) that rising bubbles tend to coalescence into larger, faster moving bubbles if more than half of the cross-sectional area of a trailing bubble overlaps with that of a leading bubble. In contrast, bubble break-up is promoted if the overlap is less than about half the cross sectional area of the trailing bubble (Otake et al. 1977). According to Otake's rule, a humpback could potentially mitigate gap formation by increasing bubble overlap, thus facilitating the rupturing of leaders into effervescence and thereby more effectively filling the gap. By minimizing gap formation in the cylinder walls with this method, the whale would again be confronted with the previously mentioned tradeoff, since increased rupturing would tend to degrade spherical cap leaders more quickly, and presumably limit the depth at which the net could be deployed.
It is concluded that a single whale cannot execute this feeding technique, since the deployment of the bubble net and the herding of the prey up from depths appear to be separate but synergistic activities.

It has previously been shown by Whitehead (1983) that foraging group size in the North Atlantic when feeding on sandlance *Ammodytes americanus* is correlated with size of the prey patch. If patch size in Southeast Alaska was the sole factoring governing pod size, and assuming that small schools are not uncommon, then one would expect to find solitary foraging individuals on a regular basis, which was not the case. Given that feeding calls elicit an avoidance response from the herring (Chapter 2), a vocalizing bubble blower (located above the school) presumably would drive prey away from the surface. It is interesting to note however, that even when herring schools were located relatively close to the surface (and thus perhaps vulnerable to single vocalizing and bubbling whale) there was no attempt by solitary whales to feed on the schools. This suggests that there may be a variety of benefits that accrue to individuals that forage in groups.

There is no evidence to suggest that more than one whale deploys the bubble net. However, most or all members of the pod appear to deploy their own bubble cloud just prior to lunging through the surface. These clouds may provide a final herding stimulus or permit each whale to fine tune the position of the prey in front of its mouth. Clouds may be helpful in containing the prey during the final lunge, as this is when the prey appears to make its most frantic escape attempt; it is often possible to observe fish leaping clear of the surface just prior to being engulfed. Clouds may also form part of the cylinder wall with open, trough (**Fig. 4.1**) shaped bubble nets. I obtained a maximum velocity of 1.1 m/s for bubbles during the swarm phases (with the 9 l deployments), however, it is likely the speed of the clouds deployed by humpbacks is considerably greater. This is due to the large volume of air that humpbacks release when producing clouds plus the fact that it appears to be forcibly ejected.

Monitoring with a hydrophone revealed that during much of the ascent phase (and often during much of the bottom search phase), one to several whales produce loud trumpet-like vocalizations ranging in frequency from 350 to 1200 kHz. It has been suggested that these calls may serve to disorient or frighten the herring and thus facilitate their capture (Baker 1985). Given that these sounds appear to be broadcast from a position below the herring schools, I suggest that they assist in herding the prey toward the surface. Further support for a herding function of these calls comes from playback studies (Chapter 2) which found that herring exhibit a strong avoidance of feeding calls.

The individual releasing the bubbles appears to regulate the size of the net to match the number of whales in the pod (personal observation). A large diameter bubble net produced by a big pod may make it difficult for the prey to perceive that they are being forced into a trap. Once the school is forced into the bottom of the bubble structure, the inward spiraling of the cylinder may then gradually constrict their movement. The tailoring of the net's diameter to pod size implies forethought on the part of the bubble blower and a cooperative basis to these groups. Perhaps whales within a group are obliged to accept new arrivals, as they might become disruptive if not permitted to participate in the feeding activity. However, the highly structured nature of these groups' dive order (unpublished data) and lunge formation (D' Vincent et al. 1985), and the rarity with which agonism is observed suggest that these pods are not based on producer-scrounger interactions or some other form of social parasitism. Given that adult herring are as fast (or faster) than an attacking whale, and that they can execute striking avoidance movements (Watkins and Schevill 1979, Pitcher and Parrish 1993) it is unlikely that any would-be cheater could benefit from prematurely rushing the school. But it does appear that through close cooperation, a fish school can be manipulated to the point where it can be successfully engulfed by the whales. Although larger pods require that the prey be divided among greater number of individuals, this cost is probably more than offset by the larger volume of prey that multiple whales can force up from the depths.

Although the sonar has been invaluable for investigating this behavior, there are a number of questions that remain unanswered. It is unclear to what extent the bubble blower contributes to the feeding calls, and at what point the bubbler halts the construction of the bubble cylinder to join the herders moving up from the depths. It is also unclear how individuals can freely join and depart these pods with little disruption to feeding activity. Perhaps most importantly, the sonar was unable to provide any insight into individual or group rates of prey intake. This information is essential for addressing questions concerning optimal group size, optimal net diameter, joining and departure decisions, and the factors underlying enduring partner preference patterns.

Despite these unanswered questions, this study was able to provide the first coherent picture of underwater events associated with socially foraging humpback whales. It was found that herring schools typically occur much deeper than bubble nets, and that the bubbling whale adjusts the net's depth so the bubbles arrive at the surface simultaneously with the fleeing fish. Using experimental bubble releases, this study also found evidence that humpbacks are confronted with an important tradeoff between net depth and the integrity of the net's walls. Perhaps the most intriguing finding of this study was the evidence of task specialization involving the bubbler and herders, suggesting that this feeding technique represents a sophisticated form of cooperation.

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	Independent Variables (Predictors)				
Variables (depth in meters)	X_1	X_2	X_3	X_4	X_5
Independent					
X1 Top of fish school	1.00				
X2 Middle of fish school	0.96	1.00			
X3 Underside of fish school	0.91	0.98	1.00		
X4 Sea floor under prey	0.90	0.96	0.97	1.00	
X5 Sea floor under bubble net	0.85	0.92	0.93	0.97	1.00
Dependent					
Y Bubble net	0.74	0.78	0.77	0.77	0.71

Table 4.1. Correlation matrix indicating the strength and direction of the association among the five independent variables and between each of the latter and the dependent variable. These correlation coefficients (r) result from analyses conducted on mean values (of dependent and independent variables) computed for each pod.

Different portions of fish school	Focal fish schools (N = 522)	Ambient fish schools (N = 161)	t-test
Top	17.1 ± 10.6	16.8 ± 10.7	P = 0.75
Middle	23.2 ± 12.2	22.9 ± 13.4	P = 0.85
Underside	29.0 ± 14.3	29.6 ± 16.5	P = 0.67

Table 4.2. Mean (± SD) depth (m) of focal herring schools (sampled within 15 m of nets) and haphazardly sampled schools (located more than 100 m from nets) and their comparison using t-tests (variances were homogeneous: Levene's test, all P values > 0.05).

		Mid-school depth (m)			Regression parameters	
Pod name	N	Mean	Max.	Range	r	P
Quest	2	10.50	11	1	NA	NA
AK Chicken	10	27.10	38	30	0.68	0.031
Akusha	9	26.00	36	16	0.55	0.122
Angoon	27	17.81	31	21	0.21	0.297
Bendel	1	17.00	17	0	NA	NA
Black Bear	20	28.40	49	32	0.49	0.028
Blackrocquat	21	16.67	24	11	0.55	0.010
Cornwallis	27	14.33	21	12	0.50	0.008
Crazy Ivan	8	42.63	51	25	0.16	0.704
Danger Pt	21	13.39	27	20	-0.06	0.795
Five Finger	17	58.24	80	45	0.27	0.293
Fog	14	15.93	25	15	0.52	0.058
Grave to Hunt	35	17.29	36	28	0.52	0.002
Hood Bay-1	31	19.71	29	23	0.37	0.037
Hood Bay-2	11	23.18	27	10	-0.50	0.119
Kennasnow	40	14.75	24	18	-0.17	0.288
Log Dumper	17	29.35	50	38	0.44	0.003
Melancholy	8	36.00	46	24	-0.09	0.823
Odyssey	10	30.80	50	29	0.45	0.186
Parker Pt	6	20.00	22	5	-0.78	0.063
Pinta	9	34.33	58	38	0.06	0.867
Pleasant Is	33	19.55	32	22	0.05	0.752
Princeton Hall	12	39.67	57	34	0.19	0.551
Radio Silence	2	58.50	60	3	NA	NA
Research	7	27.43	45	29	0.36	0.421
Richard-1	29	18.66	28	16	-0.11	0.561
Richard-2	15	19.20	28	16	-0.26	0.394
Romar	31	23.74	40	26	-0.06	0.732
Solo	2	37.50	45	15	NA	NA
Stellars	19	24.58	38	24	0.42	0.068
White Rock	7	16.57	26	15	0.61	0.145
Whitestone 2	8	11.00	16	7	-0.25	0.550
Yellow Eye	9	51.44	74	39	0.26	0.489

Table 4.3. Results of regressions conducted on successive dives of individual pods. Correlation coefficients (r) and P values are shown for simple regression analyses conducted between mid-school depth (ln transformed) and bubble-net depth. Also shown are the number of dives recorded for each individual pod and several statistics describing the depth at which fish were recorded.

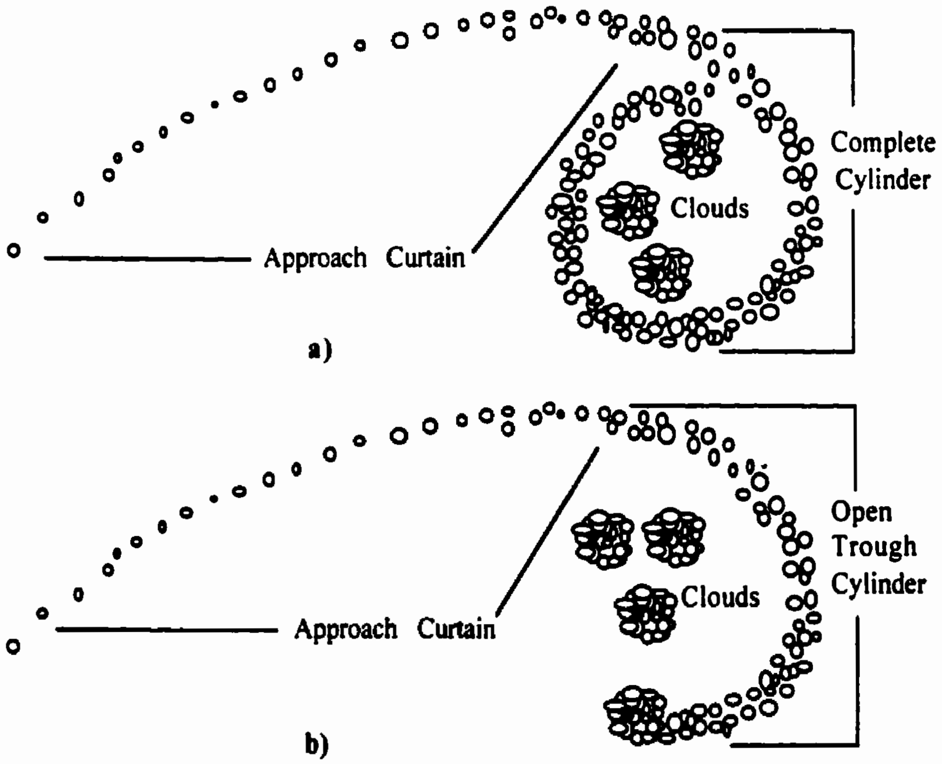


Figure 4.1. Diagram of bubble net patterns observed at the surface; a) complete cylinder, and b) open trough cylinder.

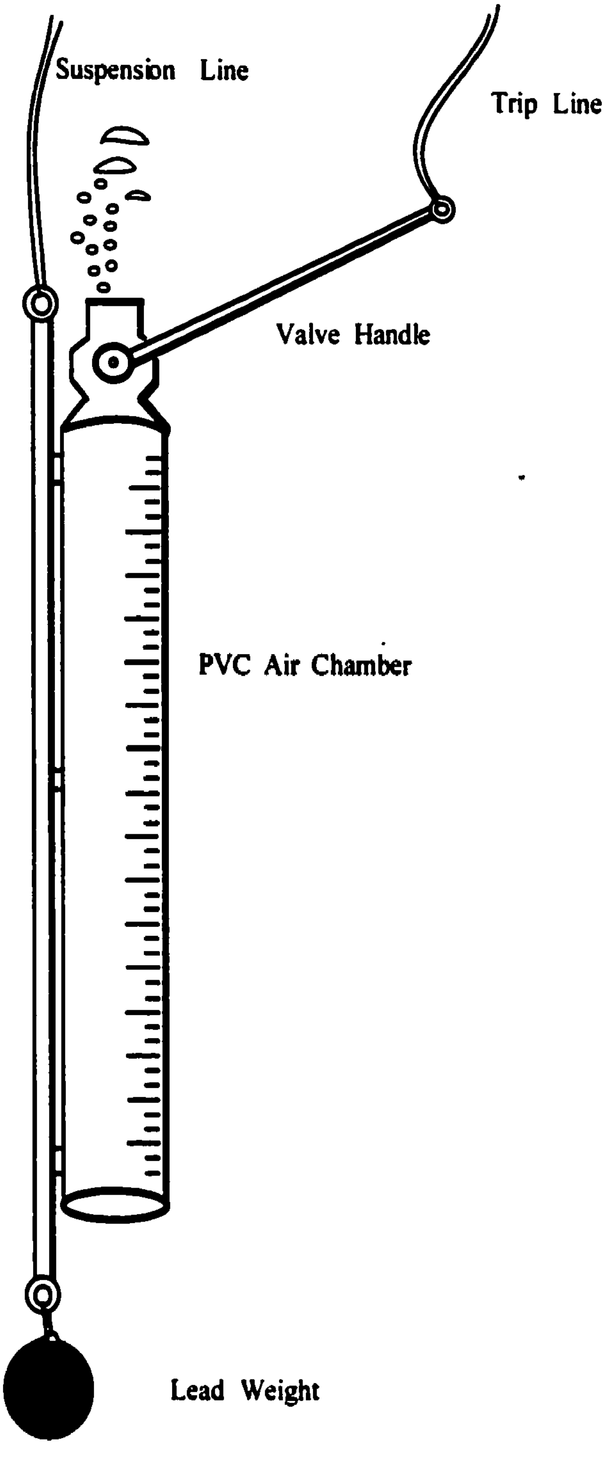


Figure 4.2. Device used for air deployment tests.

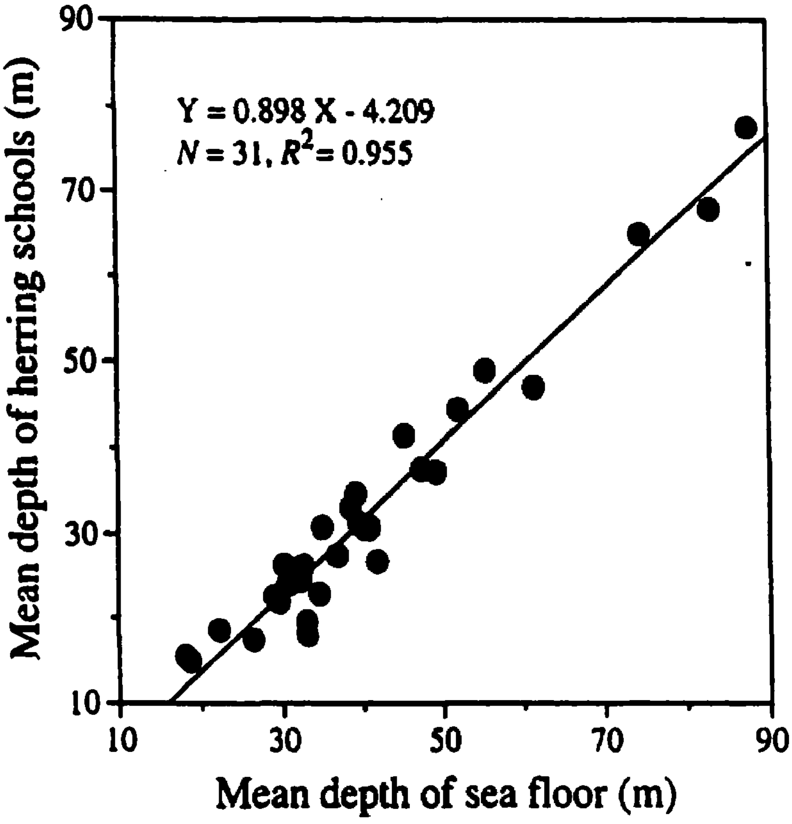


Figure 4.3. Scatter plot showing the tendency of herring to occur close to the sea floor. Each point represents the mean depth of herring (center of school) and underlying sea floor, observed in the vicinity of bubble nets released by a specific pod of humpback whales.

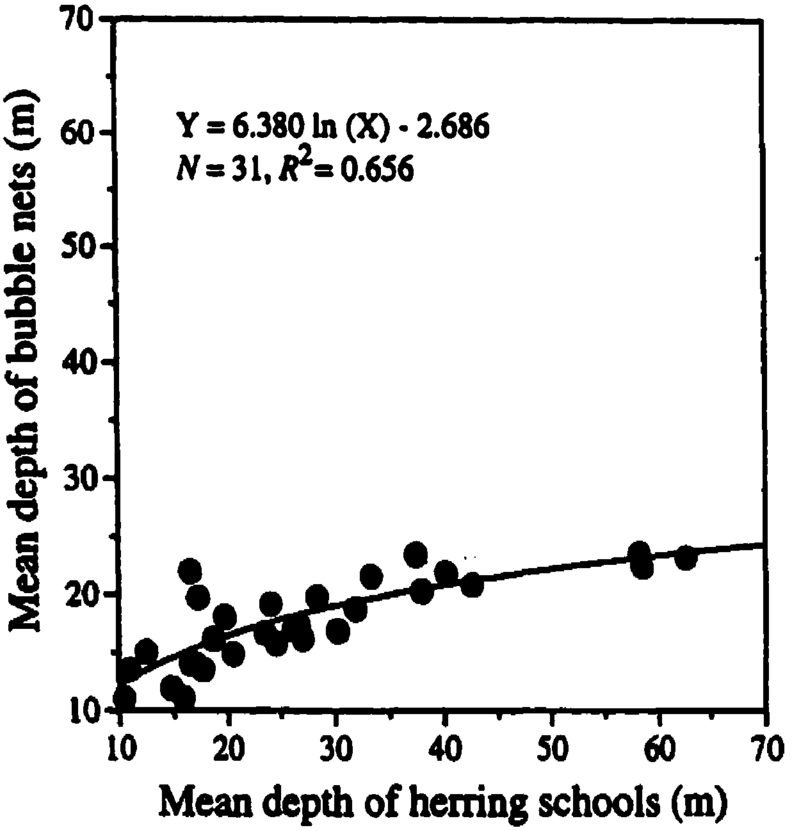


Figure 4.4. Scatter plot showing the tendency of humpback whales to adjust the depth at which they deploy bubble nets in relationship to the depth of nearby herring schools. Each point represents the mean depth of herring schools (center of school) and associated bubble nets (bottom) observed for a single pod of humpbacks.

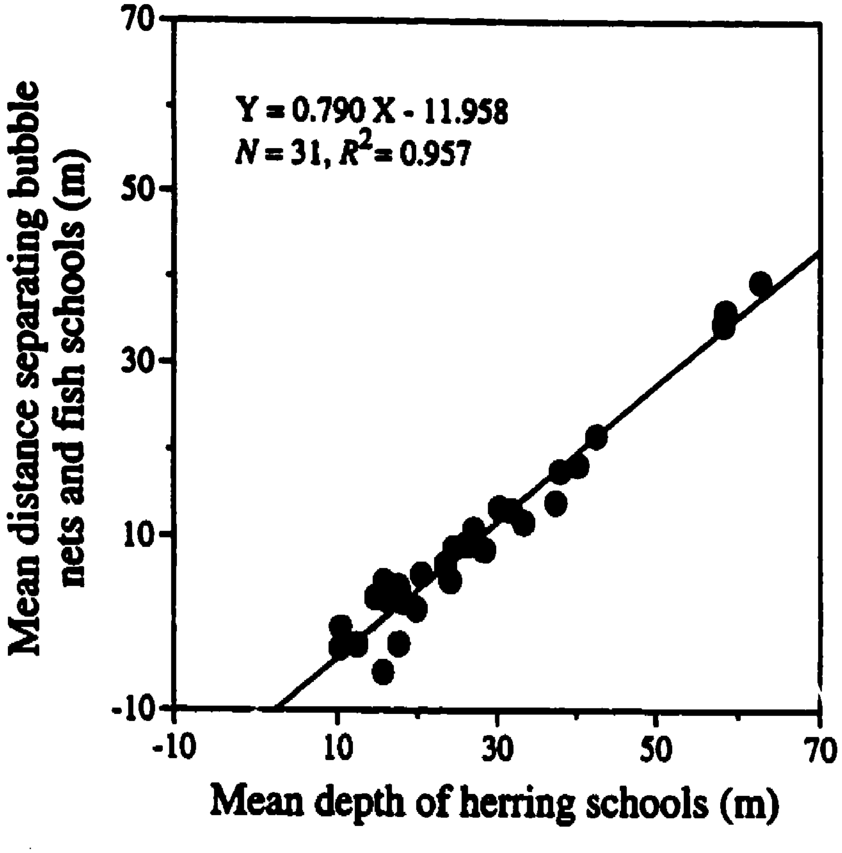


Figure 4.5. Scatter plot showing an increase in the distance separating herring schools and bubble nets with increasing depth of herring. Each point is derived from mean depths of herring schools (center of school) and bubble nets (bottom) observed for a single pod of humpback whales. Nets were generally deployed shallower than the schools, although the bubbles showed a significant tendency to be released at greater depth when the fish were situated deeper in the water.

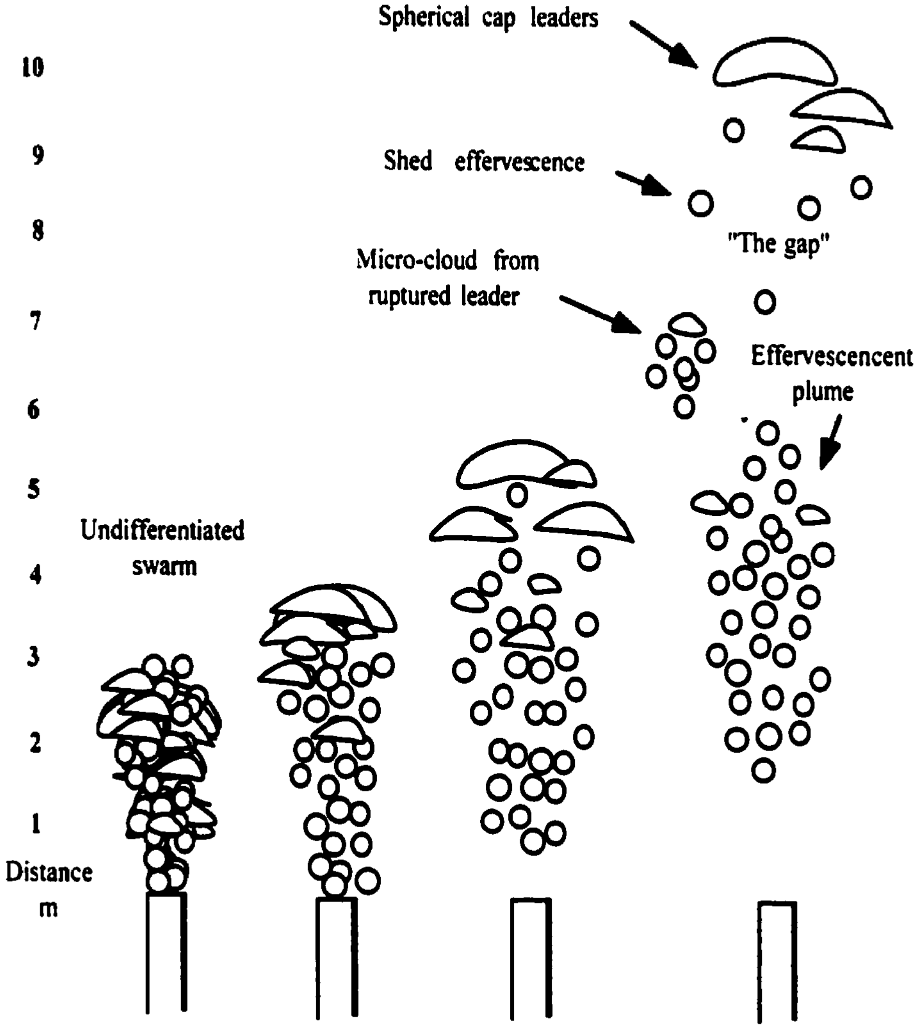


Figure 4.6. Diagram showing typical transition of a rising bubble plume. Starting with an undifferentiated swarm, the bubbles quickly sort into two basic size/speed groups: slower effervescence and faster moving spherical cap leaders.

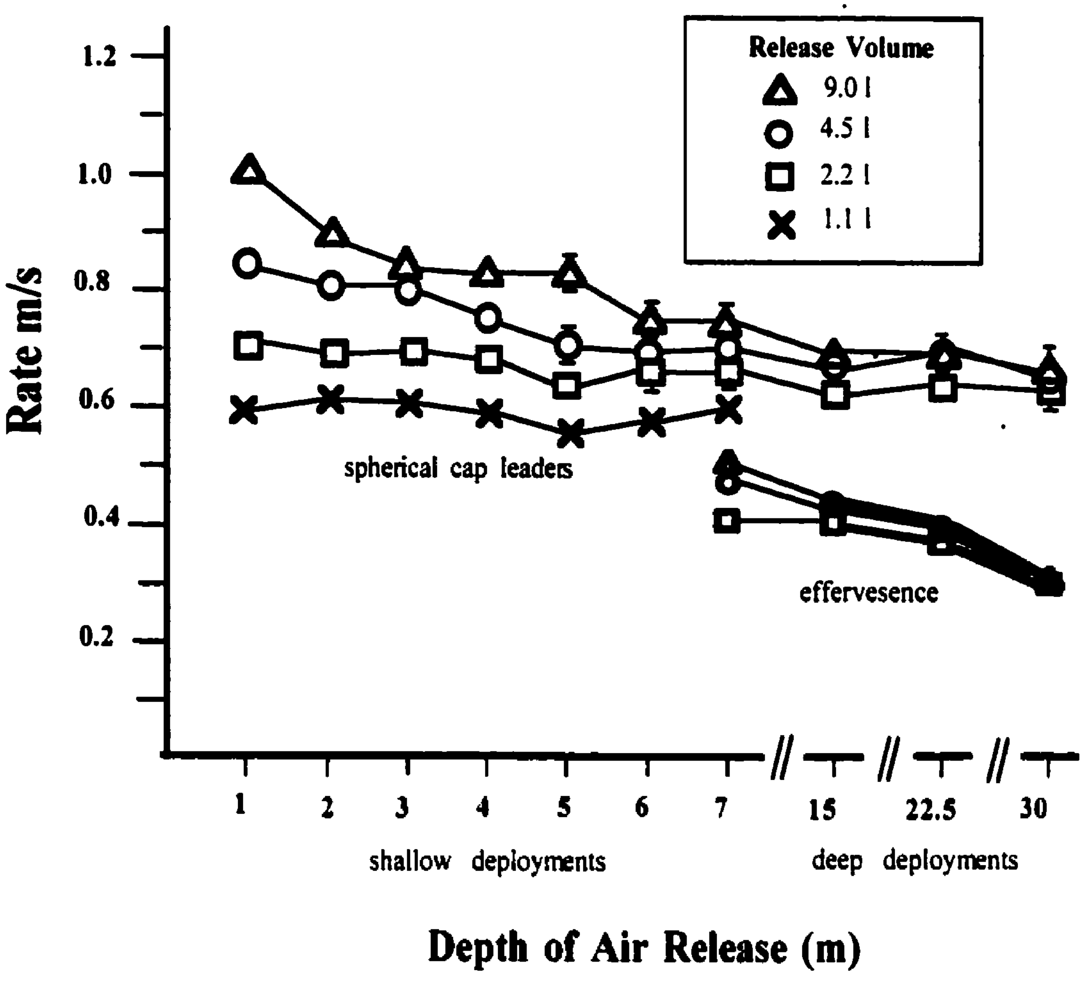


Figure 4.7. Graph of experimental releases showing the rise rates of spherical cap leaders and effervescense at four different deployment volumes and depths. Increasing the volume of air substantially increased theinitial rise rate of spherical cap leaders. Complete separation of leaders and effervescence did not occur until the plume rose for approximately six meters.

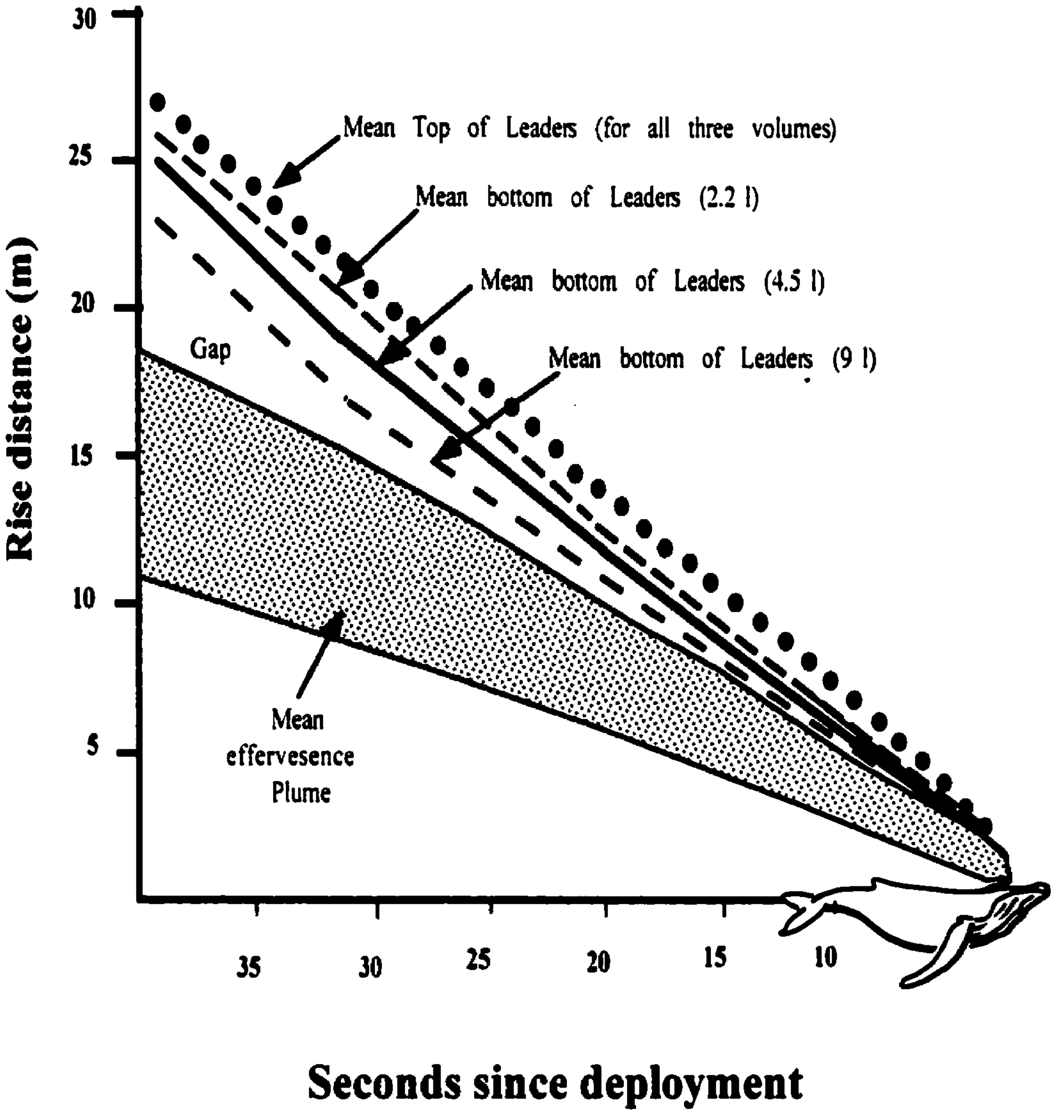


Figure 4.8. Inferred structure of rising bubble net from test deployments. Note decrease in gap size associated with increasing volume of release.

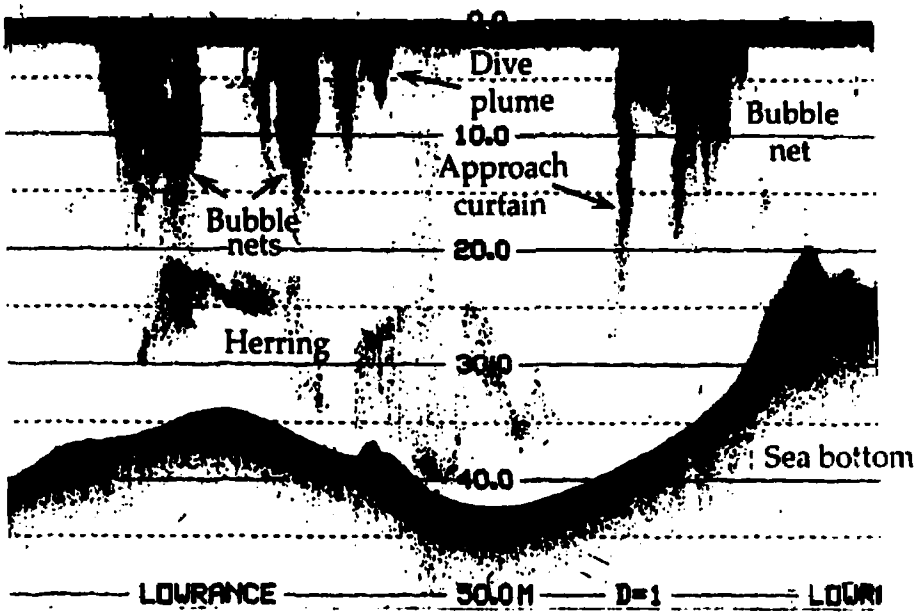


Figure 4.9a. Sonar image showing three bubble nets. Note the depth of herring schools below lower end of the bubble cylinders. The bubble net on the right reveals that the whale started releasing the approach curtain at 24 m, then ascended to 19 m when the cylinder was released.

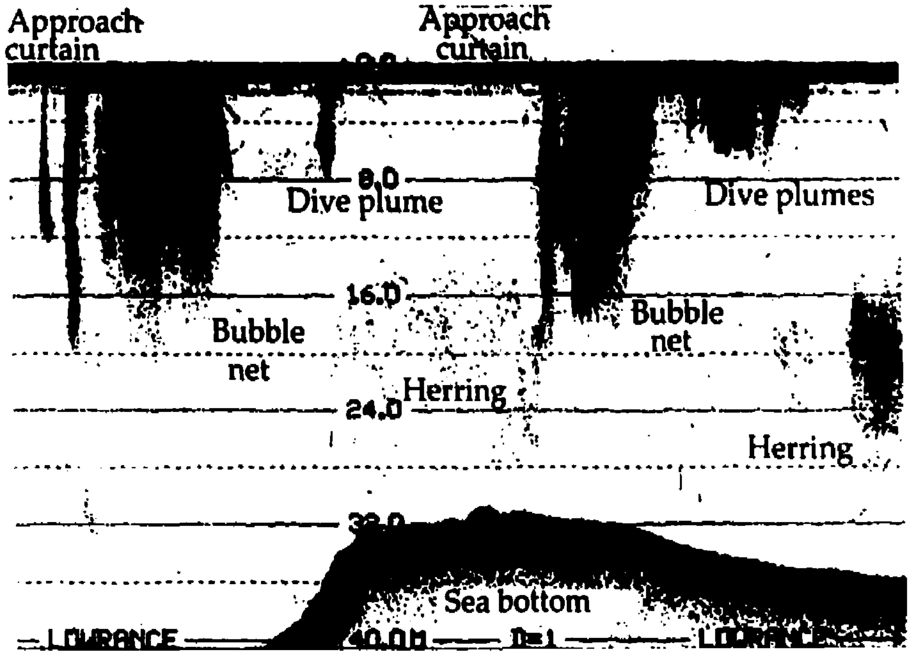


Figure 4.9b. Sonar images of two bubble nets. The bubble net on the left reveals an animal descending from 12 to 20 m as the approach curtain is deployed. The dive plume associated with the left bubble net (from a single animal), and on the right bubble net (from multiple animals) indicate that the whales descended steeply toward the bottom.

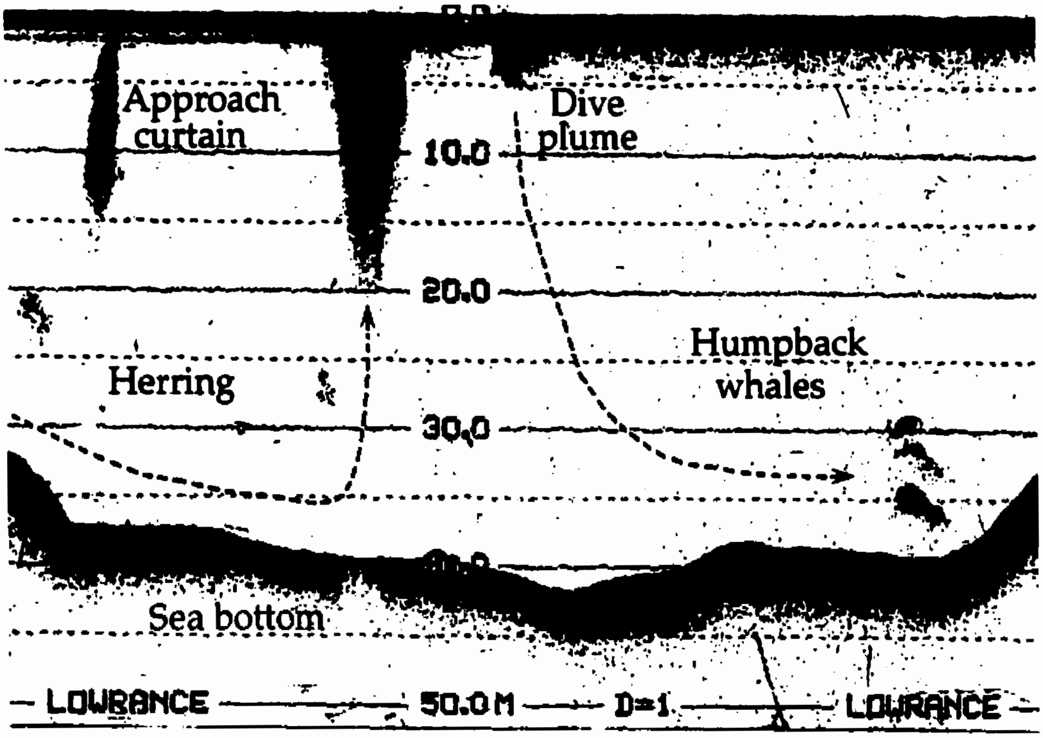
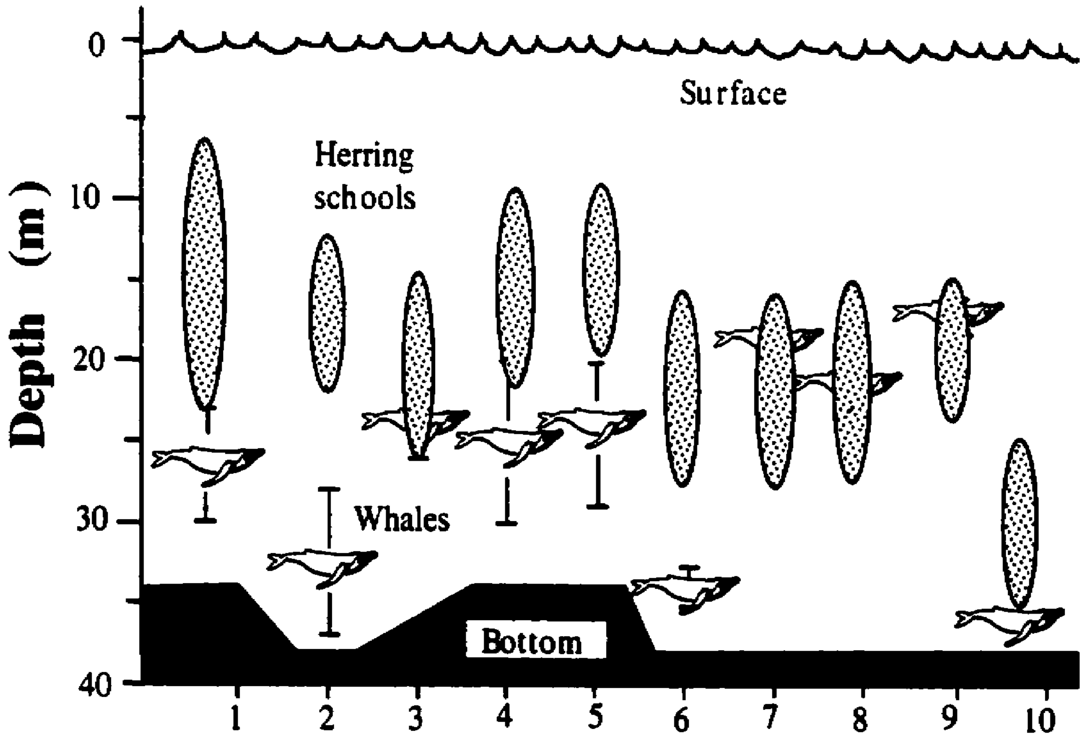
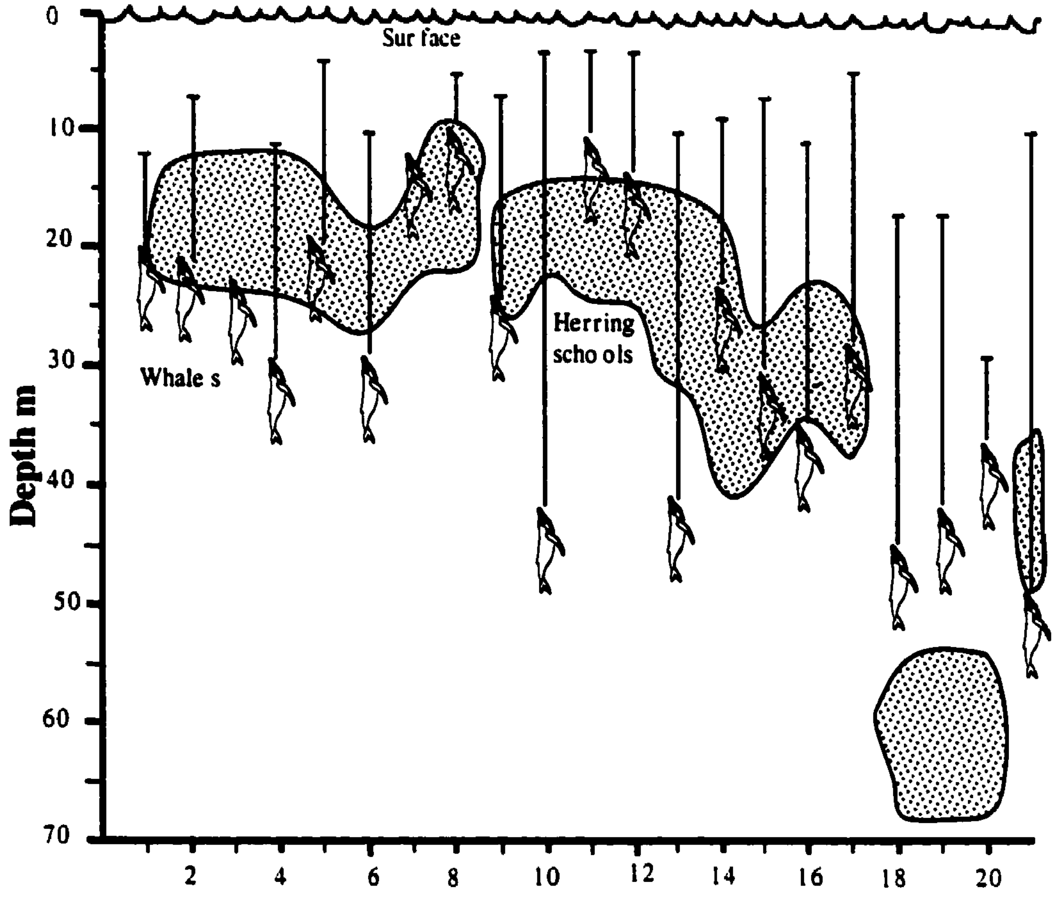


Figure 4.10. Sonar image of three whales swimming near the bottom in a vertical echelon formation. Bold dotted line represents the inferred path of these prey-herding individuals.



Encounters with hunting whales

Figure 4.11. Diagram showing relationship between hunting whales, herring schools, and bottom. Note that on the majority of the encounters, the mean depth of the whales was below the underside of the school, suggesting the humpbacks prefer to attack the herring from below.



Feeding events imaged on sonar

Figure 4.12. Diagram showing data obtained during vertical attack on the prey. Note that in the majority of the events, the whales were first imaged below the mean depth of the herring schools. Lines above the whales represent total distance recorded on sonar.

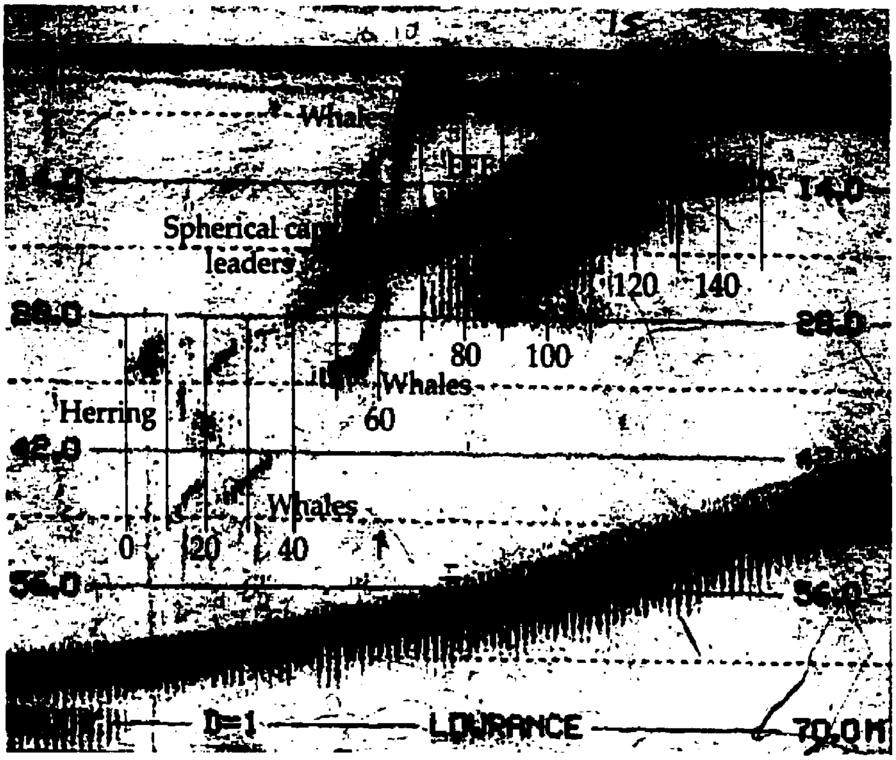


Figure 4.13 Sonar image obtained on 2 September 1994 in Icy Strait during the Pleasant Island encounter. Vertical lines represent time elapsed in seconds; horizontal lines represent depth in metres. From 0 to 25 s, herring schools were detected between 30 and 42 m. From 10 to 35 s, two herders were recorded below the school at 42 to 49 m. The image situated between 31 and 35 m at 20 to 35 seconds is difficult to interpret, but may represent the bubbler releasing the start of the cylinder (spherical cap leaders), which are clearly visible starting at a depth of 30 m at 38 s. These leaders rise 26 m in 30 s, for an average rate of 0.86 m/s. The herding whales are again recorded at 45 s, having ascended 17 m in 17 s for a rise rate of approx. 1 m/s. From this position 5 m below the cylinder's bottom, the whales begin their rapid ascent towards the surface, covering 31 m in 10 s for a rise rate of 3.1 m/s. At 67 seconds the whales lunge through the surface, synchronizing their arrival with the leading edge of the bubble cylinder. The effervescence (EFF) can be observed slowly rising to the surface from 40 to 125 s with a rise rate of 0.37 m/s. Unlike most feeding events, the herders here appear to initially force the herring school upwards relatively slowly (1 m/s) before rapidly accelerating to 3.1 m/s.

Chapter 5

Association Patterns and Relatedness of Group Foraging Humpback Whales in Southeast Alaska

Abstract

Photo-identification and molecular techniques are used to describe the social structure of group foraging humpback whales in Southeast Alaska. Group size and coefficients of association (CoA's) were found to vary over the study area depending on available prey types. In Chatham Strait (where fish abundance is high and euphausiid abundance is low), a group of 22 individuals were found to specialize almost exclusively on Pacific herring. Members of this "core community" are rarely found together in one group; instead they assemble into several widely ranging pods with a mean size of 7.4 individuals. Some partner preference is evident, although switching between groups occurs, particularly when two or more groups are in the same area. A large number of "visitors" have been observed to feed with these pods, although their residency time is relatively short. Most visitors remain for only one or two days, and are rarely observed to return in subsequent years. Calves born to core members were never observed to return and feed with their mothers in subsequent years, suggesting that these groups are not composed of first order kin. This was verified by analysis of microsatellite variation in the nuclear genome. In fact, whales in these social foraging groups were no more related than those in the population as a whole.

Unlike Chatham Strait, where individuals specialize on herring, most whales in Frederick Sound appear to be generalists and spend much of their time in small unstable groups exploiting abundant swarms of euphausiids. Consequently, when fish schools move into the Sound, individuals will join herring-feeding pods on an *ad hoc* basis, resulting in relatively weak CoA's. Group size was significantly larger in Frederick Sound, perhaps due to the high density of whales in this body of water providing many more potential recruits for fish feeding pods.

Individuals within these pods appear to be investing in by-product benefits, with the more enduring bonds between whales in Chatham Strait possibly representing combinations of individuals performing compatible tasks (i.e., bubble blower, herder, vocalizer).

Introduction

Similar to the other species of mysticete whale, the humpback whale's (*Megaptera novaeangliae*) social organization in the North Atlantic and North Pacific is characterized by small, unstable groups (Baker 1985, Clapham 1994, 2000). While on the feeding grounds, humpback associations tend to be relatively short in duration, typically lasting only a few minutes to a few hours (Whitehead 1983, Baker 1985, Weinrich 1991, Clapham 1993). Foraging group size is also relatively small, with most individuals feeding alone or in groups of two to three individuals (Baker 1985, Weinrich and Kuhlberg 1991, Clapham 1993). The absence of larger groups has been attributed to low levels of predation minimizing the need for group defense (Baker 1985, D' Vincent et al. 1990). Grouping to defend food resources is also believed to be unimportant because the patches of zooplankton and schooling fish upon which the humpback feeds tend to be variable in time and space, making them difficult to defend from conspecifics (Clapham 2000).

Despite the general tendency of humpbacks to form small, ephemeral groups, enduring associations and larger feeding pods have occasionally been noted. On the Antarctic feeding grounds, Nemoto (1964) documented two associated animals that were found together the following year when harvested by whalers. In the North Atlantic, Whitehead (1983) found that certain individuals were more "compatible" and tended to remain together despite other whales joining and departing the group. He also documented the formation of large foraging groups (up to 10 individuals) when the whales exploited large schools of sandlance *Ammodytes americanus*. In the Southern Gulf of Maine, both Weinrich (1991) and Clapham (1993) noted that a small number of individuals within the general population exhibited associations that lasted across seasons and occasionally across years (Weinrich 1991).

Some of the most extreme forms of sociality have been reported from Southeast Alaska where humpbacks feeding on Pacific herring (*Clupea harengus pallasi*) form large coordinated groups, sometimes numbering up to 24 individuals (Baker 1985, D' Vincent et al. 1989). Certain individuals within these groups have been found to remain in close association, and have been re-sighted together for several consecutive summers (Baker 1985, Gabrielle et al. 1995). The feeding tactics of these pods are also unusual, and include the production of loud trumpet-like calls, the deployment of bubble structures, and extensive waving of their large pectoral flippers at prey aggregations (Jurasz and Jurasz 1979, Baker and Herman 1984, Baker 1985, D' Vincent et al. 1985, Sharpe and Dill 1997). Whales in these groups also maintain close spatial proximity as they travel, dive, and engage in synchronized lunges on herring schools (Baker 1985, D' Vincent et al.

1985). These pods range widely throughout the Chatham Strait/Frederick Sound (CS/FS) region of SE Alaska. One pod, however, appears to occupy a relatively localized area in the vicinity of Point Adolphus in western Icy Strait (Gabrielle et al. 1995).

The objective of this study was to determine the basic social structure of herring feeding pods of Southeast Alaskan waters. Although past descriptions of their unique feeding behavior have been useful, the underlying social structure of humpback groups is poorly understood. It is not known, for example, if these groups are structured along lines of kinship. Furthermore, there is disagreement concerning whether individuals within feeding groups are competing (Watkins and Schevill 1979, B. Dolphin in Giddings 1984) or cooperating (Baker 1985, D' Vincent et al. 1985) as they attack fish schools. The first phase of this study used photo-identification to determine whether individuals within these groups 1) form distinct social units that do not mix with other pods (Multi-pod Hypothesis), 2) mix with other pods but contain sub-groups of more closely associating individuals (Meta-pod Hypothesis), or 3) represent a freely associating community where all individuals are likely to be sighted together with equal probability (Mixing pod Hypothesis).

The second phase of the study involved the collection of tissue samples from individuals within these groups for comparison with the larger humpback population in Southeast Alaska, to test the prediction that those individuals exhibiting high coefficients of association (CoA's) were close kin. The results are used to provide an overview of the social structure of Alaskan social pods, and insight into whether the relationships between individuals are based on collaborative or competitive interactions.

Methods

Studies were carried out in the waters of Chatham Strait and Frederick Sound in Southeast Alaska (**Fig. 5.1**) during the months of June to September, from 1994 to 1999. Research was conducted from either a 7 m or 15 m research vessel and two smaller inflatables. Socially foraging groups were located by traveling along the coastline (usually within 1 km of shore) within the study area. The terms group and pod are used interchangeably, and are defined here as two or more animals engaged in at least one feeding event involving the use of a bubble net, feeding vocalizations, and a synchronous surface lunge. When a group was visually located, there was an initial close approach to within 15 m to obtain ID's of all group members. To minimize disturbance to the animals, the research vessel would then retreat to an observation distance ranging from 50 to 250 m. The duration of observation periods was variable, ranging from 20 min. to 14 hrs. Once a group was encountered, it was observed until either 1) it disaffiliated, 2) it split into two groups (and one subgroup was followed), or 3) darkness or inclement weather forced termination of the observations. Individuals were identified from videotapes of the variable pattern on the underside of the flukes (Katona and Whitehead 1981) using either a Sony Digital Handycam DRCVX700 or a Sony Hi8 CCD Handycam. The identifying images were transferred to a Macintosh Quadra 840AV computer and stored on Adobe Photoshop files. Each time a new individual was documented it was given a name (listed here as a four letter code) and two hard copy images were printed. These prints were stored in two notebooks, one organized by fluke coloration, the second alphabetically by name, from which images on the field tapes were identified.

To minimize pseudoreplicating associations, group composition was sampled only once per day. The justification for sampling a given group of animals on successive days was based on the observation that most pods tend to stop feeding and disaffiliate at dusk, providing the opportunity for individuals to reassemble into "new" combinations of individuals on the following day. This nocturnal scrambling of individuals was verified by observations of visiting animals (see Results for details) who frequently disappeared from social pods overnight. If the pod split into two independently feeding groups, ID's would also be obtained from both of the resulting groups, and thus these were considered three separate encounters on a single day. Similarly, if two feeding groups joined, it was considered as three different encounters (two initial, one derived). However, if a pod continued to split and rejoin, the subsequent pods were not included in this analysis; thus only the pods associated with the first splitting or joining event were sampled. Following Gabrielle et al. (1995) a stable association is considered to occur when two individuals are sighted together on at least 25% of the observations per year for more than one year.

An overall coefficient of association (CoA) for all potential pairs was created using the simple ratio method (Cairns and Schwager 1987) which provides an estimate of the proportion of time the dyad were found in the same group:

$$\frac{X}{X + Y_{ab} + Y_a + Y_b}$$

where X = the number of encounters in which both animals were present in the same group;

Y_{ab} = number of encounters in which both animal a and b were present, but were not in the same group (always zero here);

Y_a = the number of encounters in which only animal a was present; and

Y_b = the number of encounters in which only animal b was present.

On nearly all encounters, it was possible to positively identify all members of the group. This is because when group foraging on herring, all members of the pod typically lift their flukes high into the air when diving. In addition, numerous dives were videotaped per encounter, permitting multiple confirmations of group composition. Feeding activity usually occurred in nearshore areas along a mean depth contour of 35 m (Chapter 4), permitting whales to be relatively easily located. Consequently, there appeared to be little effect of group size on sightability, so the simple ratio index was used as it is the least biased of the standard association indices (Ginsberg and Young 1992). The association indices were calculated and analyzed using SOCPROG 1.2 (H. Whitehead, programs available: http://is.dal.ca/~whitelab/index.htm).

Whale tissue samples were collected using a Teleinject biopsy rifle, or by dip-netting sloughed skin after an individual of known identity engaged in high energy surface behaviors (Clapham et al. 1993). Total genomic DNA was extracted from 46 biopsy samples, collected from Chatham Strait and Frederick Sound, using a standard phenolchloroform extraction technique as described in Baker et al. (1990). These samples were compared to an outgroup sample of 30 whales collected from the larger Southeastern Alaska region and to the mtDNA haplotype frequencies of 39 previously published samples (Baker et al. 1998). Molecular identification of sex was achieved by amplification of a short fragment of the SRY gene and using a second, larger nuclear fragment of ZFXY as a PCR control.

Mitochondrial (mt) DNA control region haplotypes were determined by digesting a 152 bp fragment with three restriction enzymes (DraI, NcoI and Sau96I), following Medrano-Gonzalez et al. (1995). The enzymes identify the three major clades found in humpback whales, world-wide. Further, the enzymes identify the two haplotypes (A+ and A-) within the A clade, which are the only haplotypes previously detected in Southeast Alaska (Baker et al. 1994). Restriction enzyme products were separated by size using gel electrophoresis (1.6% agarose/TBE gel) with a DNA mass ladder to determine size of each fragment.

Individual identification and relatedness analysis was achieved by genotyping each sample with up to nine cetacean-specific microsatellite loci. Each of the loci has previously been shown to be polymorphic in humpback whales (Schlötterer et al. 1991, Valsecchi et al. 1997, Palsbøll et al. 1997). The 5' end of one primer of each pair was labeled with a fluorescent dye (6-FAM, TET or HEX) to allow visualization on ABI autosequencer gels. After PCR amplification, following the specifications published with each primer, the microsatellites were separated by size on an ABI 373 autosequencer. Each lane included a size ladder (gs350) to allow accurate (±0.5 bp) determination of the size and intensity of each band. Microsatellite gels were analyzed using GENESCAN and GENOTYPER software (Applied Biosystems).

Relatedness was determined by using the M_{xy} approach (Blouin et al. 1996). For each locus a count is made of the number of allelic positions at which two individuals matched (0,1, or 2). Dividing by the number of loci gives M_{xy}, the average number of matches per locus between individuals x and y. The overall relatedness of the Chatham Strait and Frederick Sound population was compared to an outgroup sample of 30 whales representative of the whole Southeastern Alaska population. Relatedness by sex and by mtDNA haplotype were also calculated. Finally, a pairwise matrix of M_{xy} relatedness enabled comparison of genetic relatedness of given dyads to their coefficients of association.

Results

Association Data

A total of 257 individual whales were identified in 192 different groups. Coefficients of association ranged from 0 to 0.82 **(Fig. 5.2)**, with most individuals exhibiting a relatively weak tendency to affiliate with others. Consequently, the Multi-Pod Hypothesis (individuals form distinct social units that do not mix with other groups) was not supported. However, support was found for the Meta-Pod Hypothesis, as a small proportion of the population (n=25) were found to form stable associations (n=99) with one or more individuals **(Fig 5.3)**. Nearly all of these stable associations (n=96) were located in Chatham Strait or in a transition area between Frederick Sound and Chatham Strait **(Fig 5.1)**.

During 70% of the encounters with Chatham Strait pods (n=120) there was at least one whale present, termed a "visitor", who was not a member of the core community. A total of 92 visitors were identified and stayed with core pods for a mean of 1.9 days (SD=2.0). However, most visitors (n=63) were observed feeding with the core community only on a single day. There was a low interannual resighting rate of visitors; only 6 individuals were observed feeding with the core community in more than one year, and only one individual was resighted in 3 different years. Little effort was put into monitoring the behavior of visitors when not in a group, although on a number of instances they were noted independently feeding on euphausiids (n=10). Mean group size of pods in Chatham Strait (including both core members and visitors) was 7.4 (SD= 3.5).

In contrast to the core community in Chatham Strait, far fewer stable associations were detected among herring feeding pods in Frederick Sound (n=3). Consequently, the social structure of the herring feeding pods in this region is best characterized by the Mixing-Pod Hypothesis. Frederick Sound herring feeding pods (including those in the transition area) were found to be significantly larger in size ($\bar{x}$ = 10.1; SD = 3.2; n=72; $p \leq 0.0001$, unpaired t-test) than those in Chatham Strait. The population of whales in Frederick Sound was considerably larger, as the majority of animals were observed in Frederick Sound (n= 195) despite a lower number of survey days (n = 140). In contrast, 115 individuals were identified in Chatham Strait during 204 survey days.

Many animals exhibited strong site fidelity to either Frederick Sound or Chatham Strait, and are considered to belong to either sub-region if they were found there on 75% or more of the sightings. However, individuals from both sub-regions co-mingled in the transition area where they routinely fed together in the same pods. When Chatham whales visited this transition area, they were often in the company of other individuals from their core community. However, core members rarely ventured further east or north into Frederick Sound. The one instance when three members of the Chatham community (Bigm, Batm, Rubb; 19 Aug. 1995; Five Finger Islands) were found deep inside Frederick Sound, they approached, but did not join two actively feeding pods. They were not observed to feed in this area, and departed after one surfacing. In contrast, when visitors were sighted feeding with the core community in Chatham Strait, they generally were not in the company of other visitors.

Of the 19 core members for which sex was positively determined from their DNA, 11 were males, and 8 were females. Based on the criteria established by Straley (1994), it is likely that the 3 remaining core members (Momm, Notc, Snak) are also male, as each was observed on at least 5 different years without a calf (6, 6 and 8 years, respectively). Of the 12 strongest associations, male-female dyads were the most common (n=5), followed by female-female (n=4) and male-male dyads (n=3). Seven of the females gave birth to a calf (with 2 females giving birth in different years) resulting in total of 9 calves produced by the core community (**Table 5.1**). Two cow-calf pairs were also documented in Frederick Sound herring feeding groups. None of these calves were resighted in subsequent years feeding with their mothers or with any other whales in the study area.

Genetic Data

A total of 41 samples were genetically analyzed including 19 adults and 2 calves from the Chatham core community (**Table 5.2**). The remaining 20 samples (all adults) were collected at sites throughout the study area and included visitors to Chatham feeding groups, members of Frederick Sound herring pods, and lone individuals foraging on krill. Of the total sample 14 (34%) were determined to be female and 27 (66%) male by genetic sexing. In all but one of the samples mtDNA haplotype was determined (**Table 5.2c**). Contingency tests demonstrate a significant tendency for males to possess the A- haplotype and females to possess A+ in both the Chatham core community ($x^2 = 6.80$, $p=0.009$) and the SE Alaskan outgroup ($x^2 = 10.47$, $p=0.001$). All of the 41 individuals were also examined with a simple band-sharing (M_{xy}) approach. This analysis was conducted without information about the CoA's to avoid bias in the interpretation of the genetic relatedness coefficients. The mean relatedness was 0.420 +/- 0.131.

No clusters of related individuals were detected, as might be expected if core group individuals were kin. The 12 dyads with the highest behavioral CoA's in Chatham Strait were selected and their M_{xy} values plotted on the overall relatedness distribution. They were found to be evenly distributed throughout the normal distribution of relatedness coefficients generated by analysis of all samples (**Fig 5.4**). If the dyads were more related than by chance their M_{xy} values would be expected to lie towards the upper end of the distribution. The fact that they do not indicates that there was no relationship between CoA and M_{xy}. This was further examined by testing the ten dyads with the highest M_{xy} coefficients against the distribution of CoA values. Again, the M_{xy} values were randomly distributed, indicating no relationship.

Discussion

The findings of this study pose a number of intriguing questions. Why do humpbacks that exploit herring in Chatham Strait develop enduring bonds and moderately sized groups, while individuals exploiting the same prey in Frederick Sound have transient affiliations and larger groups? Why don't calves remain in the core community and adopt the social foraging tactics of their mothers, or return in subsequent years to feed with relatives?

Calf Recruitment

This study corroborates other findings that humpbacks do not develop familial bonds beyond the cow-calf pair. In the North Atlantic, Clapham (1993) found that only

12 of 2,690 pairs of whales containing animals with known genealogies consisted of related individuals. Preliminary mtDNA studies of this population further suggest that members of stable pairs do not represent relatives (Clapham and Palsbøll, in Clapham 2000). Similarly, in Southeast Alaska, Gabrielle et al. (1995) found that four calves born to members of the Point Adolphus group did not preferentially feed with their mothers in subsequent summers. Furthermore, two other individuals who did join the group were not the known offspring of any its members (Gabrielle et al. 1995).

For kin benefits to be transferred, relatives presumably must remain in close association. A structured kin group, however, may lack the ability to rapidly adjust its group size to match changing prey condition or make use of the different task specialists that may be available at different times. In this study, no pair of individuals was found to remain in continuous association, suggesting that partner switching is routine and perhaps the most effective strategy for exploiting herring schools.

It is unknown why the calves born to core members were not resighted in subsequent years feeding with their mothers. One possible explanation is that it is difficult for inexperienced calves to feed with adults in social foraging pods. When exploiting krill, calves appear to feed readily with their mother and quickly copy her foraging tactics (pers. obser.). This contrasts with calves in herring feeding pods, who are only infrequently observed to lunge with adults, and instead spend much of their time on the periphery of the group engaged in non-foraging behaviors. Similar to sperm whale calves who are unable to deep dive with the adults and thus remain at the surface (Whitehead 1996), humpback calves do not appear to be able to sustain the rapid pace of the adults when group feeding on herring. In addition, the sounds and disturbance associated with the calves' routine surface activities (breaching, tail lobbing) may interfere with the group's ability to manipulate the herring school using feeding calls (Chapter 2). Mothers with calves routinely depart the pod to feed on euphausiids (pers. obser.), which exposes the calf to other prey types and feeding tactics. Once weaned, the calf probably concentrates on euphausiids, which are an abundant food source (Krieger and Wing 1984, 1986) and are viewed as an easier prey to capture (Whitehead and Mann 2000).

For the first several years, juvenile humpbacks tend to be relatively asocial (Clapham 1994), limiting the likelihood of interacting with their mother or her close associates. Juvenile humpbacks are also known to disperse widely within a given feeding ground, further reducing the probability of interaction with their natal community of social foragers. Although humpback calves spend a longer period with their mothers compared to other mysticetes, relative to most social mammals humpback offspring grow rapidly (Chittleborough 1960), become independent early (Clapham and Mayo 1987, Baraff and Weinrich 1993) and attain sexual maturity at a young age (Chittleborough 1965, Clapham 1992). None of these features suggest a prolonged mother-calf interaction which could facilitate the direct acquisition of complex social skills or feeding tactics. Instead, becoming a core member probably comes later in life and may be associated with an individual's general sociability as opposed to adoption of its mother's tactics learned during its first year of life.

In other social mammals such as elephants, a single dominant bull may inseminate several females in a herd, producing a high degree of kinship within a cohort. In contrast, the promiscuous breeding system of humpbacks presumably results in core females being inseminated by different males on any given year, resulting in weak kinship ties within and across cohorts (Baker 1985). As noted by Clapham (2000), broader kin recognition is unlikely to occur in humpbacks since most calves are weaned before the birth of a sibling. There also appears to be little possibility that older animals can learn to recognize siblings via interactions with their mothers and her present calf given the low rates of re-association observed after separation (Clapham 2000; this study). Consequently, one of the few possibilities for sibling recognition would be the birth of twins, which are rare in humpbacks (Chittleborough 1960).

In most mammals, individuals of one sex disperse before maturity, which limits inbreeding (Greenwood 1980). However, if the natal group ranges widely and associates with other groups during mating activities both sexes may remain in their natal group (Connor et al. 1998), as appears to be the case with killer whales (Baird and Whitehead, 2000), and long-finned pilot whales (Amos 1993). Since humpback whales assemble on a communal breeding ground, avoidance of inbreeding is probably not an important selective force influencing calf dispersal on the summering grounds. Given that calves of core members have never been observed to feed with their mothers, both genders must disperse widely on Southeast Alaskan feeding grounds. This is consistent with findings in the North Atlantic, where young of both sexes were found as singletons significantly more often than were adults (Clapham 1994, Weinrich 1991). That juveniles disperse widely is also corroborated by observations that young are the first to recolonize new areas (Swingle et al. 1993). Althought limited by small sample size, the different haplotype frequencies between the sexes suggests that female whales exhibit greater site fidelity in the Chatham Strait-Frederick Sound area, and that males are moving into this area from the larger population.

Herring Feeding: Chatham Strait vs. Frederick Sound

CoA's between individuals group-foraging on herring in Chatham Strait are much higher than those herring-feeding in Frederick Sound. Hydroacoustic surveys have found that Frederick Sound is characterized by high concentrations of euphausiids and relatively low densities of fish schools (Krieger and Wing 1984, 1986, Dolphin 1987). Conversely, Chatham Strait is characterized by high concentrations of fish and low abundance of euphausiids (Krieger and Wing 1984, 1986, Carlson 1984, pers. obser.). Consequently, most whales in Frederick Sound have been found to exploit euphausids (Krieger and Wing 1984, 1986, Baker 1985, Dolphin 1987), while group feeding on herring in this area appear to be relatively uncommon and opportunistic. The abundance of krill in Frederick Sound favors small unstable groups (Baker 1985) from which individuals are drawn to form the groups foraging on herring. Consequently, when herring schools move into Frederick Sound, feeding groups appear to develop on an *ad hoc* basis from the ranks of krill feeders. Individuals in Frederick Sound also join and depart herring feeding groups at a significantly higher rate than social pods in Chatham Strait which further depresses CoA's (Baker 1985, unpubl. data). An extreme example of this fluidity was noted on 18 August 1995 when a pod of approximately 10 animals fed for 5 hours at Five Fingers Island. During this time, the composition of the pod gradually continued to change, until none of its original members were present at the end of the observation period. The much larger number of whales in Frederick Sound (Krieger and Wing 1984, 1986, Baker 1985, Straley 1994) also appears to have a dilution effect, increasing the likelihood that individuals will reassociate with different partners. Only five individuals exhibited stable associations in Frederick Sound. This includes a widely roving dyad (Notc and Vult) who are considered members of the Chatham core community which occasionally make forays into the transition area and Frederick Sound. Three other Frederick Sound individuals exhibited a tendency to associate within and across years (Berm, Viki, Vict). However, additional sightings will be required to determine if these individuals are re-associating more frequently than by chance, and if they exhibit any of the intriguing patterns noted in the Chatham core community (i.e., preferred lunge positions, specific dive orders, and consistent production of feeding calls).

The tendency for whales to form significantly larger pods in Frederick Sound appears to be associated with the larger population size in this area (Krieger and Wing 1984, 1986; Straley 1994). During the course of a feeding season over 400 individuals visit the sound (Straley 1994) and at any one time there can be 100 or more whales present (pers. obser.). In contrast, Chatham Strait is rarely inhabited by more than a few dozen individuals at any one time (Krieger and Wing 1984, 1986; pers. obser.). It has previously been shown by Whitehead (1983) that foraging group size in the North Atlantic when feeding on sandlance *Ammodytes americanus* is correlated with prey patch size. It is certainly possible that prey characteristics also influences pod size between Chatham Strait and Frederick Sound, given the different size and bathymetric features between these two areas. This question merits further investigation in the future.

There appear to be a number of factors that facilitate the reformation of social pods in Chatham Strait, and increase the likelihood that certain individuals will reassociate. Herring schools are often found at predictable locations in association with upwellings and submerged reefs (e.g., Pt. Gardiner, Morris Reef, Killisnoo Is.). This increases an individual's probability of encountering other core members simply by traveling to these sites. The ability of feeding calls to propagate over considerable distances may also permit individuals to locate and join social groups. Whales have been observed rapidly traveling up to 10 km directly toward a group of feeding whales, suggesting that individuals can track calls over considerable distances (D' Vincent et al. 1989). Given the ability to readily identify different calls using computer techniques (Sharpe et al. 1998, Cerchio and Dahlheim in press) and even with the human ear (Sharpe et al. 1998) it is likely that humpbacks can also recognize individuals producing the call. This would permit whales to relocate specific individuals or pods with whom they have compatible foraging positions or tasks. The rate of sound production could also provide information about the foraging rate of different groups or the overall abundance of prey (Cerchio and Dahlheim in press, Sharpe et al. 1998).

There is no evidence to suggest that individuals live in closed or semi-closed groups in which members are hostile to non-members. Instead, individuals freely join and depart groups with a remarkable absence of agonism or disruption to feeding activity (pers. obser.). The low level of conspecific aggression suggests that social pods are not characterized by strong dominance interactions. One possible explanation for the apparent absence of competition may be the relatively equal payoffs for each position within the lunge formation. Even if the profitabilities between positions differ, agonism may not be favored so long as individuals within a group do better than they could foraging alone. In addition, there may be little incentive to engage in agonistic interactions, as this could disrupt the highly coordinated herding of the prey that requires synchronization with the rising bubble net (Chapter 4).

Another factor preventing aggressive interactions may be the difficulty of dislodging an individual from a position within a group. During male breeding competition, it has been found that principal escorts are only infrequently displaced by challengers despite boisterous displays and aggressive physical contact (Tyack and

Whitehead 1983, Clapham et al. 1992). Escalating displays in males frequently include the release of bubble streams, head lunging and the production of social calls, activities that would presumably interfere with the carefully timed feeding event or manipulation of the herring school. Humpbacks appear to respect individual ownership of spatial position, much in the manner that female lions *Panthera leo* respect each other's feeding sites at carcasses (Packer 1986) and male lions respect the consortship of other males (Pusey and Packer 1998).

Another factor promoting enduring bonds and cooperative capture of prey may be the difficulty of cheating in this system. In other social hunting mammals, such as the African lion, heavy-bodied prey is targeted, often resulting in a large carcass that is divided up after the kill. This provides the opportunity for individuals to cheat by abstaining from the potentially injurious and energetically expensive hunt, but then joining the group to feed at the carcass. Cheating may be far more difficult with group feeding mysticetes because the prey aggregation is consumed instantaneously, so only those individuals participating in the hunt would have access to the food resource. Humpbacks are not at risk of injury from their prey, nor is the cost of locomotion high for large bodied mysticetes, further eliminating the incentive to cheat by abstaining. In addition, there is probably little impetus for an individual to rush the prey prematurely, as this would probably scatter the herring school and result in a low capture rate for all.

Conclusion

This study has demonstrated that there is a correlation between specialization on herring and the development of large, stable feeding groups. Individuals exploiting herring are also known to differ from euphausiid feeding whales in terms of their acoustic behavior (Baker 1985, Sharpe et al. 1998) and habitat use (D' Vincent et al. 1989). That diet preference can have a major influence on social behavior has been demonstrated in two populations of killer whales inhabiting the waters of the eastern North Pacific (Felleman et al. 1991, Jefferson et al. 1991, Baird et al. 1992). Assortative matings within each of these sympatric populations of killer whales has led to differences in morphology (Bigg et al. 1987), and genetics (Stevens et al. 1989, Hoelzel 1991). Since most humpbacks in Alaska assemble on a communal breeding ground in Hawaii, any genetically-based foraging trait associated with exploitation of herring probably becomes swamped through gene flow via mating with animals from other foraging populations. The relatively low levels of band sharing in the M_{xy} analysis, and that fact that offspring of core females do not remain in close association with their mothers suggests that the high CoA's cannot be attributed to kin selection.

If social pods represent collections of non-related individuals investing in by-product benefits, then why do persistent coalitions form? By-product mutualisms can favor partner preferences (Wrangham 1982) which are an expected outcome of individual variation in the ability to dispense or utilize by-product benefits (Connor 1996). It has previously been suggested by Weinrich (1991) that stable grouping in the North Atlantic may represent associations of individuals with compatible feeding styles. The stable associations observed in SE Alaska may similarly represent combinations of individuals that perform compatible tasks (i.e., bubble blower, herder, vocalizer). Task specialization may be critical in this system, where the deployment of bubbles and the production of feeding calls may represent mutually exclusively tasks (Chapter 4). The development of long term bonds between individuals to facilitate the capture of mobile, elusive prey has been proposed for other species such as killer whales (Baird and Dill 1995) and lions (Strander 1992). The best way to test this hypothesis in humpbacks would be to obtain a direct measure of intake rates between individuals in pods in Chatham Strait and those in Frederick Sound. However, given the difficulty of obtaining this type of data for wild humpbacks, it is likely that other surrogate measures will have to be employed, such as rate of lunging, and ratio of aborted to successful attempts.

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a) Chatham Strait Core Community

	1994	1995	1996	1997	1998	1999	2000
Asym		Ratc					
Batm							Boyw
Bigm	Bish						
Doll				Senc			
Rake		Shan		Bodk			
Slin			Bucc				
Zapm	Nike			Lena			

b) Frederick Sound

Pars					Aset		
Absq				Nano			

Table 5.1. Calves born to mothers in a) the Chatham Strait core community, and b) Frederick Sound.

a)

Pairwise Individuals	**CoA**	**Gender**	**Haplotype**	**M_{xy}**
Slin/Batm	0.73	F-F	A+/A+	0.500
Batm/Cimm	0.71	F-M	A+/A-	0.300
Slin/Cimm	0.71	F-M	A+/A-	0.400
Rubb/Asym	0.62	M-F	A-/A-	0.714
Asym/Rake	0.60	F-F	A-/A+	0.286
Asym/Slin	0.60	F-F	A-/A+	0.429
Slin/Capt	0.58	F-M	A+/A-	0.357
Rake/Rubb	0.55	F-M	A-/A-	0.357
Scra/Butt	0.52	M-M	A-/A-	0.500
Trum/Butt	0.48	M-M	A-/A-	0.429
Trum/Scra	0.46	M-M	A-/A-	0.500
Zapm/Bigm	0.39	F-F	A+/A+	0.357

b)

	Gender	**M_{xy}**	**n**
SE Alaska	M-M	0.44 ± 0.14	225
(Baker et al. 1998)	M-F	0.40 ± 0.12	280
	F-F	0.43 ± 0.14	72
Chatham Core		0.42 ± 0.131	20

c)

Chatham Core (N=20)

	M	**F**
A+	2	6
A-	10	2

Study Area non-core (N=20)

	M	**F**
A+	3	6
A-	11	0

d)

	A+	**A-**
SE Alaska (Baker et al. 1998)	23.1	76.9
Chatham Core	40.0	60.0
Study Area non-core	45.0	55.0

Table 5.2. a) Top 12 behavioral associations of the Chatham Strait core community showing gender, haplotype, and M_{xy} values. b) M_{xy} values for the SE Alaska outgroup, and the Chatham core community. c) Contingency tables showing significant tendency of males to possess A- haplotype and females to be A+ in both the Chatham core community and the none-core study area. d) Frequency of haplotypes by gender.

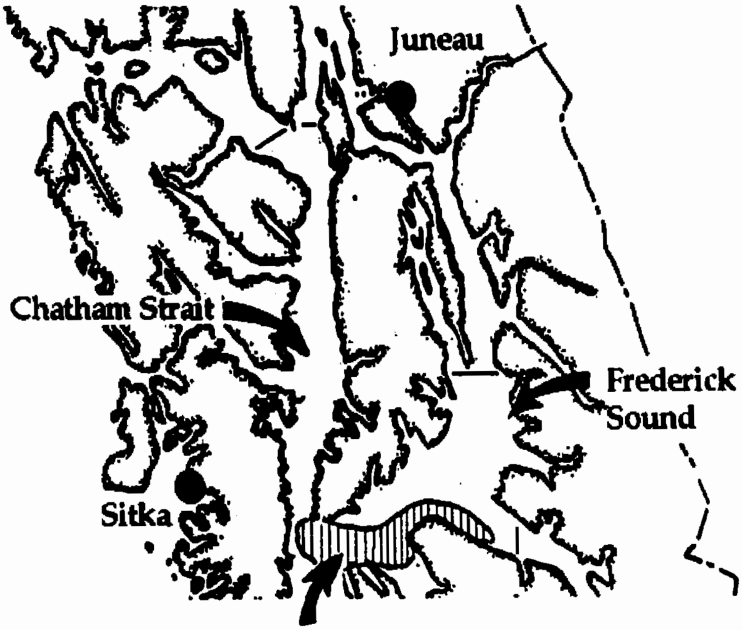

Figure 5.1. Map of study area showing primary subregions; Chatham Strait, Transition Area, and Frederick Sound.

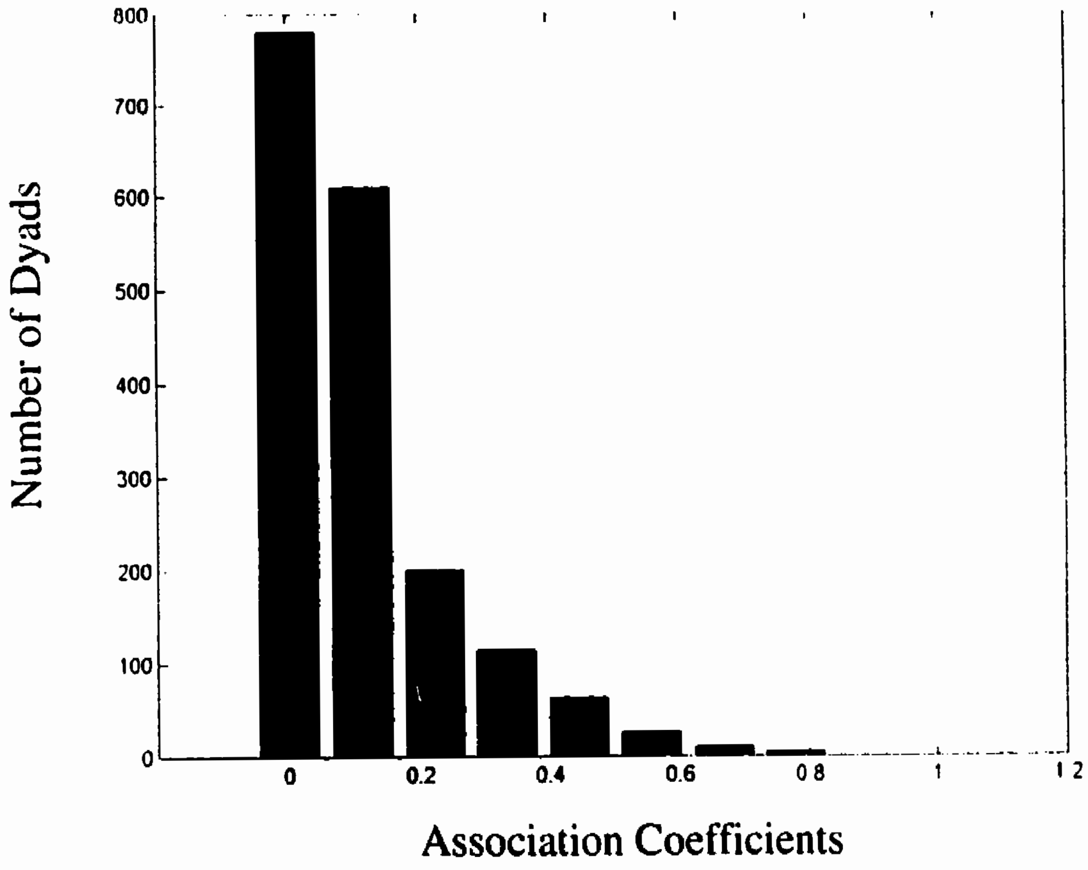

Figure 5.2. Distribution of association coefficients for all individuals in the study area observed more than twice.

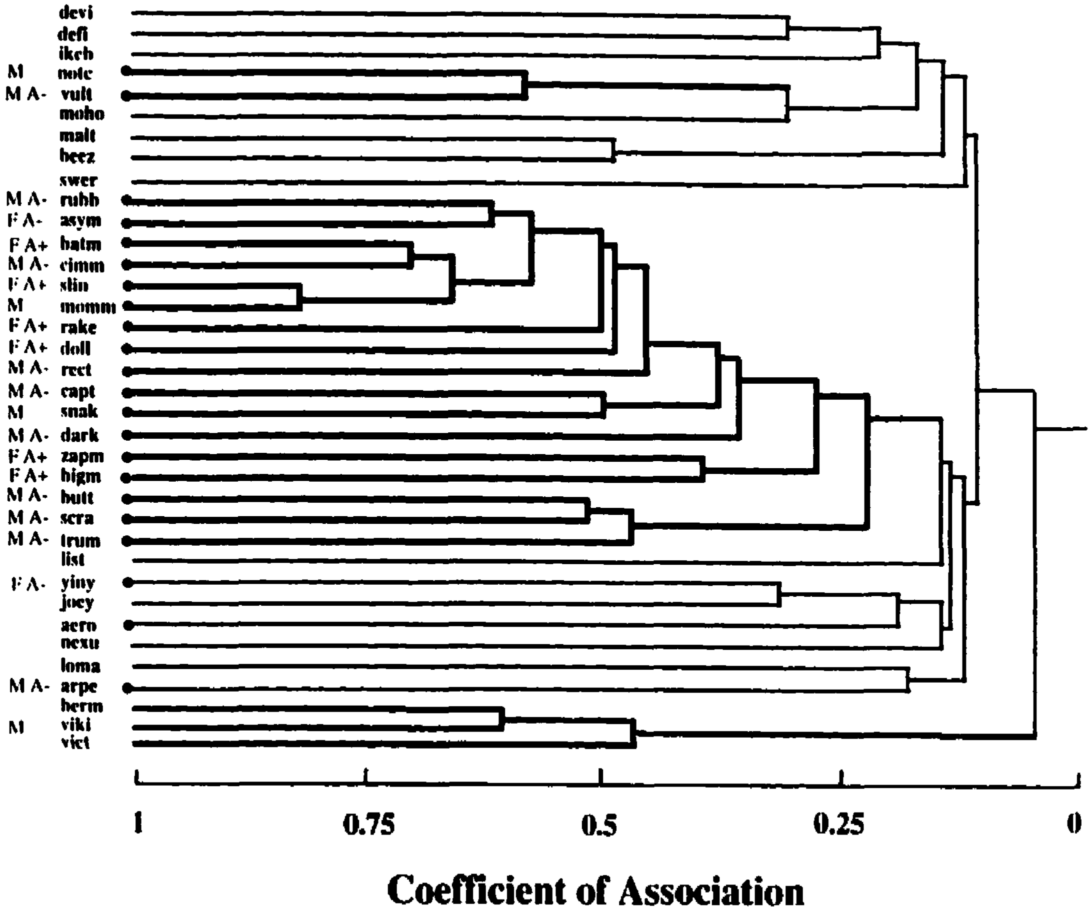

Figure 5.3. Dendrogram of humpback whales observed in social pods 7 or more times in the study area. A minimun of seven encounters was used as this prevented artificially inflating the number of stable associations by including individuals observed together on only a few occasions. Dark lines represent stable associations (whales sighted together on at least 25% of the observations per year for more than one year Gabrielle et al. 1995). The bullet denotes membership in the Chatham Strait core community. M = Male, F = Female. Capital A designates if an individual's haplotype is A+ or A-.

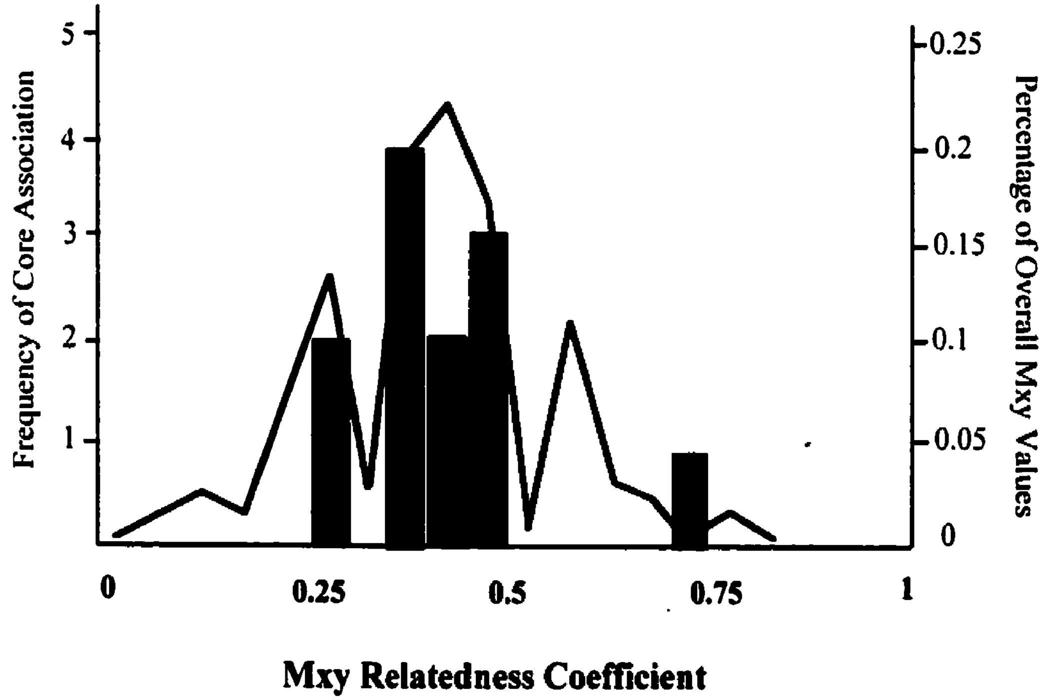

Figure 5.4. Distribution of the 12 dyads with the highest behavioral CoA's in Chatham Strait core community (bars) plotted against the overall relatedness distribution of whales within the study area (line).

Concluding Remarks

This thesis represents the first attempt to understand baleen whale foraging behavior by conducting laboratory studies on prey responses. This approach, in conjunction with field observations, has led to several novel inferences concerning social foraging in humpback whales. The laboratory tests revealed that herring exhibited predictable avoidance behaviors to bubbles, feeding calls, and flipper movements. This lends support to the hypothesis that these behaviors are used for prey manipulation and suggests that humpback whales may be exploiting prey defenses which evolved to thwart other predator guilds. Additional studies, however, will be required to conduct a more formal test of the rare enemy effect (similar to Jablonski 1999). Since it is not currently feasible to 1) make observations on captive humpbacks, 2) modify their vocal apparatus or pectoral flippers, or 3) accurately measure rates of prey intake, other approaches will be required. This could include determining the frequency of humpback predation on herring relative to other predators to ascertain if humpbacks in fact represent rare predators.

The absence of predation and territoriality, and the strong seasonal separation between feeding and reproduction, appear to favor "unconstrained" social relationships in the humpback whale. This produces grouping patterns that develop primarily due to foraging considerations. These stable foraging associations appear to be most well developed in Chatham Strait, where individuals exploiting herring form large groups with strong bonds and may specialize on specific tasks. Although task specialization has been documented in several species of group hunting birds and mammals, including Harris hawks *Parabuteo unicinctus* (Faaborg and Bednarz 1990), chimpanzees *Pan troglodytes* (van Lawick-Goodall 1968), African wild dogs *Lycaon pictus* (McFarland 1985), and lions *Panthera leo* (Strander 1992), this thesis provides the first evidence for specialization in baleen whales. This evidence comes from the spatial separation of whales in the water column (Chapter 5), indicating that whales adopt different roles during the lunge feeding event. Task specialization is also suggested by the fact that certain individuals 1) tend to occupy the same spatial positions on each lunge (D' Vincent et al. 1985), 2) consistently dive in the same order (unpub data), and 3) consistently produce the vocalizations (Cerchio and Dahlheim in press, Sharpe et al. 1998).

I have shown that humpback whales in one region of Southeast Alaska (Chatham Strait) form enduring social bonds that are not kin-based. These whales engage in apparently cooperative group foraging on herring schools using a suite of foraging tactics to manipulate prey responses. Deeper insight into this unusual community of whales will be obtained by finer resolution studies that examine changes in partner preference within and across years. In addition, comparative studies in locations where group feeding is rare will also provide further insights into the evolutionary basis of these unique behaviors and social organization.

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