

**Three dimensional prey aggregations and fine scale foraging patterns of Humpback whales
(*Megaptera novaengliae*) in Stellwagen Bank Marine Sanctuary**

Elliott L. Hazen, Ari Friedlaender, Dave Wiley, Michael Thompson, Colin Ware, and Mason Weinrich

Prior research has quantified prey densities at depth in association with foraging whales and suggests that these predators require a minimal prey density threshold for effective foraging. Even in the few cases where individual whales have been the focus of a directed study, however, it has been difficult to observe the behavior of individual whales in a three-dimensional environment. We addressed such information gaps directly by employing a novel research approach to study the fine-scale behavior of Humpback whales (*Megaptera novaeangliae*) and simultaneously measuring the distribution and density of their prey, sand lance (*Ammodytes americanus*). Non-invasive multi-sensor acoustic data logging tags measured whale movement and behavior in three dimensions. Concurrent synoptic prey data were collected using 120 and 38 kHz EK60 echosounders with simultaneous ADCP measurements of current direction and velocity. CTDs were used to measure vertical profiles of the water column during feeding bouts. Combining these measurement techniques allows us to monitor and quantify changes in whale foraging relative to oceanographic and prey conditions. Determining threshold densities of prey required for whale foraging, the effects of predation on prey school size and behavior, and examining the effects of oceanographic conditions on predator-prey interactions can augment knowledge regarding foraging theory of top predators in marine systems.

Keywords: Acoustics, Sand lance, predator-prey, foraging theory, oceanography

Contact author: Elliott L Hazen, 135 Duke Marine Lab Rd., Beaufort, NC 28516, USA [tel: +1 252 728 3941, email: elliott.hazen@duke.edu].

Introduction

Throughout their cosmopolitan range, humpback whales (*Megaptera novaeangliae*) migrate seasonally to high latitude areas to forage. These locations maintain predictable and high prey concentrations across years, and are characterized by proximity to shore, dynamic bathymetry, upwelling, and increased productivity (Gaskin 1982, Piatt 1990, Thiele et al. 2004, Friedlaender et al. 2006). The spatial distribution of baleen whales is linked in a scale-dependent manner to the distribution and abundance of their prey (Piatt and Methven 1992). For humpback whales, both the type of prey and its relative abundance over time contribute to fidelity or changes in foraging ground selection in the Western North Atlantic (Whitehead and Carscadden et al. 1985, Payne et al. 1986, Weinrich et al. 1997, Stevick et al. 2006).

Stellwagen Bank in the Gulf of Maine provides crucial habitat for foraging humpback whales particularly in late summer and early fall (Payne 1986, Weinrich 1998). Feeding humpback whales often aggregate in areas of high upwelling and productivity (Gaskin 1982) specifically where prey are most abundant (Piatt 1990). Surface foraging behavior on Stellwagen bank is diverse, previously characterized as lunge feeding (Watkins and Schevill 1979), bubble-netting (Hain et al. 1982), and lobtail feeding (Weinrich et al. 1992). These behaviors facilitate foraging by aggregating schools or corralling prey towards the surface where they are consumed. In the Gulf of Maine, Humpback whales have been observed feeding on sand lance (*Ammodytes americanus*), Atlantic herring (*Clupea harengus*), and krill (*Euphausia spp*). Atlantic herring are a primary prey source and are in highest abundance further offshore from Stellwagen Bank such as near Georges Bank, Nantucket Shoals, or Jeffrey's Ledge (Anthony and Waring 1980, Garrison 2000, Auster et al. 2001, Overholtz 2001). Humpback whales have also been observed foraging on krill off the northern edge of Stellwagen bank (Weinrich et al. 1997). Sand lance abundance is proposed as the primary prey species and driver of distribution for Humpback whales on the shallow waters of Stellwagen bank (Overholtz and Nicolas 1979, Weinrich et al. 1997).

Stellwagen bank has long been known to be an important habitat for northern sand lance (Auster et al. 2001). Bathymetric contours around the bank serve to upwell nutrients increasing productivity and prey resource for sand lance (Robinson and Lermusiaux 2002). As tidally driven waters pass over the shallow bank, turbulent flow creates internal waves that propagate along density gradients and can serve to aggregate zooplankton (Lennert-Cody and Franks 1999, Warren et al. 2003). In addition, bottom substrate on the bank includes the coarse grained sandy habitat that sand lance utilize for predator refuge (Meyer et al. 1979). Variations in climatic regimes, prey availability, and predation pressure have lead to high variability in sand lance abundance on the bank across multiple years (Weinrich et al. 1997). Increased fishing pressure on predators could be responsible for higher sand lance abundance

(Fogarty and Murawski 1998, Garrison 2000) and the subsequent rise in their importance as prey for humpback whales. Understanding the variability in humpback whale prey is crucial in understanding humpback whale ecology and behavior.

Little quantifiable information exists regarding the foraging ecology of baleen whales. Recent advances in tag technology though have allowed researchers to better investigate the underwater behavior of large predators. Using a tag which sensed motion in only 2 axes, Calambokidis *et al.* (2003) documented feeding lunges in blue whales using changes in acceleration. The DTag developed by Johnson and Tyack (2003) has been used to visualize underwater behavior by obtaining precise depth measurements, by measuring acceleration in three axes, allowing measurements of individual fluke strokes (Miller *et al.* 2004a, Ware *et al.* 2006), as well as recording acoustic cues (Nowacek *et al.* 2003, Miller *et al.* 2004b). These sensors can be also used to discriminate when humpback whales are actively feeding as humpback whales typically feed by lunging through a prey patch, engulfing a large volume of water and prey, and then expelling the water through their baleen plates. This sequence of activity may be detectable as a discrete series of movements captured by the DTag sensors.

While it is possible to measure the three-dimensional distribution of fish using trawls, the spatial and temporal resolution is extremely coarse. Fisheries acoustics offer a minimally invasive technique for collecting data on biomass at fine horizontal and vertical spatial scales throughout the water column (Simmonds & MacLennan 2005). Acoustics have been used to observe changes in distribution and behavior such as herring school size and shape while feeding (Misund *et al.* 1998, Mackinson *et al.* 1999) and under predation (Nøttestad *et al.* 2002). Measurements of prey distribution have less frequently been combined with data on foraging behavior.

To date, Croll *et al.* (1998, 2005) have completed the most integrated study of the fine scale foraging behavior of individual baleen whales. Croll *et al.* (2005) attached microprocessor-controlled time-depth recorders (TDRs) to two blue whales and correlated the vertical profiles of their dives to the vertical distribution and density of euphausiid swarms in the area. Euphausiid density was approximately two orders of magnitude greater in areas where whales concentrated their foraging efforts than elsewhere in the study area (Croll *et al.* 2005). These investigators note that “as measurements of prey were directed at patches where whales were foraging, we feel that this provides, for the first time, an estimate of the magnitude of prey densities for large whales.” Dolphin (1987) used qualitative sonar scans to describe the behavior of humpback whales in Alaskan coastal waters, which appeared to be foraging in the upper 120 m of the water column and associating with the shallowest and most dense prey patches. Friedlaender *et al.* (2006) recently analyzed the distribution of humpback whales off the western Antarctic peninsula, finding a significant spatial relationship with hydro-acoustically inferred krill patches < 140 m deep. Most recently, Ware *et al.* (2006) has described various

stereotyped underwater behaviors of humpback whales equipped with DTags off Stellwagen Bank, Massachusetts. However, there have been no studies linking the diving behavior of humpback whales to the distribution and abundance of their prey in a testable and quantitative way.

By combining acoustic measures of prey density with precise measures of whale movement and foraging behavior, our project examines the following hypotheses regarding foraging humpback whales in Stellwagen bank. In addition, we aim to understand which environmental variables are most correlated with prey abundance.

- 1) Specifically, we believe sand lance are highly correlated with increased bathymetric slope, relative fluorometry, and bottom type.
- 2) While we cannot unconditionally test whether whales are cueing their search behavior to similar environmental variables or are sensing large prey distributions, we believe whale foraging will be highly correlated with similar environmental variables as well as areas of high prey distribution. Before beginning to feed, whales might cue to environmental gradients to search for prey but do not begin foraging until a certain threshold is reached.
- 3) Building upon the previous hypothesis, we predict that humpback whales will begin foraging a specific density of prey and stop foraging below that threshold.

We believe this approach will allow us to elucidate the foraging ecology of both predator and prey relative to environmental features.

Methods

Data Collection

Our research took place aboard the R/V Nancy Foster in the Gulf of Maine, Stellwagen National Marine Sanctuary from July 6-20th, 2006 with the goal of measuring environmental gradients, prey distribution, and predator behavior. Before and after Dtag deployment, acoustic surveys were conducted to determine the relative size and distribution of prey aggregations in the survey area. Prey distribution was measured using 38 kHz and 120 kHz SIMRAD EK60 echosounders towed off the port side A-frame at a frequency of 10 pings per second and pulse widths of 512 ms and 256ms respectively. Prey species were identified primarily as sand lance which are common in the sandy habitat of Stellwagen Bank in the summer (Weinrich et al. 1997) through photography of escaping individuals during whale feeding bouts and by visual observation of prey at the surface. Boat speed while towing varied between 3 and 5 knots depending on sea state and currents. Due to the proximity of our vessel to foraging whales, midwater tows were not feasible during this study. Physical data was measured using continuous shipboard measurements of relative surface fluorometry and surface temperature. Existing data sets such as previous bathymetric multibeam and bottom

typing surveys were also incorporated to understand which physical parameters drive prey distribution and predator foraging.

Top predator behavior was examined using DTags which can be used to analyze the fine-scale movement patterns and foraging behavior of large marine animals. The DTag is small, lightweight, pressure tolerant and has a substantial data recording time and rate of 50 Hz (Johnson and Tyack 2003). The DTag is capable of recording the animal's pitch, roll, and heading as well as depth, and acoustic information. Data from the pitch record allows for analysis of fluke stroke rates and relative stroke amplitudes and combined with behavioral observation allows the identification of foraging bouts and quantification of their intensity and maximum depth. Behavioral data collected from the tagged whale and associates from a 16' rigid hull inflatable (RHIB) with position recorded using laser range finder binoculars with a realtime GPS data feed. At times when behavioral sequencing was unavailable (e.g. night time), positions were estimated using the research vessel's position and relative proximity to the tagged whale as judged by the amplitude of VHF transmitted radio signals.

Before tagging, the boat would search for whales to tag while collecting acoustic data, essentially providing a control set of prey data in the absence of whale predators. Once a whale was located and tagged, a RHIB served as the follow boat recording individual whale behaviors while the R/V Foster measured surrounding prey and environmental variables. If the tagged whale was traveling, a zig-zag design was used to survey prey distributions passed over by the whale (1.4km long transects). If the tagged whale was foraging, an expanding box design allowed the measurement of prey abundance and distribution at varying scales, with the center of the box moving with the whale. The sampling design around resting individuals was identical, with an expanding box to examine the prey distribution in the absence of foraging. As animals perceive and react to their environment at a range of scales, there is clearly no single scale correct for studying ecological relationships (Levin 1992) therefore we tried to resolve prey and predator distribution at similar scales.

Analysis

In order to test our research hypothesis, behavioral data from tagged whales was integrated with physical data and measurements of prey patch distribution and density collected during the synoptic acoustic surveys. Acoustic data were processed using Sonardata Echoview software (version 4.20). The sounder detected bottom was manually rectified and an exclude below line was created incorporating a half-meter backstep. Individual schools were marked, integrated, and exported using the school detection algorithm at both 38 kHz and 120 kHz with a -75 dB threshold. Acoustic biomass was subsequently gridded into 50 meter horizontal cells by 1 meter vertical cells and integrated with a -90 dB threshold to examine smaller prey aggregations. All exported backscatter data including 2-dimensional school

parameters (density, length, mean height, mean depth), integrated cell biomass (density per 50m), and bottom depth were imported into ESRI's ArcGIS 9.2 for spatial analysis.

Surfacing and behavioral observations of tagged whales were coded into feeding and non-feeding events and imported into ArcGIS. Depth of feeding events and time spent per feeding event were analyzed using Trackplot (Ware et al. 2006) and incorporated into sighting data. Surface feeding was identified using ascent rates and whale orientation and were often accompanied by one to three loops. Behavioral sequencing data were used to ground truth DTag observed foraging behaviors to ensure that behaviors we were identifying from the DTag track were observed at the surface. In the absence of behavioral sequencing data, the iterative process gave us confidence in behaviors identified by DTag analysis.

In order to sample data for each event, school parameters (length, height, area, density, depth), logarithmic measures of acoustic biomass (dB), surface temperature (°C), and relative fluorometry (volts) were interpolated into temporally segregated raster grid cells using an ordinary kriging function while adjusting variograms to minimize RMS error (Petitgas 1993, Maravelias et al. 1996). Additional previously measured physical parameters (distance to slope, bottom depth, bottom type) were also incorporated in sampling. Tidal height measured in Boston Harbor was temporally linked to each data point. For prey analyses, individual 50 m cells were used to sample the environmental variables. Each sighting following a surface foraging or non-foraging event was used to sample interpolated environmental and school parameters. The resultant samples were imported into Insightful's S-Plus 7.2 for statistical analysis.

For prey data, generalized additive models (GAMs) were used to examine the non-linear relationship between backscatter and environmental variables using a Gaussian distribution. A generalized linear model (GLM) was used to examine the linear effects of each environmental variable on backscatter. In order to examine predator behavior, a Classification and Regression Tree (CART; Redfern et al. 2006) was run with whale surface behavior as the response variable. Optimal recursive partitioning combined with a cross-validation using explained deviance ensured that only the most significant breaks were included in the final model. Generalized additive models (GAMs) were then used to examine the non-linear relationship between CART selected variables and whale foraging behavior using a binomial distribution. We also examined foraging dive depths with mean prey school depth to look for correlation in behavior.

Results

During the duration of the cruise, we deployed DTags on 15 individuals in the Stellwagen Bank National Marine Sanctuary for over 95 hours of tag data: 66 hours during daytime and 29 hours at night (Figure 1). A total of 2384 prey schools were detected at 38 kHz with 2980 schools detected at 120 kHz. Results are presented primarily for 120 kHz data for simplicity and because scattering was estimated to be greater compared to 38 kHz for similar sized fish lacking swimbladders (Gauthier and Horne 2004). Eleven of the fifteen whales were observed surface feeding at some point during the data record. Out of a total of 892 sampled surfacings, 393 were surface feeding events and 499 were non-surface feeding behaviors. Prey backscatter was patchily distributed (Figure 2) with school lengths up to 4km and heights up to 30m. Detected schools had an average density -57.7 dB with a range from -72.9 dB up to -33.1 dB. The mean school length at 120 kHz was 139m and the mean height was 7.9m. While most of the effort was concentrated near the western edge of the bank due to the abundance of whales, prey density was visibly greatest near high slope bathymetry along the western bank edge.

Examining the longest track for whale 196a (~21.5 hrs), surface foraging bouts occurred at three distinct times (Figure 3). The whale was foraging when the tag was attached at 8:51 and stopped at 10:00. Surface foraging commenced again at 19:00 and continued until 20:16. The final foraging bout began at 5:00 the next morning and continued until the tag released at 6:30. The total number of surfacing observations was 153 with 40 of them recorded as surface foraging events. For example, during the first foraging bout whale 196a was observed lobsailing followed by a bubble net in 66 meters of water (Figure 4a). Large surface schools were visible in the acoustic data surrounding the behavior. On a broader scale, two out of three of the foraging bouts overlapped with high prey density while the third was about one kilometer from the nearest high density patch. However, a regression of foraging depth against mean prey school depth had a low R^2 value (0.11) with high variability in the relationship.

The effects of environmental variables on prey density from the GAM found all of the variables to have a significant non-linear effect on backscatter (Table 1). However, time, temperature, and bottom depth explained most of the variability in the model (Table 1). Backscatter values in the water column were greatest around 04:00 with a decline in the evening and lowest after 20:00 (Figure 5). We also observed a large amount of backscatter on the shallow shelf, 20 m declining with depth up to 35 m. There is a positive relationship between backscatter and depth from 35m to 100m deep. As well, we find a negative relationship with relative fluorometry where backscatter is greatest at values of 0.05 volts declining to 0.07 and leveling out at values greater than that. There also was a greater amount of backscatter near areas of high bathymetric relief, such as the bank edge. Prey were found in greatest abundance over bottom types of sand and mud with less pelagic backscatter over

gravel. There was a cyclical relationship with tidal height as well with a peak in backscatter at 8m tidal height but a decline with greater and lesser values.

Whale surface foraging was best predicated by a number of thresholds as revealed by the CART (Figure 6). Surface foraging was not observed after 20:29 at night or before 4:40. In addition, at low relative fluorometry levels (<0.06) 163 out of 192 observations were foraging individuals. If the tide height was greater than 7.3 meters or observations were close to the slope whale behavior was commonly surface foraging. At higher fluorometry levels, high tide height (>6.28), shallow school height (<12 m) and high backscatter (>-65.3 dB) were correlated with surface foraging events. The shape of these relationships was illustrated and tested for significance using a GAM.

Of the environmental variables and school parameters tested, only temperature, bottom depth, and school depth did not have a significant non-linear effect on whether whales were surface feeding (Table 2). Time, tidal height, relative fluorometry, and backscatter explained the largest amount of deviance in the foraging model. Whale foraging showed a peak around 7:00 and began to decline around 18:00, peaking about 2 hours after prey density was greatest (Figure 7). Whale foraging behavior increased in likelihood at high tidal heights (4 m) with a peak at 9 m. There was an increase in foraging behavior at mud and sand bottoms compared to gravel and a notable decline in foraging behavior as relative fluorometry increased. Foraging was observed more often at deeper depths with a decline with increasing distance from slope edge. For the school parameters, a large increase in foraging behavior occurred up to -63 dB with a smaller increase with higher backscatter values. There was a positive relationship with foraging behavior and school height and area although a negative relationship with mean school depth and school length. These results are useful in elucidating potential foraging thresholds as well as the environmental variables that could influence search behavior.

Discussion

While synoptic surveys of environmental variables, prey distribution, and predator behavior can be difficult to align at temporal and spatial scales, it is a requisite towards understand the foraging ecology of marine apex predators. Recent technologies in high frequency sampling devices have made such multidisciplinary studies more feasible. By using fisheries acoustics to measure prey, real time sensors to sample surface temperature and fluorometry, and measuring fine scale 3-D movement patterns of predators, we were able to examine how ocean features and prey distribution affect the foraging ecology of humpback whales. Nonetheless, our results indicate a high correlation between prey abundance and the measured environmental variables while humpback whale foraging events were best predicted by prey school shape, density, as well as a number of environmental variables.

Although split-beam acoustics only measures a slice in the water column, we were able to sufficiently map the general two dimensional shape and density of sand lance schools on Stellwagen Bank. Time of day explained most of the variation in prey distribution which supports previous studies of sand lance behavior. Adult sand lance are present in the water column during daytime foraging upon small zooplankton, while they bury in sandy substrate at night (Meyers et al. 1979, Hobson 1986). While sand lance foraging might rely on sunlight because they are active feeders, substrate burial at night is believed to be primarily a method of predator avoidance (Hobson 1986). While sand lance abundance peaked around 4:00, whale foraging did not peak until 6:00 suggesting whale foraging did not commence until densities of sand lance were substantial enough to be energetically valuable, or that the average search time before whales were able to find prey patches to feed was around two hours. However, it is not clear whether foraging whales are mimicking the behavior of the sand lance that bury in the substrate at night (Meyer et al. 1979), or whether bubble netting is a visually based foraging behavior.

Acoustic biomass of sand lance was greatest above sandy and mud substrates. While sand lance utilize the sandy shelf for refuge, mud habitats are predominant immediately off the western slope with the edge of the bank indicating high upwelled productivity. Tagged whales also foraged more often above mud habitats and less so above sand habitats. Part of the reason may be that sand lance are more likely to bury when threatened above sand habitats. Surface foraging may be aided by increased depth as indicated by the relationship of increased foraging with depth; mud substrate was also present in these deeper environments. Although the relationship between prey density and temperature was significant, the relationship was complex. A general decline in abundance occurs at the lowest and highest temperatures although the standard error is particularly high as well. There was a dip in biomass at a surface temperature of 17.5 degrees but the reason for this association is not obvious. This relationship was not present at the higher trophic level; whale foraging was not significantly correlated with temperature.

While increased sand lance density would conceivably be associated with increased productivity (Meyer et al. 1979), an opposite trend was observed in this study. Both whale surface foraging and prey distribution showed a strong negative correlation with surface fluorometry. Cascading trophic interactions offer a plausible explanation for this relationship (Carpenter et al. 1985); high productivity would result in increased density of small zooplankton that would with time graze down phytoplankton levels. In turn, increased zooplankton abundance would attract high densities of sand lance eventually resulting in increased surface foraging for humpback whales. Contrary to a closed lake system, upwelling events reset the process with an initial increase in fluorometry, an eventual increase in grazers and resultant decrease in phytoplankton, and culminating in an increase in sand lance and humpback whales.

This temporal lag between predator and prey is also apparent in the relationship with tidal height.

Tidal height was incorporated into the analysis as a crude proxy for upwelling and internal wave formation. Nonetheless, the high correlation with prey and predator was surprising. Acoustically measured prey were most abundant at a tidal height of 8 feet while whale foraging peaked at a height of 10 feet. Internal wave packets are generated during ebb tide as a lee wave over the western edge of Stellwagen bank (Haury et al. 1979). As the tide turns, the waves begin propagating towards shore and undulations develop as the waves stack up redistributing chlorophyll and zooplankton (Haury et al. 1979). This lag suggests that prey are aggregating well after the formation of internal waves on the west edge of the bank with a further delay before whales begin foraging. The increase in prey distribution and increased observance of whale foraging behavior near the slope edge also supports this conclusion. Fine scale measurements of internal wave production, propagation, and nutrient upwelling would aid in understanding the exact timing of the trophic cascades on Stellwagen Bank.

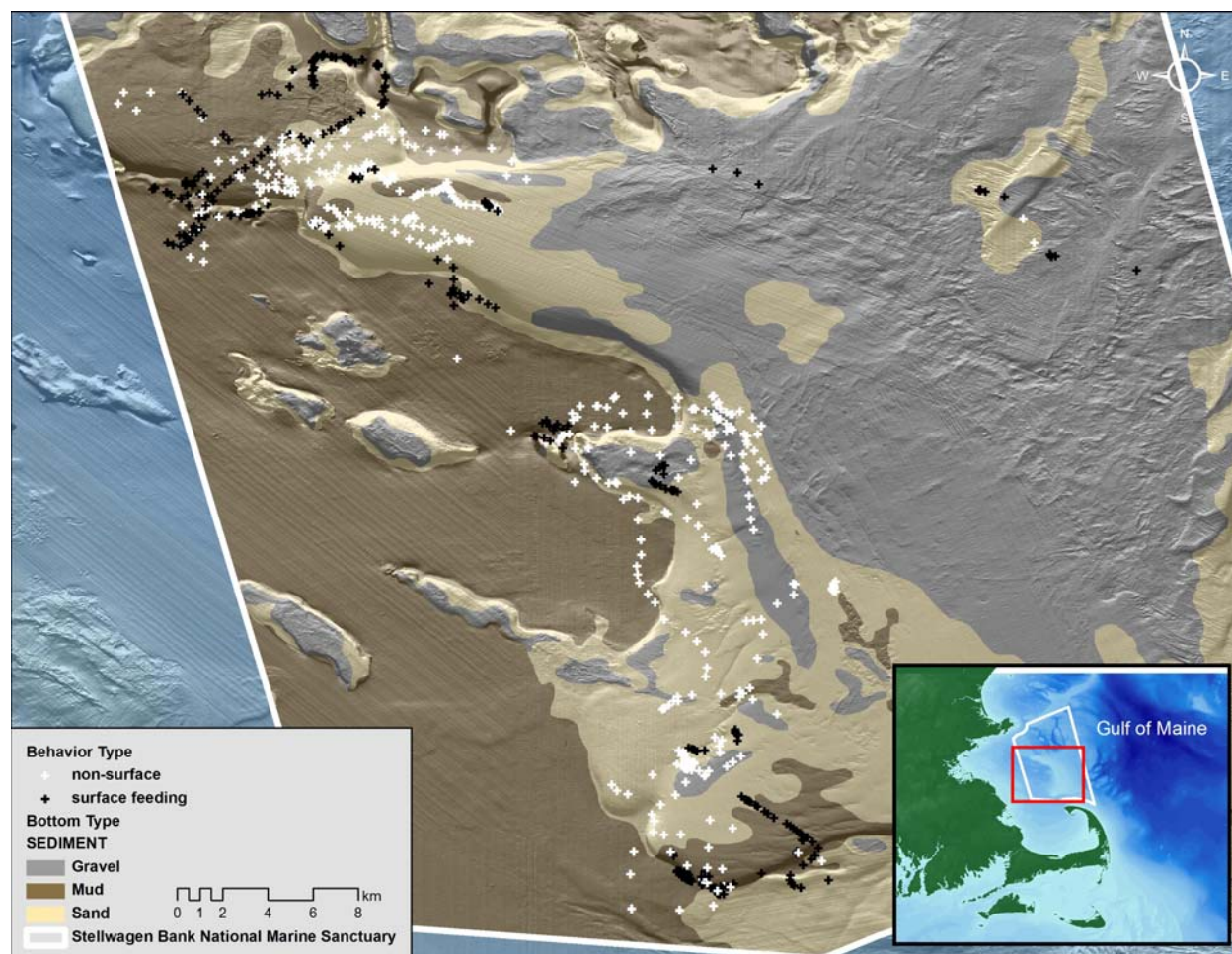
Whale surface foraging was significantly affected by prey school shape. Surface foraging occurred more often around schools with a large area, taller height, and shorter length. Because surface foraging involves a bubble corral to aggregate prey followed by a vertical lunge (Hain et al. 1982, Hain et al. 1995), taller schools would make this behavior more profitable. Longer schools were often associated with a thin layer (<2.5 m tall) in the water column, potentially more difficult or less cost-effective to consume. The lack of a clear relationship between foraging depth and mean school depth may be due to the whale foraging only on the top portion of schools or a corralling of deeper schools toward the surface. A more detailed analysis of foraging depth relative to both pycnocline depth and mean school height is necessary. In addition, because bubble net feeding can be cooperative (Hain et al. 1982), the tagged whale may not be producing the bubbles, but only be making the final foraging loops; multiple tags on cooperating foragers will be necessary to better elucidate this relationship.

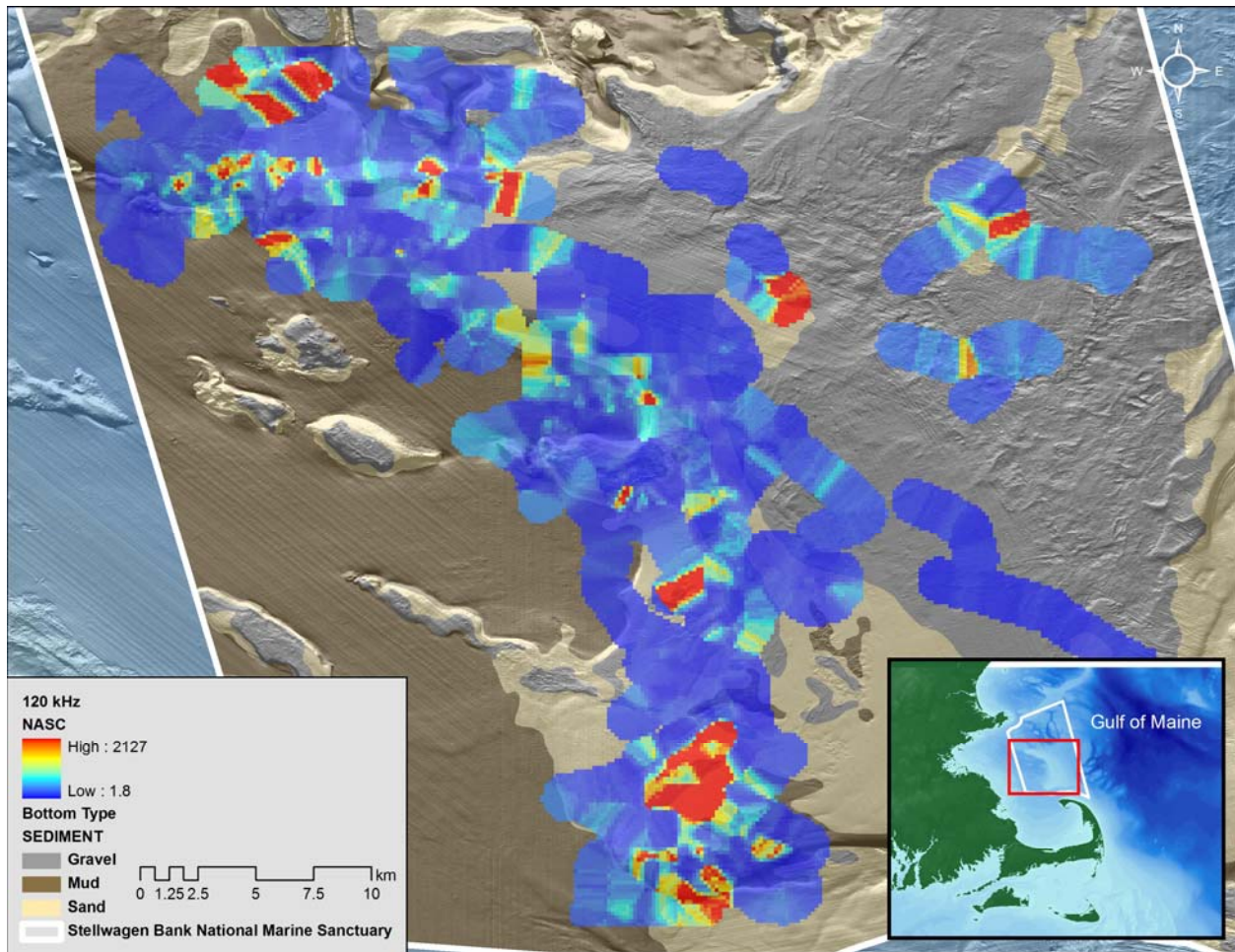
Predator aggregation most often occurs as a non-linear function of increasing prey density (Holling 1965, Murdoch and Oaten 1975), leading to a threshold foraging behavior typical of higher vertebrates (Piatt and Methven 1992). Using a Eulerian approach, Piatt and Methven (1992) conducted hydroacoustic surveys for capelin concurrent with visual surveys of baleen whale abundance in Witless Bay, Newfoundland to determine whether these whales exhibited a threshold response to prey density. These researchers documented a lower limit of prey density per km below which foraging was unprofitable and aggregation of whales did not occur (Piatt and Methven 1992). This lower limit is likely set by the metabolic demands of the whales and their unusual foraging style of engulfing prey (Nagy *et al* 1984, Goudie and Piatt 1991). Piatt and Methven (1992) suggest that because humpback whales have wider jaws and a greater filtering volume for their size than fin or minke whales, they may be able to subsist on

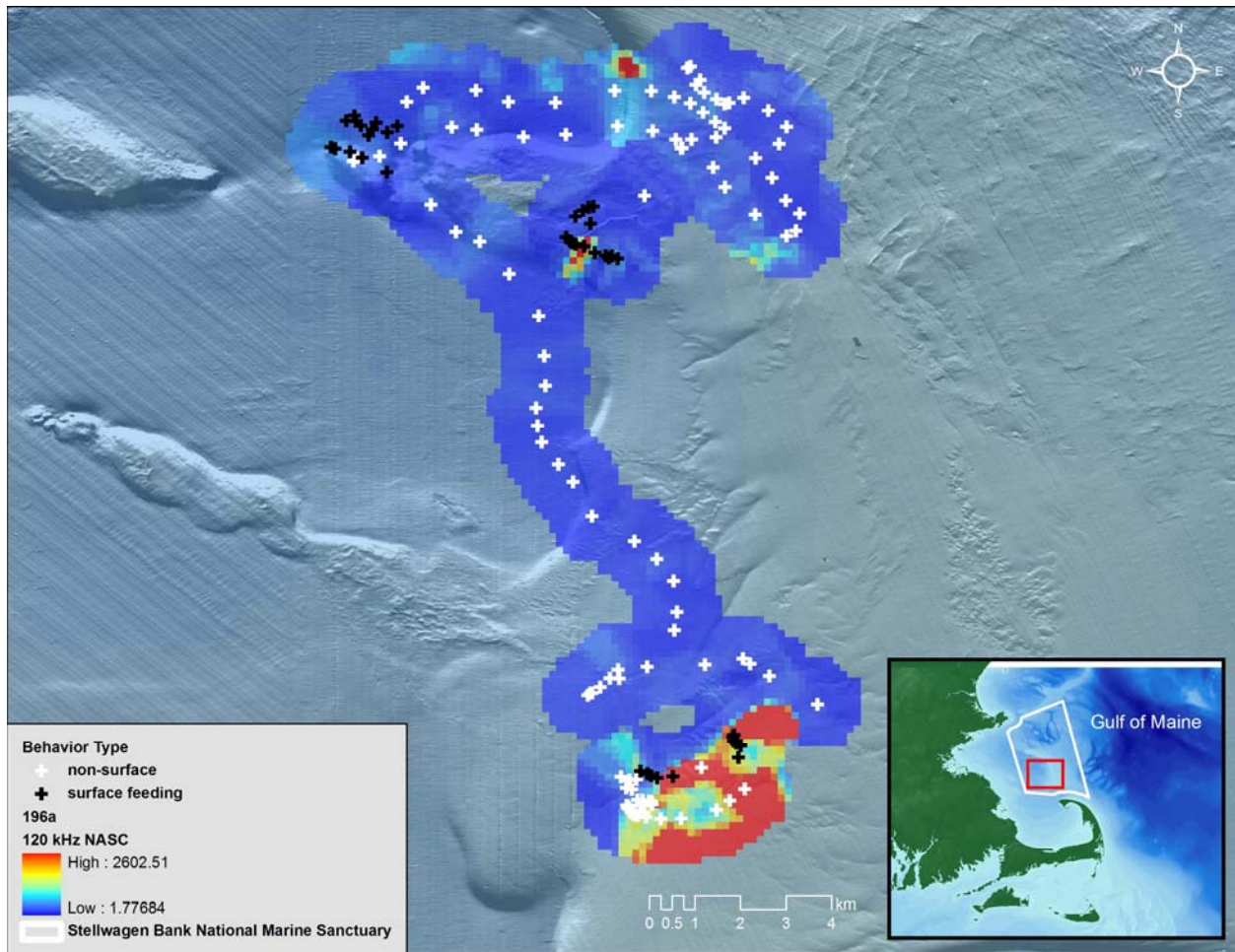
lower density prey aggregations. One of our goals was to measure this threshold for foraging humpback whales. Using GAM and CART models, we observed that surface foraging was more likely above -65 dB and the ascent with prey density decreased around -62 dB. However, using a minimum school detection threshold of -75 dB, we did not observe a lower threshold, below which foraging did not occur. Part of this might be explained by the sampling methodology. While we attempted to approach the foraging whale as close as was safe, the research vessel could not sample at the exact spatial and temporal location of the foraging whale. In addition, these thresholds may vary based on the number of patches in an area. It is not clear whether whales are more likely to feed on smaller but numerous prey patches or on large but spatially distinct patches. Additional analyses are necessary to examine which condition is preferred by an individual foraging whale.

In order to determine whether or not a humpback whale chooses or ignores a prey patch, we need to know how much of the surrounding environment the whale perceives. At the present time, we have no empirical information on which to make this determination. Humpback whales negotiate their surroundings over spatial scales ranging from 1000's of kilometers (migration routes) to a 10's of meters (foraging on prey patches). Kenney *et al.* (2001) suggest that while in seasonal foraging areas, northern right whales sample prey density using tactile perception as zooplankton make contact with vibrissae around the mouth. Whether this is true or not for humpback whales is not known. Our research provides a fine scale analysis of apex predator behavior and prey distribution relative to environmental variables and has allowed us to examine possible cues for foraging. In addition, we were able to identify an upper threshold of relative prey density (-62 dB) above which surface foraging likelihood becomes asymptotic. Understanding foraging behavior at the scale of an individual whale is an important addition to our ecological understanding and is necessary to properly institute conservation goals.

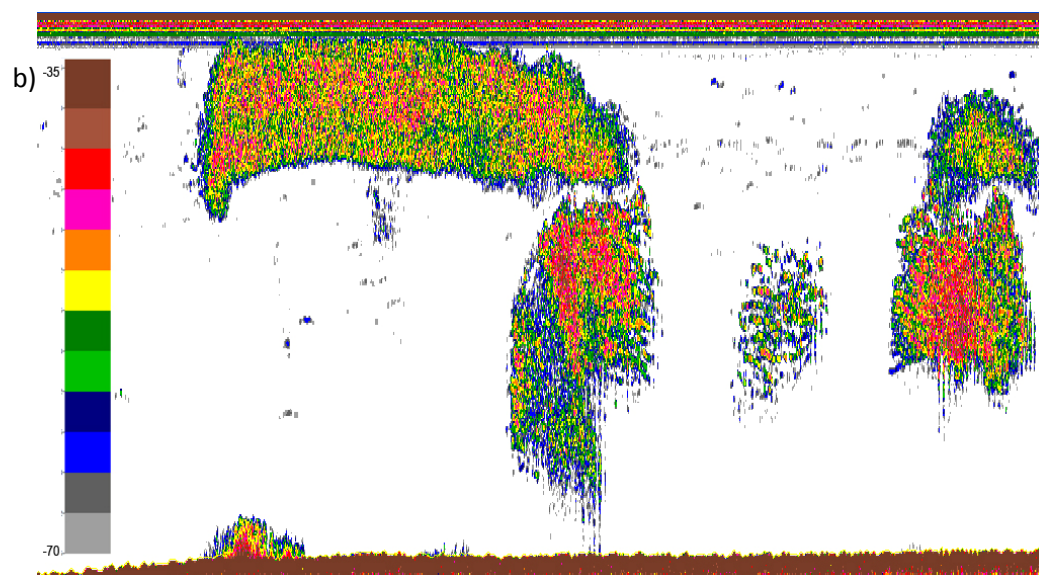
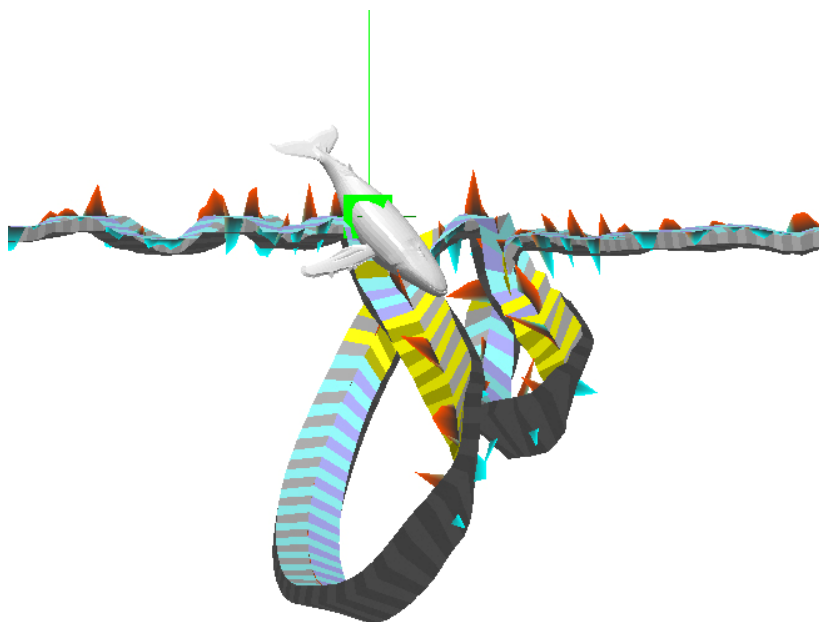
Figures

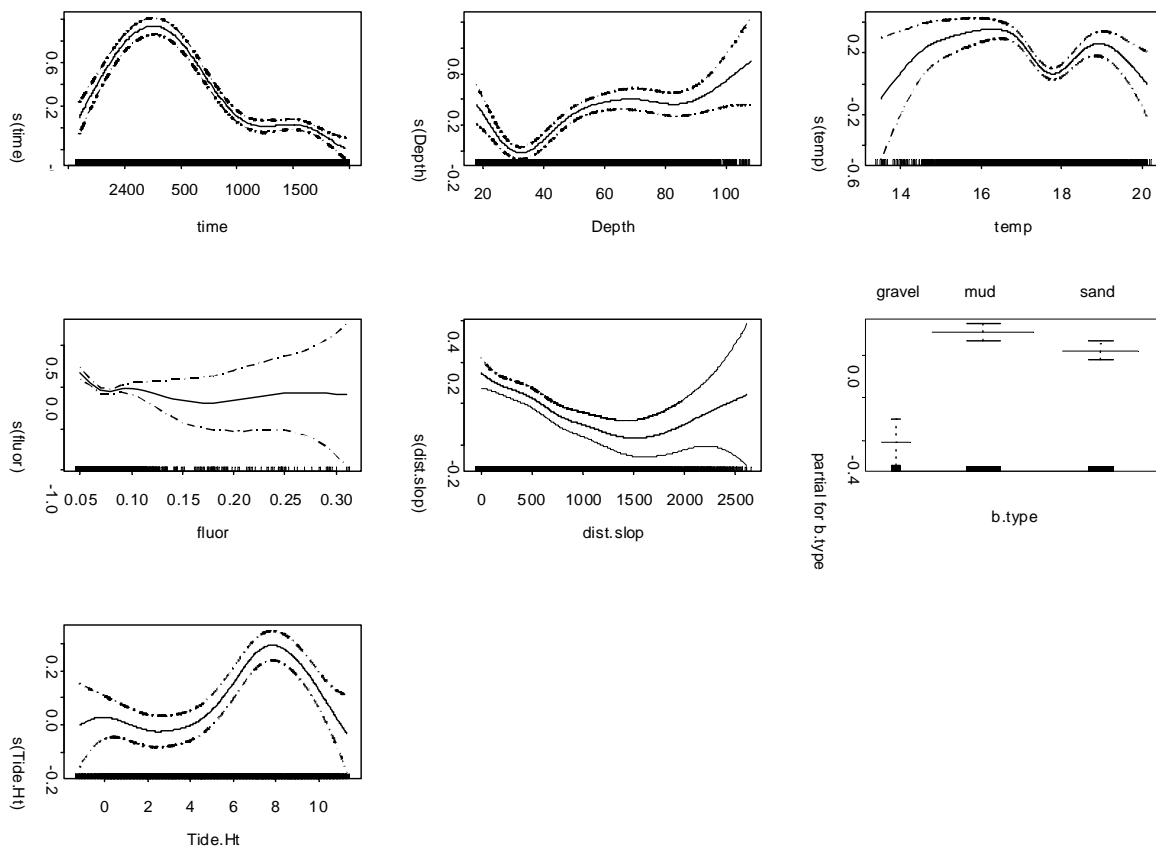


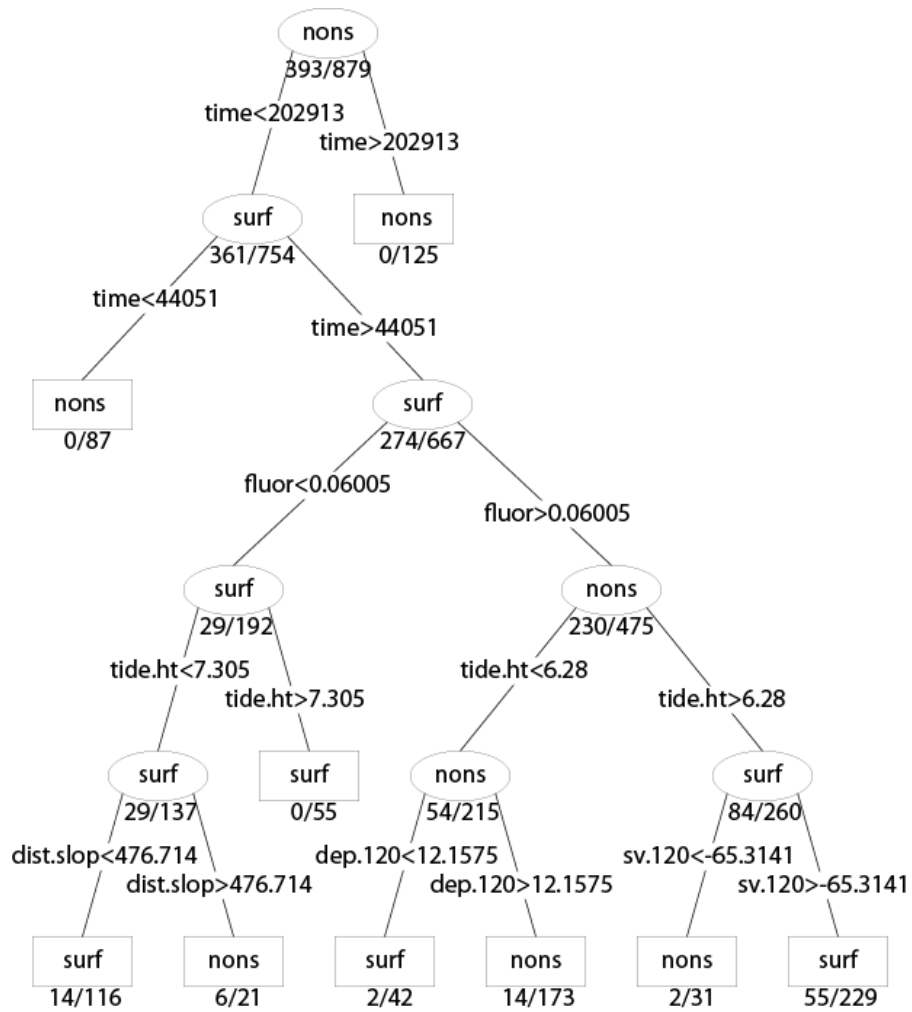




a)







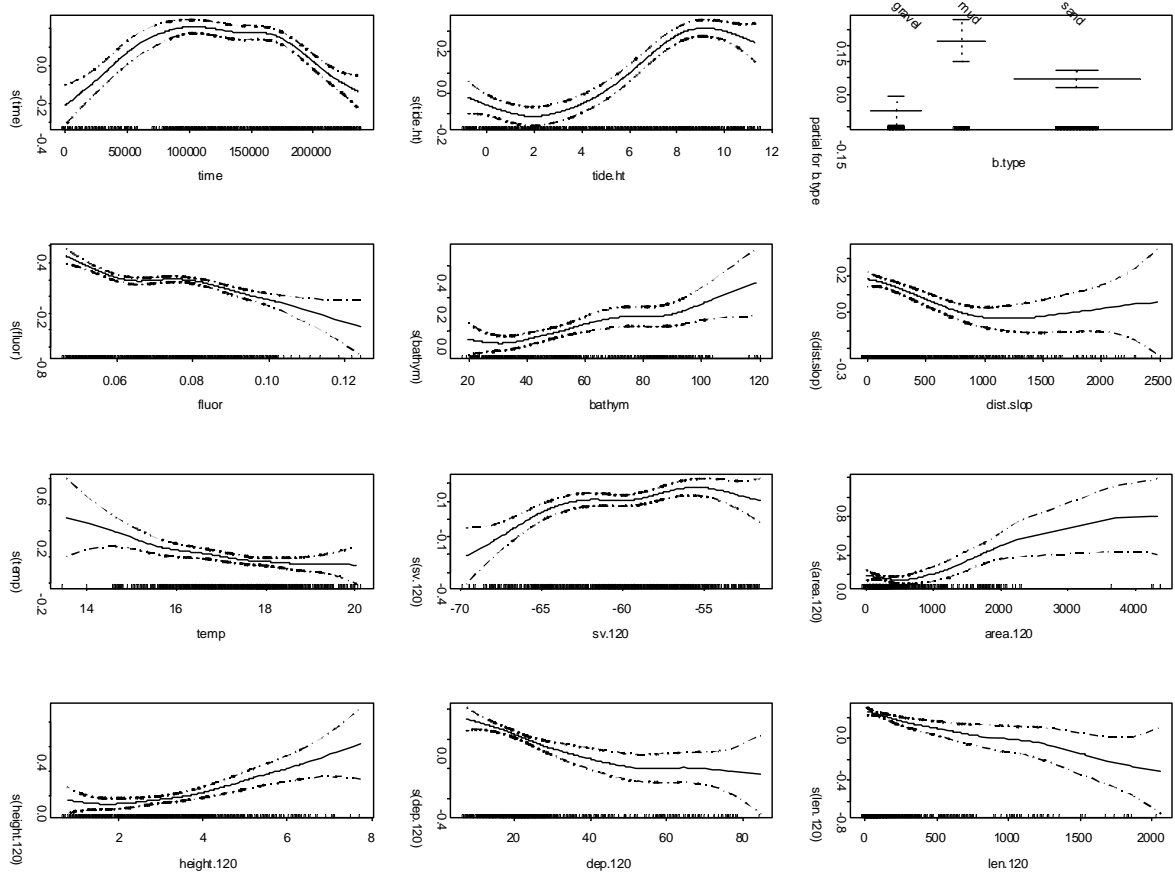


Figure 1. The Stellwagen Bank National Marine Sanctuary is shown in the subset image with our tagged whales in the red rectangle. On the main image, Dtag measured foraging behavior is shown in black with non-foraging surfacing shown in white for all 15 whales tagged. Bottom type is represented with dark brown for mud, light brown for sand, and grey for gravel.

Figure 2. EK60 measured backscatter interpolated within 1km of the ship track every 12 hours. Red represents high backscatter with blue representing low backscatter. The inherent patchiness of the prey is readily apparent.

Figure 3. Individual whale track in the southwest corner of the sanctuary for animal 196a, from 9 am on July 15 to 6am on July 16. Interpolated prey abundance is shown with high backscatter in red and low backscatter in blue.

Figure 4. a) Trackplot image of whale 196a at 9:27 in the morning beginning a characteristic double loop foraging behavior. Fluke strokes are shown using blue and red triangles. Behavioral sequencers observed a lob-tail and bubble net during this dive. **b)** At 9:24 a large prey patch was observed in the water column in 66 meters of water. Red represents high acoustic biomass with white representing acoustic biomass below the threshold (-75 dB).

Figure 5. Generalized Additive Model (GAM) plots for prey biomass (log sA) as a function of time, depth, temperature, relative fluorometry, distance to slope, bottom type, and tidal height. Strong relationships were observed between time of day, tidal height, and bottom type, and distance from slope edge.

Figure 6. Classification and Regression Tree (CART) for behavioral state of tagged humpback whales: surface feeding or non surface feeding. Breaks were chosen based on deviance explained with values shown on each branch of the tree. Numbers below each terminal node represent the number of misclassified observations out of the total number of observations. Time of day was the most definitive split for surface foraging and non-surface foraging behaviors.

Figure 7. Generalized Additive Model (GAM) plots showing whale behavioral classification as a function of environmental variables and mean school parameters (density, area, height, depth, and length). Time of day and tidal height explained most of the variability in foraging while school density and area were important as well.

Parameter	Linear Effects			Nonlinear effects		
	df	χ^2	$\Pr(\chi^2)$	df	F	$\Pr(F)$
Time	1	23427.52	0.000	3.00	82.06504	0
Tidal Height (ft)	1	21815.59	0.000	3.00	16.84461	0
Bottom type (M/S/G)	2	23139.42	0.000	N/A	N/A	N/A
Temperature (°C)	1	23397.27	0.057	3.00	37.01386	0
Relative Fluorometry	1	23396.49	0.377	3.00	9.64755	2.35E-06
Distance to Slope (m)	1	23288.42	0.000	3.00	4.82115	0.002348
Bottom Depth (m)	1	23400.89	0.000	3.00	30.01492	0

Table 1. GAM results for areal backscatter (sA) as linear and non-linear relationships of environmental variables. Significant p-values (< 0.05) are shown in bold.

Parameter	Linear Effects			Nonlinear effects		
	df	χ^2	$\Pr(\chi^2)$	df	F	$\Pr(F)$
Time	1	214.32	0.174	3.00	32.73	0.000
Tidal Height (ft)	1	205.07	0.002	3.00	14.17	0.000
Bottom type (M/S/G)	2	190.39	0.001	N/A	N/A	N/A
Temperature (°C)	1	157.49	0.106	3.00	1.62	0.183
Relative Fluorometry	1	173.05	0.000	3.00	9.13	0.000
Distance to Slope (m)	1	160.10	0.007	3.00	3.64	0.013
Bottom Depth (m)	1	167.28	0.016	3.00	0.95	0.418
School sA (dB)	1	148.45	0.003	3.00	6.21	0.000
School Area (m ²)	1	140.42	0.005	3.00	4.22	0.006
School Height (m)	1	137.71	0.100	3.00	2.78	0.040
School Depth (m)	1	134.94	0.096	3.00	1.83	0.141
School Length (m)	1	97.02	0.295	3.00	2.76	0.041

Table 2. GAM results for likelihood of whale surface foraging as linear and non-linear relationships of school parameters and environmental variables. Significant p-values (< 0.05) are shown in bold.

Literature Cited

- Auster, P. , Joy, K. and Valentine, P. (2001) Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example. *Environ. Biol. Fish.* 60: 331–346.
- Anthony, V. C., Waring, G. (1980). The assessment and management of the Georges Bank herring fishery. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 177: 72–111.
- Baumgartner M.F., Cole T.V.N., Campbell R.G., Teegarden G.J., Durbin E.G. (2003). Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Mar Ecol Prog Ser* 264: 155–166.
- Calambokidis J.E. Oleson, M. McDonald, B. Burgess, J. Francis, G. Marshall, M. Bakhtiari, and J. Hildebrand. (2003). Feeding and vocal behavior of blue whales determined through simultaneous visual-acoustic monitoring and deployment of suction-cup attached tags. *15th Biennial Conference on the Biology of Marine Mammals*, Greensboro, North Carolina, USA, December 14-19 2003.
- Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. (1985). Cascading Trophic Interactions and Lake Productivity. *Bioscience*, 35: 634-639.
- Casey JM, Myers RA (1998) Diel variation in trawl catchability: is it as clear as day and night? *Can J Fish Aquat Sci* 55:2329-2340.
- Croll D.A. *et al.* (1998) An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research Part II* 45: 1353-1371.
- Croll, D. A., Marinovic, B., Benson, S., Chavez, F. P., Black, N., Ternullo, R. and Tershy, B. R. (2005). From wind to whales: trophic links in a coastal upwelling system. *Mar. Ecol. Prog. Ser.* 289,117 -130.
- Fauchald, P., Erikstad, K.E. & Skarsfjord, H. (2000). Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81, 773–783.
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ. (2006). Whale distribution in relation to prey abundance and oceanographic processes in the Western Antarctic Peninsula shelf waters. *Marine Ecology Progress Series* 317: 297-310.
- Fogarty, M.J. and S.A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: Fishery impacts on Georges Bank. *Ecol. Appl.* 8(1) Supplement:S6-S22.
- Garrison LP (2000) Spatial and dietary overlap in the Georges Bank groundfish community. *Can J Fish Aquat Sci* 57: 1679–1691
- Gaskin DE (1982) *The Ecology of Whales and Dolphins*. Heinemann, London.
- Hain, J.H.W., Carter, G.R., Kraus, S.D., Mayo, C.A. and Winn, H.E. (1982). Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fishery Bulletin* 80:259-268.
- Hain, J. H. W., Ellis, S. L., Kenney, R. D., Clapham, P. J., Gray, B. K., Weinrich, M. T., and Babb, I. G. (1995) Apparent bottom feeding by humpback whales on Stellwagen Bank. *Marine Mammal Science* 11: 464-479.
- Haury, L.R., Briscoe, M.G., and Orr, M.H., (1979). Tidally generated internal wave packets in Massachusetts Bay. *Nature*, 278:312-317.
- Hobson, E.S. 1986. Predation on the Pacific sand lance *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. *Copeia*. 1: 223-226.
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs to the Entomological Society of Canada* 45:1-60

- Johnson, M.P. and Tyack, P.L. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28: 3-12.
- Kenney R.D., Mayo, C.A., Winn H.E. (2001) Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. *Journal of Cetacean Research and Management Special Issue* 2:251-260.
- Lennert-Cody, C. E., and Franks, P. J. S. (1999). Plankton patchiness in high-frequency internal waves. *Marine Ecology Progress Series*, 186: 59–66.
- Levin, Simon A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1976.
- Mackinson S., Nøttestad L., Guenette S., Pitcher T., Misund O.A., and A. Ferno. (1999). Cross-scale observations on distribution and behavioural dynamics of ocean feeding Norwegian spring-spawning herring (*Clupea harengus* L.). *ICES Journal of Marine Science* 56: 613-626.
- Maravelias, C.D., Reid, D.G., Simmonds, E.J., Haralabous, J.. (1996). Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:1497-1505.
- Meyer, T.L., R.A. Cooper & R.W. Langton. (1979). Relative abundance, behavior, and food habitats of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. *U.S. Fish. Bull.* 77: 243-253.
- Miller, P. J. O., Johnson, M. P., Tyack, P. L. & Terray, E. A. (2004a). Swimming gaits, passive drag, and buoyancy of diving sperm whales (*Physeter macrocephalus*). *J. Exp. Biol.* 207, 1953–1967.
- Miller, P. J. O., Johnson, M. and Tyack, P. L. (2004b). Sperm whale behaviour indicates use of echolocation click buzzes 'creaks' in prey capture. *Proc. R. Soc. Lond. B* 271: 2239-2247.
- Misund O.A., Ferno A., Pitcher T., and B. Totland. (1998). Tracking herring schools with a high resolution sonar. Variations in horizontal area and relative echointensity. *ICES Journal of Marine Science* 55: 58-66.
- Murdoch, W.W. and Oaten, A. (1975). Predation and population stability. *Adv. Ecol. Res.* 9:1-131.
- Nowacek, D. P., M. P. Johnson, and Tyack, P.L. (2004). "North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli." Proceedings of the Royal Society of London, B 271(1536): 227-231.
- Nøttestad L., Fernö A., Pitcher T., Mackinson S., and Misund., O.A. (2002). How whales influence herring school dynamics in a cold front area in the Norwegian Sea. *ICES Journal of Marine Science* 59:393-400.
- Overholtz, W. J., and Nicolas, J. R. (1979). Apparent feeding of the fin whale, *Balaenoptera physalus*, and the humpback whale, *Megaptera novaeangliae*, on the American sand lance, *Ammodytes americanus*, in the northwest Atlantic. *Fish. Bull.* 77:285-287.
- Overholtz, W.J. 2002. The Gulf of Maine - Georges Bank Atlantic herring (*Clupea harengus*): spatial pattern analysis of the collapse and recovery of a large marine fish complex. *Fish. Res.* 57(2002):237-254.
- Payne PM, Nicolas JR, O'Brien L., Powers KD (1986). The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. *Fish. Bull U.S.*: 271-277.
- Petitgas, P. (1993). Geostatistics for fish stock assessments: a review and an acoustic application. *ICES J. mar. Sci.* 50: 285-298.
- Piatt JF (1990) The aggregative response of common murre and Atlantic puffins to schools of capelin. *Studies in Avian Biology* 14:36-51.
- Piatt JF, Methven DA (1992) Threshold Foraging Behavior of Baleen Whales. *Marine Ecology-Progress Series* 84:205-210

- Read, A. J. and C. R. Brownstein. 2003. Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine. *Conservation Ecology* 7: 2.
- Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M., Forney, K.A., Ballance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S., Read, A., Reilly, S., Torres, L., Werner, C., (2006). Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series* 310, 271–295.
- Robinson, A.R. and Lermusiaux, P.F.J. (2002) Data assimilation for modeling and predicting coupled physical–biological interactions in the sea. In: Robinson, A.R., McCarthy, J.J. and Rothschild, B.J., Editors, 2002. *The Sea* vol. 12, Wiley, New York, pp. 475–536 Chapter 12 .
- Simmonds EJ, MacLennan DN (2005) Fisheries acoustics : theory and practice, Vol. Blackwell Science, Oxford ; Ames, Iowa
- P. T. Stevick, J. Allen, P. J. Clapham, S. K. Katona, F. Larsen, J. Lien, D. K. Mattila, P. J. Palsbøll, R. Sears, J. Sigurjónsson, T. D. Smith, G. Vikingsson, N. Øien, P. S. Hammond (2006) Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology* 270 (2), 244–255.
- Thiele DC, Chester ET, Moore SE, Sirovic A, Hildebrand JA, Friedlaender AS (2004) Seasonal variability in whale encounters in the Western Antarctic Peninsula. *Deep Sea Research II* 51:2311-2325
- Ware, C., Arsenault, R., Plumlee, M., Wiley, D. 2006. Visualizing the Underwater Behavior of Humpback Whales. *IEEE Computer Graphics and Applications* 26: 14-18.
- Warren, J.D., Stanton, T.K., Wiebe, P.H., and Seim, H.E. (2003). Inference of biological and physical parameters in an internal wave using multiple-frequency, acoustic-scattering data. *ICES Journal of Marine Science*, 60: 1033-1046.
- Watkins, W.A., and Schevill, W.E. (1979). Aerial observation of feeding in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. *Journal of Mammalogy* 60: 155-163.
- Weinrich M. (1998) Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). *J Mammal* 79: 163–170.
- Weinrich, M, Schilling, M.R., and Belt, C.R. (1992). Evidence for acquisition of a novel feeding behavior: lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behavior* 44: 1059- 1072.
- Weinrich M, Martin M, Griffiths R, Bove J, Schilling M. (1997) A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine. *Fish Bull* 95:826–836.
- Whitehead , H.P. and Carscadden, J.E. (1985). Predicting inshore whale abundance: whales and capelin off the Newfoundland coast. *Canadian Journal of Fisheries and Aquatic Science*. 42: 978-981.