

Prey densities and foraging of humpback whales, *Megaptera novaeangliae*

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Summary. Analysis of simultaneous sonar scans from a surface vessel and film from a remotely operated underwater camera show that euphausiids form extremely dense micropatches upon which humpback whales feed. Krill densities were found to be several orders of magnitude greater than values previously reported from results of towed net samplings and were sufficiently dense to allow capture of the whales calculated minimum daily caloric requirements in a matter of several dives. Dive depth during foraging episodes can be predicted with a high degree of confidence from ventilatory, surfacing, and diving patterns of a whale.

Key words. Humpback whales; euphausiids; foraging ecology; sonar; underwater cameras.

The question of how whales gather sufficient prey in a highly heterogeneous environment is of considerable interest to ecologists and biological oceanographers alike. However, there is little information on the feeding ecology of rorqual whales other than scattered surface observations and results of necropsies from the whaling industry. Further, despite extensive investigations¹, little is known about the behavior and distribution of krill, the primary prey of many baleen whales, at sea. Studies I have conducted since 1979 on the feeding behavior of the humpback whale (*Megaptera novaeangliae*) in Frederick Sound, Alaska (57°N, 134°W.) have necessitated an intensive examination of the whale's prey items, 50–80% of which I have found to consist of krill, principally *Thysanoessa raschi* and *Euphausia pacifica*. Based upon photographic identification data, an estimated 350–500 humpback whales utilize the study area between July and September annually during which time they spend approximately 80% of the daylight hours feeding (Dolphin, unpublished). The remaining months are spent in the low latitude waters of Hawaii where calving and mating occur, but little or no feeding takes place^{2,3}.

The spatial and temporal distribution of zooplankton are of considerable importance for their role in predator-prey relation-

ships. Patchy distributions of krill, on a scale of tens of meters, are predicted by most biological oceanographers^{4,5} but have been little studied. Sampling of small aggregations is difficult due to their brief temporal duration and dilution effects resulting from necessarily large volumes through which nets must be towed. Integration and averaging of the obtained results certainly do not reflect the true zooplankton distribution, and the krills' active avoidance of moving nets exacerbate the problem⁶. Sonar sampling techniques have greatly assisted in the examination of small scale zooplankton distributions^{7–9}. The frequencies employed in these studies to yield high resolution (0.5–3.0 MHz), however, preclude penetration to the depths necessary for examination of the prey of whales during any but the shallowest feeding situations.

Inconsistencies arise when one attempts to integrate calculated daily energy requirements of whales with the reported average densities of their prey. Using the average maximum caloric values of 2.72 kJ g⁻¹ (1 kcal = 4.1868 kJ) for the euphausiid *T. raschi* (the primary euphausiid prey item in Frederick Sound) given by Mauchline¹¹, and the energy requirements calculated by Lockyer¹² (30 g kg⁻¹ day⁻¹) the daily intake of the average active 3.27 × 10⁴ kg humpback whale can be estimated at roughly

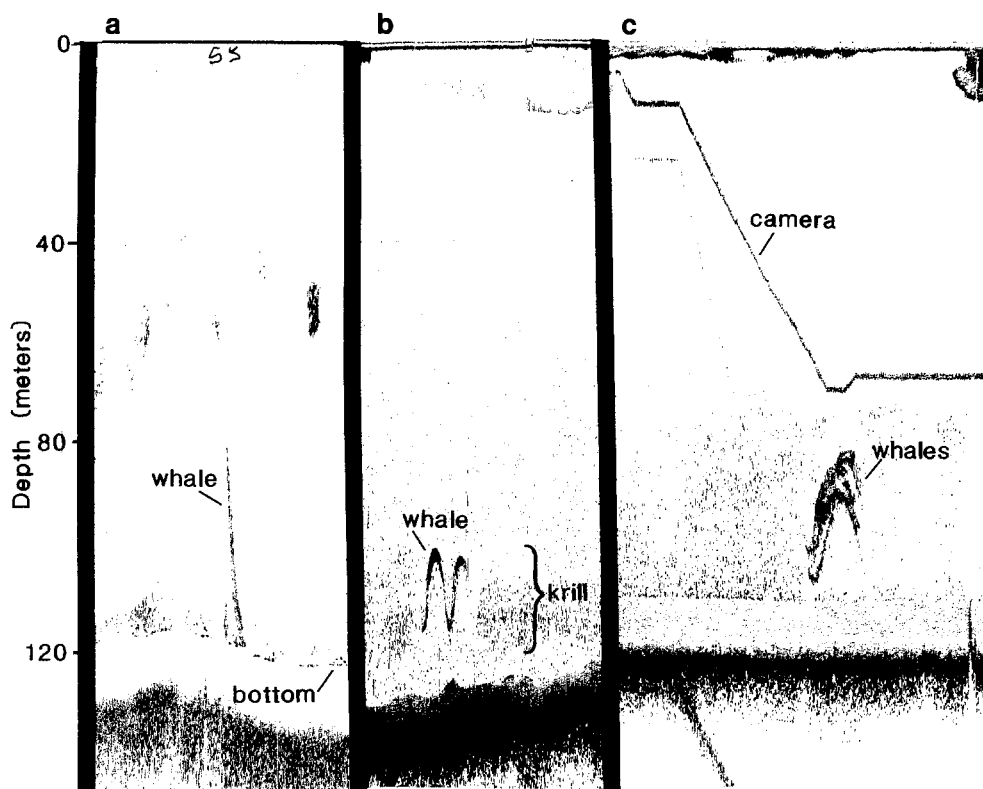


Figure 1. Sonar tracings of: a a single whale descending directly to a depth of 118 m; b a single whale swimming at a depth of 100–115 m. The sinusoidal oscillations are approximately 15 m in amplitude, corresponding to one body length of the whale. The whale's path takes it through the densest concentration of krill. In c 3 whales are visible swimming (one cycle shown) at a mean depth of 98 m. The camera is visible just above the whales at 68 m.

2.67×10^6 kJ during the June–September feeding period. Researchers working with towed nets in the study area obtained maximum densities ranging from 4.1^{13} to 23.5 euphausiids m^{-3} ¹⁴ which translates to an upper value of approximately 1.84 kJ m^{-3} . It becomes clear that for a whale to gather either the volumes of krill found in their stomachs¹⁵ or to obtain their calculated caloric requirements, they must feed upon densities considerably higher than those reported. Humpback, and other rorqual whales, are not continuous filter feeders, but are instead ‘gulpers’¹⁶, capturing and ingesting their prey in discrete mouthfuls. They are, therefore, selective, discontinuous samplers. Either the calculated energy requirements of the whales are seriously in error or the prey density estimates obtained from towed nets grossly underestimate the actual situation.

To resolve the above discrepancy I first determined the depth to which the foraging whales were diving (correlating surface and sonar observations) which allowed me to identify, and subsequently examine in detail, the target prey patch. Using sonar I was able to determine the depth and vertical extent of potential prey patches. For analysis purposes prey patches were partitioned into 20-m interval categories based upon mean patch depth. Humpbacks, while diving, swimming at depth (presumably foraging), and returning to the surface, could frequently be followed using 120 kHz, narrow beam sonar (Datamarine Kodiak SLR). In this manner the actual depth to which the whales dived could be ascertained (fig. 1), as could the depth of available prey in the immediate area.

Figure 2. *a* Depth of dive plotted against the time required to reach that depth ($r^2 = 0.91$, $F = 504.9$, $p < 0.001$, $n = 57$). Each point represents the time and depth measurement for a single dive. In *b* and *c* velocity of ascending and descending whales are plotted against depth. Descent velocity was not significantly correlated with depth of dive ($r^2 = 0.05$, $F = 2.34$, $p > 0.1$, $n = 42$), whereas ascent velocity did exhibit a significant correlation with the depth to which the whale had dived ($r^2 = 0.50$, $F = 12.77$, $p < 0.05$, $n = 15$). Data obtained from sonar tracings.

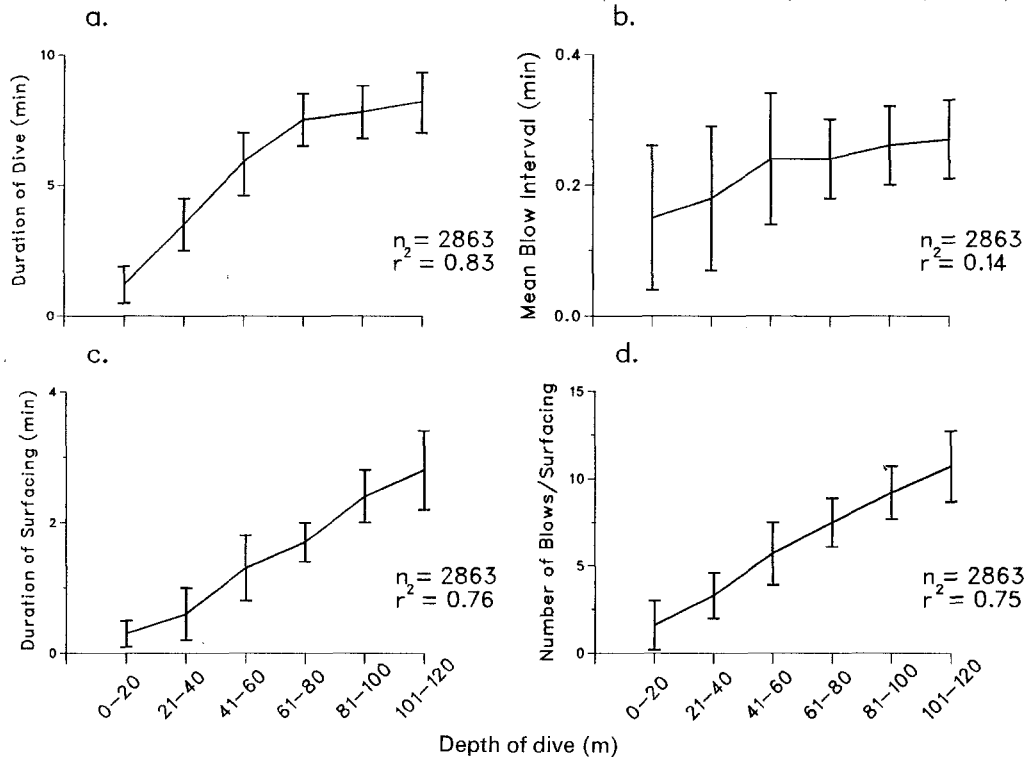
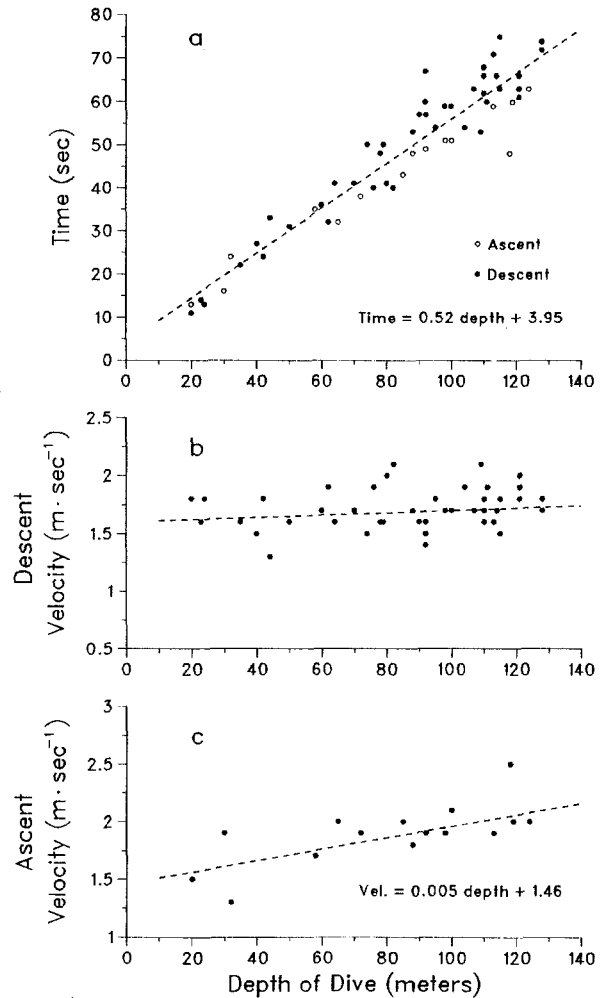


Figure 3. *a* Dive time (DT), *b* mean blow interval (MBI), *c* surface time (ST), and *d* number of blows during surfacing (NB) plotted against depth of dive. All are significant at $p < 0.001$. Vertical bars represent 1 SD unit.

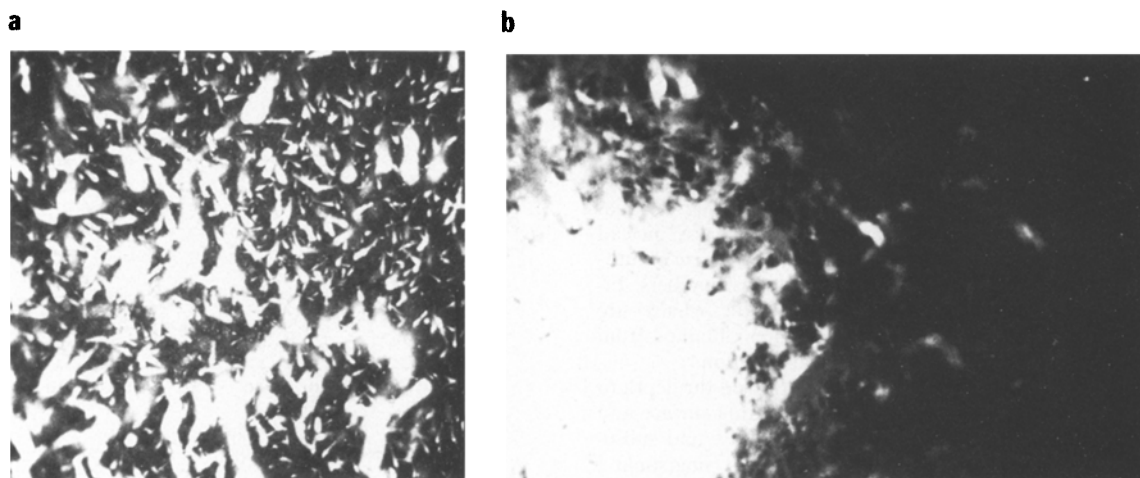


Figure 4. *a* Photograph of a dispersed euphausiid layer taken at 68 m. Density was estimated at 9.1×10^2 euphausiids m^{-3} . *b* The edge of a dense euphausiid patch at 98 m. Density in the center of the patch was estimated at ca 5×10^4 euphausiids m^{-3} . Euphausiids were identified from capture in towed nets as *Thysanoessa raschii* and averaged approximately 1.6 cm in length.

The path and rate of descent and ascent could be directly determined from sonar tracings, and it is clear that feeding humpback whales dive and ascend both steeply and directly. Descent and ascent velocity averaged 1.8 ± 0.20 m s^{-1} (fig. 2). Ascent velocity, however, increased with depth. (These values are comparable, but somewhat lower, than those reported for captive beluhka, *Delphinapterus leucas*¹⁷, and bottle-nosed dolphins, *Tursiops truncatus*¹⁸).

Humpback whales appear to restrict their foraging to the top 120 m of the water column. Of 284 dives traced with sonar, only 8 (less than 3%) exceeded this depth, and no cases were found in which a humpback surpassed 150 m, despite numerous records of dense prey at depths to 200 m. Reasons for this restriction in dive depth are not clear, however, thermal stress and avoidance of incurred O_2 debt may be involved¹⁹.

Feeding bouts to which I could confidently assign a target prey, and therefore depth to which the whales were diving, were used to test correlations of non-calf humpback whales between ventilatory variables (dive time DT, surface time ST, number of blows at the surface NB, and mean blow interval MBI) and depth of dive between 0–120 m (fig. 3). 2863 complete ventilation-dive cycles were analyzed. DT, ST, and NB were all highly correlated with the depth of dive.

The ability to ascertain the depth to which a whale is diving in a given feeding situation is critical to the study of their foraging behavior. Whales are tied to the surface by the necessity to breathe; all activities are consequently subjugated to ventilatory patterning in a manner more profound than for any terrestrial mammal. It was anticipated that the ventilation patterns of the whales would be excellent indicators of their behavioral and physiological state. To test this assumption a discriminant analysis was run using those feeding situations in which the minimum depth to which a whale dived was accurately determined with sonar. A discriminant function was calculated based upon this subset of data. This discriminant function was subsequently run on the larger combined data set consisting of feeding situations to which a depth category had been assigned. The predicted depth category (using the discriminant function) was calculated and compared with the a priori feeding category assignment. Using the variables DT, MBI, ST, NB, and the computed variable PCST (percent of time spent at the surface (calculated as $ST/(TDT+ST) \times 100\%$) an 84.3% agreement was found between the predicted as assigned (observed) feeding category. Thus the depth of the target prey patch can be assigned with a high degree of confidence based upon easily collected ventilatory, surfacing, and diving patterns.

Having ascertained the depth of the target prey it was necessary to obtain an estimate of prey density. To do so a remotely operated underwater camera and strobe (Benthos Edgerton Deep Sea Utility Camera model 371 and Utility Strobe model 381) were used in conjunction with an attached television camera. This system allowed for continuous viewing of the underwater field via a monitor aboard a boat at the surface.

When the depth at which humpbacks were feeding was determined (and respiration patterns of individual whales established) the camera was lowered (fig. 1, c) and photographs taken at multiple depths. In this way those patches upon which the whales preyed as well as those bypassed could be characterized. Whales invariably fed in areas of the shallowest, densest prey in the top 120 m. Analysis of film, using stereological techniques^{20,21}, indicated that krill on occasion formed extremely dense (estimated 3.0×10^4 to 5.0×10^4 individuals m^{-3}) micro-patches, ellipsoid or spherical in shape, and having diameters frequently of less than 3 m (fig. 4). Patches often consisted of uniformly oriented individuals moving rapidly with clearly delineated edges, and should be considered schools²². Swarms of randomly oriented krill were most frequently seen in association with high densities of phytoplankton and were presumably feeding. The krill did not appear to respond to the presence of the camera nor to the 200 W video floodlamps (fishes, however, showed a distinct response to the lamps: a positive phototropism during the nighttime hours, negative response during daylight). The flash of the strobe elicited a tailflip from the krill in some cases; however, there were no indications of spontaneous molts in these euphausiids as have been reported in the Antarctic *E. superba* upon being startled²³.

The minimum euphausiid patch density upon which the humpbacks were determined to feed was 50 euphausiids m^{-3} . This is more than twice the maximum value obtained from towed nets in the study area. More usual densities were in the range of 3.0×10^3 to 10.0×10^3 euphausiids m^{-3} . A 12-m baleen whale can be expected to ingest roughly 13 m^3 in a single mouthful, accounting for throat distension²⁴. The average time to complete a foraging surface-dive cycle was 3.6 min, corresponding to a dive depth of 21–40 m. Thus, an overall average dive rate of 17 dives h^{-1} was found for feeding whales during the study. Assuming a single swallow per dive, and a 50% escape rate of the krill (probably high) one arrives at an hourly ingestion rate of roughly 2.98×10^3 kJ h^{-1} when feeding on prey densities at the lower limit of 50 euphausiids m^{-3} . At this rate of intake 895 h of feeding would be needed to achieve the calculated requirement of 2.67×10^6 kJ day^{-1} . However, at a higher density of 10×10^3

euphausiids m^{-3} , 4.5 h of feeding would be sufficient for the whale to meet its daily energy requirements, and only 1.5 h would be needed at densities of 3×10^4 euphausiids m^{-3} . Deeper feeding dives result in a longer surface-dive cycle time, and consequently, more time spent feeding will be needed to meet the daily energy requirements. For example, the surface-dive cycle time for dives of depths to 81–100 m is 10.1 min with a resultant dive rate of approximately 6 dives h^{-1} . In this situation 12.7 h of foraging could be necessary to gain the daily energy requirements if feeding on patches of density 10×10^3 krill m^{-3} . It is apparent that the distribution of patches in the water column, in addition to patch density, can profoundly influence the rate of energy acquisition.

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- 1 Mauchline, J., in: *Advances in Marine Biology*, vol. 18, p. 245. Eds J. H. S. Blaxter, F. S. Russel and M. Yonge, 1980.
- 2 Gambell, R., 'Discovery' Rep. 35 (1968) 31.
- 3 Nemoto, T., *Sci. Rep. Whales Res. Inst., Tokyo* 12 (1957) 33.
- 4 Haurly, L. R., McGowan, J. A., Wiebe, P. H., in: *Spatial Patterns in Plankton Communities*, p. 277. Ed. J. H. Steele, 1978.
- 5 Harris, G. P., *Can. J. Fish aquat. Sci.* 37 (1980) 877.
- 6 Fleminger, A., and Clutter, R. I., *Limnol. Oceanogr.* 10 (1965) 96.
- 7 Richter, K. E., *Deep-Sea Res.* 32 (1985) 163.
- 8 Greenlaw, C. F., and Johnson, R. K., *J. acoust. Soc. Am.* 72 (1982) 1706.
- 9 Holliday, D. V., and Pieper, R. E., *J. acoust. Soc. Am.* 67 (1980) 135.
- 10 Richter, K. E., *Deep-Sea Res.* 32 (1985) 149.

This paper has shown that target prey depth of the whales can be determined either directly using sonar, or indirectly based upon surface collected ventilation and dive variables. Whales can be followed in their dive using sonar, thus determining not only the depth to which the whale dived, but ascent and descent rates as well. Slight variations in the distribution and abundance of krill could be of major ecological significance due to the profound influence which they exert on the higher trophic levels. With the remote camera I have observed that krill form extremely dense aggregations surrounded by areas of relatively low concentrations. These results explain the low average densities obtained with towed nets. It is apparent that whales feed selectively on these dense patches within the upper 120 m.

- 11 Mauchline, J., cited in Mauchline¹.
- 12 Lockyer, C. H., in: *Mammals in the Seas*. FAO Fish. Series, vol. III. Rome 1981.
- 13 Bryant, J. P., Nichols, G., and Miller, K., *J. Mamm.* 62 (1981) 427.
- 14 Wing, B. L., and Krieger, K., *Final Report to N.M.F.S., N.O.A.A., Auke Bay, Alaska*, 1983.
- 15 Brodie, P. F., Sameoto, D. D., and Sheldon, R. W., *Limnol. Oceanogr.* 23 (1978) 1264.
- 16 Nemoto, T., in: *Marine Food Chains*, p. 241. Ed. J. H. Steeles, 1970.
- 17 Ridgway, S. H., Bowers, C. A., Miller, D., Schultz, M. L., Jacobs, C. A., and Dooley, C., *Can. J. Zool.* 62 (1984) 2349.
- 18 Ridgway, S. H., Scronce, B., and Kanwisher, J., *Science* 166 (1969) 1651.
- 19 Dolphin, W. F., *Can. J. Zool.* 65 (1987) 354.
- 20 Reid, M. H., *Med. Phys.* 9 (1982) 346.
- 21 Reid, M. H., *Med. Phys.* 9 (1982) 361.
- 22 Mauchline, J., cited in Mauchline¹, p. 613.
- 23 Hamner, W. M., Hamner, P. P., Strand, S. W., and Gilmer, R. W., *Science* 220 (1983) 433.
- 24 Lambertsen, R. H., *J. Mamm.* 64 (1983) 76.

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