

Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis*

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ABSTRACT

In order to define the trophic requirements of the North Atlantic right whale, a series of experiments were designed to examine the food capture characteristics of the species. The food filtering efficiency of the baleen of an immature right whale was tested in a flume using graded samples of zooplankton, primarily calanoid copepods, collected in the path of surface-feeding whales. The filtering capacity decreased with decreasing prey organism size, so that greater than 95% of the available caloric content of the zooplankton samples was captured in size fractions collected on 333 μ mesh nets. The experiments demonstrate that the filtering efficiency of the baleen narrowly focuses the right whale's feeding on an energy-rich, yet spatially and temporally variable, portion of the mid-water food resource.

KEYWORDS: FEEDING; EUPHAUSIIDS/COPEPODS; NUTRITION; RIGHT WHALE; NORTH ATLANTIC

INTRODUCTION

With a population of about 350 individuals (Fairfield, 1990; NMFS, 1991; Knowlton *et al.*, 1994; IWC, 2001), the North Atlantic right whale (*Eubalaena glacialis*) is among the rarest of the world's baleen whales. Although intensive whaling which began in the 17th century initially depleted the right whale stock (Reeves *et al.*, 1978; Reeves and Mitchell, 1986), lack of recovery today is thought to be the result of a number of factors including mortality caused by collision with ships and entanglement in fishing gear (Kraus, 1990; IWC, 2001). The recovery plan for the northern right whale (NMFS, 1991) also identifies disruption of critical habitats as a potential contributing factor to the lack of recovery. Although the impact of such disruption on the health of the population is not easily assessed, both the recent decline in calving rate (Kraus *et al.*, 2001) and the decreased use of historically exploited feeding areas (A. Knowlton, pers. comm.) could reflect profound changes in food resources. Hence, the relationship between the whales and the marine ecosystem is an important consideration in the effort to conserve the species.

The most obvious connection between the whale and its habitat is embodied in the whale's feeding activities. To capture food, the right whale filters its zooplanktonic prey from seawater. The efficiency of the right whale's filtering structure fundamentally defines the relationship between the whale and its mid-water resources and thus characterises the whale's reliance on marine planktonic productivity.

The filtering structure of the right whale is formed by two rows of keratinous baleen plates whose function and morphology are reviewed by Pivorunas (1976). Rows of between 250 and 390 plates per side (Leatherwood *et al.*, 1976) form tightly packed filtering walls, or racks, beneath the lateral margins of the upper jaw. With the mouth open, seawater enters the buccal cavity through a gap at the front of the mouth between the racks. In the mouth, filaments arising from the frayed inner edges of adjacent plates overlap across the narrow openings between the plates, forming a filter mat through which water trapped in the mouth is expelled. Because such filter feeding is relatively indiscriminate with respect to food types, food consumption

is determined by two characteristics of available mid-water prey items, filterability and avoidance behaviour.

Planktonic food resources in most of the North Atlantic habitats where right whales are thought to feed are dominated by the calanoid copepods *Calanus finmarchicus* (Winn *et al.*, 1986; Wishner *et al.*, 1988; Murison and Gaskin, 1989; Woodley and Gaskin, 1996), *Pseudocalanus* sp. and *Centropages* spp. (Mayo and Marx, 1990). Although a variety of other food organisms including euphausiids (Hammer *et al.*, 1988), swarming galaethiads (N. Patenaude, pers. comm.) and colonial siphonophores (C. Mayo, unpublished data) have occasionally been reported or inferred as the food of right whales worldwide, the dependency of North Atlantic right whales on calanoid copepods is widely accepted. Copepods and other forms found in the zooplankton community range from approximately 0.05–10.0mm in length, thus requiring for their capture the fine mesh filter mat found in right whales. Movement and orientation of the whale at many scales as it chooses to find patches of zooplankton may permit some degree of prey selection. However, during feeding it is likely that selection is passive and determined solely by the filtering capacity of the baleen once the water has entered the mouth.

Although important in assessing the relationship between the whale and the ecosystem, the filtering efficiency of right whale baleen has not been quantified. This paper estimates the capture efficiency of baleen from the results of filtration experiments using zooplankton collected on the edge of the feeding paths of right whales in Cape Cod Bay, Massachusetts, USA and baleen extracted from the mid-rack of a dead, immature whale.

METHODS

To test zooplankton capture efficiency, a series of experiments were designed to flush water containing plankton through a section of a rack of right whale baleen. In these experiments, we did not compensate for the escape behaviour and orientation of living copepods, for tissue changes in preserved zooplankton, or for the possible

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influences on filtration resulting from the Bernoulli effect at the outer plate margins hypothesised by Orton and Brodie (1987) and Lambertsen *et al.* (1989). The effects on filtration of active or passive conditioning of the filament mat by the whale as suggested by P. Brodie (pers. comm.) were also not controlled for in this study. Instead, the experiments were designed to use food organisms encountered by right whales to test baleen capture efficiency in a simple experimental environment controlled for the density of zooplankton, the velocity of flow and the total filtration time.

The baleen used in the tests was extracted from a 10.1m, 18 month old female (North Atlantic catalogue #1504, P. Hamilton, pers. comm.) killed in a collision with a ship off Cape Cod in August 1986. Our estimates of zooplankton capture efficiency thus refer to the characteristics of #1504's baleen. The section of the left rack used in the experiments included plates 125-150, counting from the front and the test area was approximately 35cm below the upper margin of the plates. During the year between the collection of the baleen and its use in the filtration tests, the baleen was washed and conditioned with a commercial hair conditioner every four months. While the baleen became brittle after collection and drying, the periodic washing and conditioning appeared to restore the supple quality of the filaments found in fresh material.

The zooplankton samples used in the filtration tests were collected in Cape Cod Bay. During the winter of 1987, thirty-nine samples were collected by towing a 471 μ mesh conical plankton net within 3m of the path of right whales feeding at the surface. Samples of zooplankton in the 170-471 μ size range were collected separately using fine mesh nets. All collections were combined to make a standard zooplankton test sample with a density distribution approximating the mean density of the 1987 feeding path collections (Fig. 1). Zooplankton samples were preserved in 10% formalin and graded into seven size fractions by washing through screens. To determine the filtration efficiency of the baleen for different zooplankton sizes, five to nine individual tests were run using each graded fraction. To control for density effects, a sample of a size fraction was counted and injected into the flume to produce a density that approximated that found in the feeding path of the whales. The preserved zooplankton samples were used in the tests within 14 months of collection and preservation.

To flush water through the baleen section, a flume (Fig. 2) was constructed of plywood. It was built around a reservoir containing approximately 125 litres of water and a submersible pump rated at 167 litres/min⁻¹. Connected to the reservoir were input and return channels, each 1m long and 15 × 15cm in cross section. Water was pumped by hose from the reservoir into the input channel with the volume of flow controlled by a restrictor. Water flowed in a loop from the reservoir through the restrictor and input channel and back to the reservoir via the parallel return channel. The baleen section with its plate surfaces parallel to the flow was sealed to the end of the return channel by support frames clamped on each side of the rack section. Thus, the matted filtering surface of the baleen blocked the flow of water returning to the reservoir.

During each experiment, a counted sample was injected into the flow of the return channel 30cm before the water reached the baleen. A window in the face of the return channel permitted the operator to observe the progress of the plankton injection and capture. Observation of the plankton and baleen surface assured that no holes developed in the baleen mat and that the zooplankton was distributed evenly through the water column at the point of impact with the

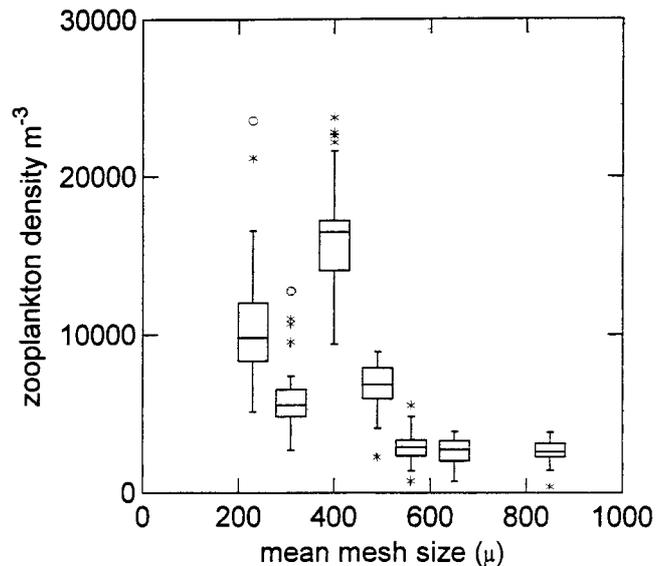


Fig. 1. The distribution of zooplankton collected in the path of feeding right whales in 1987. The size fractions are expressed as the mean of the mesh sizes used to grade the standard 1987 zooplankton sample.

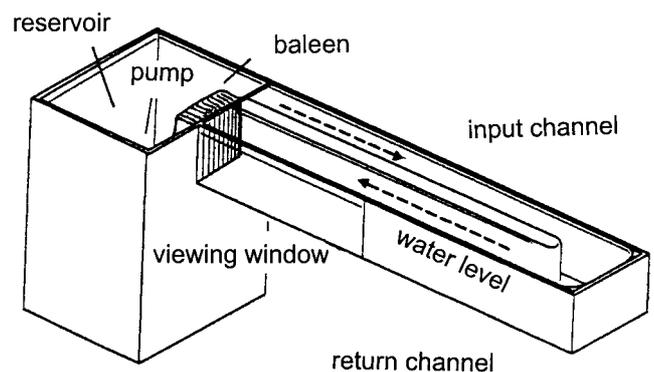


Fig. 2. The experimental flume.

filaments. Such experiments were conducted for 2.5mins to approximate the mean interval between behaviour that Mayo *et al.* (1987) proposed may indicate harvesting of plankton from the baleen surfaces.

In order to set the water transport volume of the flume to the approximate velocity with which water passes through the baleen of a feeding whale, we used the relationship:

$$Vb = (Ag/Ab) \times Vs$$

where:

Vb is the estimated velocity through the baleen filtering surface;

Ag is the area of the free gape of the mouth of whale #1504;

Ab is the surface filter area of the baleen of whale #1504;

Vs is the mean swimming velocity of feeding whales observed during our studies.

To determine the size of the gape, the mouth of #1504 was measured, a 1/20 scale model of the head constructed, and the approximated free gape projected on a grid. The left baleen rack was removed from the mouth intact, measured and similarly projected on a grid to estimate the filtering area.

Swimming speed was determined from plotted tracks of the research vessel following surface feeding whales. Onto these tracks were superimposed the paths of the whales using the methods described by Mayo and Marx (1990). Twenty-three segments of right whales' feeding paths from approximately eight hours of observations were analysed to determine swimming velocity during feeding.

With the pump running at the end of a test, the captured zooplankton was removed from the surface of the baleen by siphoning the sample off the mat and into fine mesh screens. The baleen segment was then lifted from the reservoir and any organisms adhering to the filaments were collected. An estimate of the filtration efficiency for the zooplankton size fraction being tested was obtained by comparing the number of zooplankton captured on the baleen filaments with the number injected. To determine both the injection density and the capture numbers, organisms were counted using a dissecting microscope.

In order to examine the energetic implications of the zooplankton capture characteristics of the baleen, the caloric content of the size fractions used in the filtration tests was estimated. Laurence (1976) determined the mean dry-weight caloric content of the adult forms of several taxa of copepods collected from the shelf waters of the northeastern USA, including three taxa that dominated the 1987 Cape Cod Bay feeding path samples: *Calanus finmarchicus* (6,425 kcal kg⁻³); *Centropages* spp. (4,999-5,245 kcal kg⁻³); and *Pseudocalanus minutus* (5,071 kcal kg⁻³). To permit a comparison with Laurence's estimates of caloric content, five weighed sub-samples of the mixed test sample were frozen and the caloric content of each was determined by bomb calorimeter. Three additional sub-samples of each size fraction were counted and weighed to produce an estimated wet weight per organism and, using the calorimeter data, a caloric content per organism was determined. The wet weight to dry weight values were converted using the 1/5 fractional relationship between wet and dry weight caloric content in order to compare our caloric content estimate with those reported by Laurence (1976).

RESULTS

By projecting the opening of the mouth on a scaled grid, the area of the gape at the front of the racks was determined to be 1.21m². The left side rack area was estimated by projection to be 4.35m², yielding a total baleen surface area of 8.70m² for whale #1504. The mean velocity of feeding whales determined from our field observations was 1.34±0.41m sec⁻¹ (SE=0.08) with a range of 0.41-2.20m sec⁻¹ for the 23 segments of feeding paths analysed. This swimming velocity differs from that reported by Mayo and Marx (1990, 0.63m sec⁻¹, SE=0.03) because of the incorporation of information not previously available. For comparison, the velocity of feeding right whales was roughly estimated by Watkins and Schevill (1979) at 3kts or 1.54m sec⁻¹.

From the above values, the calculated mean through-baleen velocity for feeding whales was estimated at 0.188m sec⁻¹. To approximate this velocity, water was pumped from the reservoir of the flume into the channels and through the baleen at 0.11-0.19m sec⁻¹ (mean=0.13m sec⁻¹).

The mean caloric content of the zooplankton sub-samples was 914 kcal kg⁻¹ wet weight. Although this value was approximately 10% lower than the caloric content reported

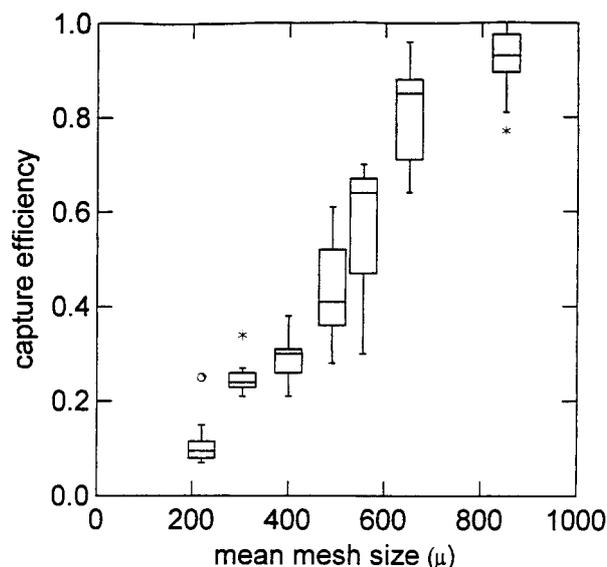


Fig. 3. Baleen capture efficiency determined from flume experiments. The size fractions are expressed as the mean of the mesh sizes used to grade the standard 1987 zooplankton sample.

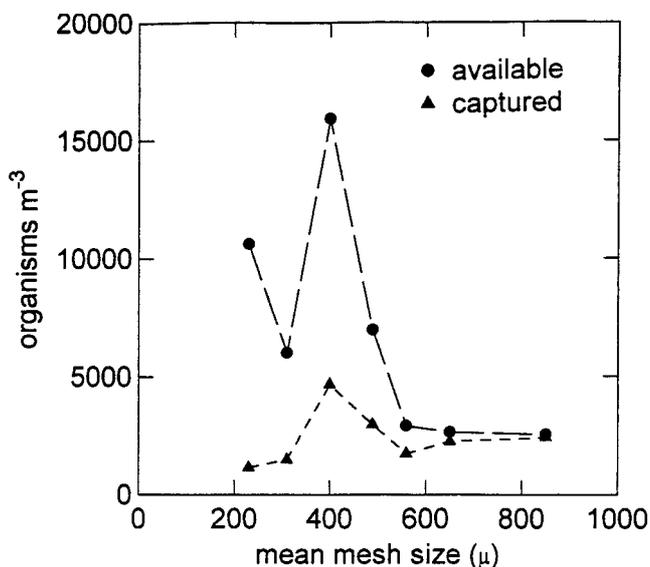


Fig. 4. The estimated mean number of zooplankton organisms available in and captured from the 1987 feeding path samples.

by Comita (1966) and Laurence (1976), it was used here as a conservative estimate of the quality of the zooplanktonic food of right whales in Cape Cod Bay.

Sixty-six flume tests were run using the zooplankton size fractions. The zooplankton capture efficiency summarised in Fig. 3 is reported as the number of organisms captured divided by number injected. The effect of the mesh size on the capture of zooplankton is shown by comparing the number of organisms available and captured (Fig. 4). The calculated wet weight and caloric content of individual zooplankters in each size grade are reported in Table 1. Combining the filtering efficiency with the estimated caloric content by test fraction, permits a comparison between the cumulative caloric content of zooplankton available to right whales and the predicted cumulative caloric capture and loss during filtration (Fig. 5). In our tests, greater than 95% of the available energy was obtained from zooplankton sizes greater than those captured on a 333μ mesh net, despite the significant number of organisms available in the lower size fractions of the test sample.

Table 1
Characteristics of 1987 zooplankton size fractions used in the filtration experiments.

Experimental fraction (m)	Capture efficiency	Mean no. organisms m ⁻³	Weight/organism in g x 10 ⁻⁵	Available kcal m ⁻³	Captured kcal m ⁻³
170-280	0.11	10,621	1.46	0.15	0.02
280-333	0.25	6,012	1.63	0.09	0.02
333-471	0.29	15,922	2.00	0.30	0.09
471-510	0.42	6,997	4.05	0.27	0.11
510-600	0.60	2,915	5.76	0.16	0.09
600-700	0.85	2,661	15.30	0.38	0.33
700-1,000	0.95	2,555	46.50	1.12	1.06
Total		47,683		2.47	1.72

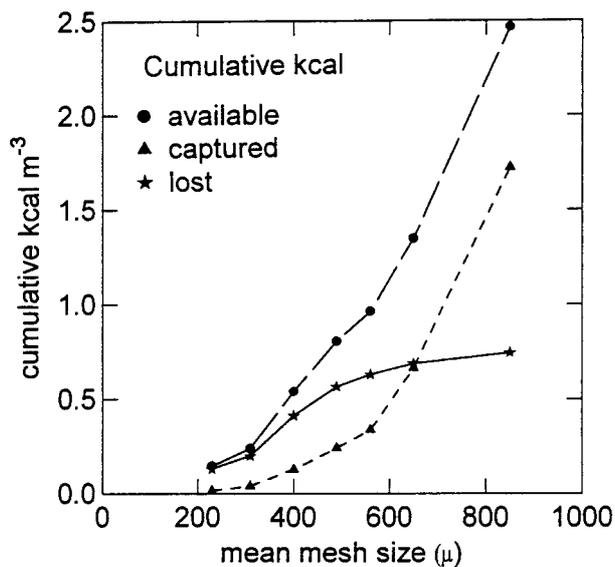


Fig. 5. The cumulative caloric availability, capture and loss during the filtration of 1m³ of seawater in the path of feeding right whales in 1987.

DISCUSSION

There are a number of factors that it was not possible to control for in the experimental design which should be considered when applying our findings to a full consideration of right whale foraging efficiency. The stiffening of the baleen filaments in the dried test rack and the softening and shrinkage of copepod tissues resulting from preservation may have decreased the filtering efficiency in the experimental apparatus as compared to that in a foraging whale. Furthermore, in living whales the filtration rate might be greater than in our experiments as a result of increased flow through the mat because of pressure differences hypothesised by Orton and Brodie (1987) and Lambertsen *et al.* (1989). The considerable escape behaviour of living copepods should also be considered as a factor influencing an application of our results to the living whale. However, our interpretation of the experimental results compensates for the effects of escape behaviour because the estimation of available zooplankton in the path of the whales was calculated from net tows also influenced by copepod avoidance behaviour. The activity of a captured copepod on the surface of the baleen may also increase the escape rate, thus reducing the efficiency of filtration in foraging whales (P. Wiebe, pers. comm.). In our study, it was not possible to assess the impact of the hypothesised differences between

the filtration rates in the living whale and in our experiments. Nevertheless, it seems likely that the identified influences balance one another to some degree, making the results of the experiments useful in assessing the limitations of the right whale's capacity to capture food organisms.

The relationship between capture efficiency and zooplankton size (Fig. 3) is expected if the filter surface is of non-uniform pore size, as are the matted filaments of the baleen rack. In such a filter system, the capture of zooplankton would be expected to increase in efficiency as the size of the available organism increases. In a feeding right whale, this direct relationship between filtration efficiency and organism size would probably continue until the motility of the prey becomes significant. In collections from the feeding paths of whales from Cape Cod Bay, large, mobile organisms such as euphausiids are not encountered and our observations do not, therefore, establish the upper limit of successful foraging. Organisms available as food within the feeding path samples in Cape Cod Bay have a relatively low motility and, once trapped within the mouth, are selected on the basis of the filterability demonstrated in our experiments. Thus, the right whale is well adapted to the harvest of larger, energy-rich zooplankton organisms such as the later life-stages of *C. finmarchicus*, but is less effective at capturing smaller prey items. These smaller prey are both inefficiently filtered and produce less caloric content per organism and are, therefore, less valuable to foraging whales. Nevertheless, right whales feeding in midwater environments dominated by exceptional densities of small zooplanktonic forms could be successful if the density of organisms is so great as to overcome the coincident factors of low efficiency and low organism mass. Fig. 5 demonstrates the importance of the larger size zooplankton fractions in caloric capture by feeding right whales in Cape Cod Bay, where the potential prey is dominated by late larval and adult stages of calanoid copepods. In the bay and perhaps in the other remaining feeding habitats of the western North Atlantic, the right whale's feeding options are therefore limited. Restricted to the capture of large zooplankton by the baleen's filtering characteristics, yet limited in their ability to harvest larger and more mobile nektonic prey by their ponderous filtering apparatus, the right whale's trophic position is narrowly focused on the most productive but labile part of the marine food web. The success of the right whale, as for all filter feeders, is thus determined by the availability of a limited variety of prey organisms whose occurrence may vary widely and unpredictably in the natural system.

Our observations have implications for the methods of zooplankton sampling used to measure the quality of right whale habitats. Using the results of the zooplankton capture tests, it is possible to estimate the size of the net mesh which best approximates the filtering characteristics of the baleen. This estimation is also useful because it presents an approach to evaluate the quality of habitats for which the zooplankton resource has been described from studies using various sampling techniques. We propose that the net mesh that best approximates the capture characteristics of right whale baleen is 333μ, based on the assessment here that more than 95% of the energy captured during the tests came from size fractions captured on mesh greater than 333μ. However, the use of the 333μ mesh as a general functional model of right whale baleen is dependent on the assumptions that the distribution of planktonic prey is similar to the distribution found in our study and that baleen filtration characteristics do not vary significantly with the demographic class of the whales.

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