The Urban Whale

North Atlantic Right Whales at the Crossroads

EDITED BY

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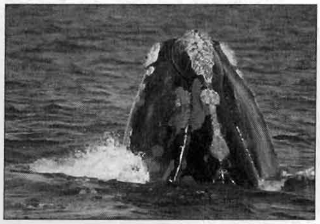
HARVARD UNIVERSITY PRESS
Cambridge, Massachusetts
London, England · *2007*



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Enormous Carnivores, Microscopic Food, and a Restaurant That's Hard to Find

MARK F. BAUMGARTNER, CHARLES A. MAYO, AND ROBERT D. KENNEY

April 1986
Cape Cod Bay

We'd known for a long time that there were places east of Cape Cod where powerful tidal impulses meet the sluggish southward-moving coastal current, places where right whales lined up along the rips where plankton concentrate. On a windless day in early April 1986, we decided to see if right whales had found such an area. The winter season, when right whales come to Cape Cod, had been a hard one, and calm days like this were few, so we could at last get to the more distant convergence and, as local fishermen do, see what we could catch.

It was gloomy and nearly dark when we left the port. For those of us who study whales, expectations are usually tempered by reality; we were looking for one of the rarest of all mammals in the shroud of the ocean. Today, however, spirits were high as the daybreak was filled with springtime promise. Along the great outer beach of the Cape, so close to shore that we could smell the land nearby, the first right whale was spotted working along one of those current rips. And as the sun climbed out of the haze, the whale rose and opened that great and odd mouth and skimmed the surface in a silence broken only by the sizzle of water passing through its huge filtering *apparatus. Our earlier optimism was warranted, and for several hours we drifted just clear of the linear rip that the whale was working, recording the complex pattern of its movements.*

This whale, one well known to those of us studying right whales, was a young female identified as Eg #1223, but given the nickname "Delilah." As the hours passed, Delilah's movements became more convoluted as the current convergence, seen as wavelets on the glassy surface, seemed to be shrinking and moving toward the land. Our work involved collecting samples of the food on which Delilah was feeding with intense focus. Marilyn Marx, in charge of documentation, recorded what appeared to be a declining concentration of the orange plankton that drifted in the rips nearly unseen and that we, like Delilah, could filter from the water with a fine-mesh net. Back and forth along the current edge, Delilah skimmed the surface. It was a magical time, as always when right whales are about and performing.

As the day wore on to afternoon, Delilah's feeding path shifted slowly toward the beach until we could see clamshells on the bottom and hear the chatter of the gathering crowd of beach walkers! Then things began to change, perhaps as the currents driven by the tides changed, and we were soon surrounded by the shrinking rip that marked the conditions causing the food to concentrate. In some incomprehensible way Delilah knew that things were changing in her murky, liquid-green world. Her patterns of movement matched exactly the rip along the surface into which we, perhaps a large piece of flotsam to her, had drifted. She skimmed ever closer. For the very first time that day, Delilah closed her mouth, turned toward us and dove, a lumbering black ghost. She passed below the boat, then stopped suddenly and hung just beneath us. Only a moment passed until, rising against our starboard side, Delilah rolled and firmly struck the side of our vessel with her flipper. With point made (whatever it was, we could not know), she slid silently away, only to rise, mouth opened again, to continue her surface feeding for several more hours.

What was in the mind of Delilah? Certainly this whale was processing information with senses that must have been finely tuned to feeding on an unimaginably different kind of food resource in a sea of uncertainty. And what message was Delilah sending when she momentarily stopped her feeding, came to us, and delivered a firm slap to the boat? We came to understand only the rudiments of right whale foraging that day as Delilah displayed the basic components of a behavior built from millennia of learning and adaptation. Sadly, we will gain no more knowledge from our old and *one-time cantankerous friend, as she was struck and killed by a ship six years after our encounter in the coastal rip.*

Charles (Stormy) Mayo

Right whales are among the Earth's largest animals, but they feed on creatures that are the size of fleas. In regard to the ratio of a right whale's mass to that of its prey (50,000 kg to 1 mg, or 50 billion to one), right whale feeding is equivalent to humans feeding on bacteria. Perhaps as strange, right whales are carnivores that feed without manipulating their prey or their environment in any way. Unlike chimpanzees that use their hands to gather food, spiders that build webs to trap insects, ants that farm fungi, lions that ambush and run down their prey, or dolphins that herd fish into tight balls to more easily capture them, right whales simply open their mouths, swim forward, and feed on whatever happens to fall in. They rely utterly on the environment to organize their prey into mouth-sized aggregations of millions to billions of organisms.

Right whale feeding is often likened to grazing by cows (an image bolstered by their shared evolutionary roots), which is essentially correct if the cow is in the desert, looking for a small, continuously moving oasis of grass, blindfolded. So instead of considering right whales to be lazy or dumb, bear in mind that the challenge of finding prey aggregations in the ocean is enormous; with all of our modern technology, researchers cannot find the kinds of superabundant aggregations that the whales can. For example, the largest concentrations of their primary prey ever recorded have come from zooplankton samples collected near right whales (Wishner et al. 1995; Beardsley et al. 1996). This chapter explores what right whales eat, how they feed, and how they might go about finding food, but first it examines their unusual feeding apparatus and its implications for how they make a living in the sea.

Why Baleen?

The mouth of a mysticete, or baleen whale, is an extraordinary morphological adaptation to life in the sea. Gone are the calcified teeth that most mammals use to capture, kill, and chew food, and in their place are 160–400 baleen plates, each with hundreds to thousands of filaments that together act as a sieve (Nemoto 1959) (Fig. 5.1a). These filaments are made of keratin, the same protein that fingernails and hair are made of, and the size and number of the filaments determine the filtering efficiency of the baleen. Right, bowhead, and sei whales have the finest and most numerous baleen filaments of all the mysticetes (Fig. 5.1b), which allow them to capture zooplankton, the tiny weak-swimming animals of the sea. Like a sieve, baleen filters only those organisms that are larger than a certain minimum size. Mayo et al. (2001) estimated that the filtering efficiency of right whale baleen is similar to that of the 0.333-mm net commonly used by marine ecologists to sample zooplankton. Organisms smaller than 0.333 mm (just over 1/100 of an inch) are too small to be efficiently retained on the baleen, and most simply pass through it.

Right whales typically swim slowly (ca. 1.5 m/s) while feeding for sustained periods, likely because the work required to push their baleen through the water increases exponentially with their swimming speed. Moreover, optimal flow characteristics through the mouth and baleen are probably maintained at slower speeds (Hamner et al. 1988; Werth 2004). Consequently, the right whale's diet is restricted by the swimming speed of their prey. Small fish such as herring and mackerel are far too fast to be captured by slow-moving right whales, and even some adult euphausiids (krill) may be able to avoid capture by detecting the oncoming whale and swimming to safety. The restrictions on the minimum and maximum size of prey that are imposed by the filtering efficiency of baleen and the right whale's slow swimming speed, respectively, severely limit the number and type of prey species available for capture. For these reasons, right whales feed primarily on a few species of large zooplankton.

To understand why right whales would evolve to focus on such a limited range of prey species, one must consider the way energy is transferred through the food web. Trophic efficiency in marine ecosystems has been estimated at roughly 10 percent (e.g., Ryther 1969; Pauly and Christensen 1995), meaning it takes 1,000 kg of phytoplankton to produce 100 kg of herbivores (e.g., herbivorous zooplankton), 10 kg of zooplantivores (e.g., herring, right whales), and 1 kg of piscivores (e.g., silver hake, humpback whales). The amount of biomass in the ocean can be thought of as a pyramid, with phytoplankton at the wide bottom, and top predators at the narrow apex. Predators evolved to feed at a particular level of the pyramid, and there is considerably more food available to a predator that feeds lower on the pyramid than higher on the pyramid (e.g., there is more biomass available to be eaten when feeding on phytoplankton than on seals). Most marine mammals feed on fish or squid that are relatively high on the pyramid, but right whales take advantage of the increased biomass available at lower levels of the pyramid by feeding on large zooplankton.

Figure 5.1. (a) Head of Eg #1004 with left lower lip and mandible removed to reveal the very large tongue and baleen (note the tip of the tongue has been removed). Michael Moore / Woods Hole Oceanographic Institution. (b) Baleen of Eg #1014 in near-pristine state. Regina Campbell-Malone / Woods Hole Oceanographic Institution.

However, zooplankton concentrations vary widely from location to location and from year to year because of changes in zooplankton production and the processes that aggregate zooplankton. Right whales, therefore, rely on a sometimes unreliable food resource, and because their behavior and morphology are so rigidly adapted to capturing zooplankton, they cannot switch to another prey resource, such as small fish, during times of low zooplankton availability. With such a small population size, the right whale's restrictive filtering apparatus makes it particularly vulnerable to fluctuations in prey abundance caused by environmental variability. Although it is efficient during times of zooplankton plenty, the right whale's remarkable feeding adaptations might doom the species should the zooplankton resources decline.

Right Whale Food

Numerous studies have demonstrated that a single species of zooplankton, the 2- to 3-mm-long calanoid copepod *Calanus finmarchicus* (color plate 6), is the primary prey of North Atlantic right whales in each of the major feeding habitats: Cape Cod Bay (Mayo and Marx 1990), Great South Channel (Wishner et al. 1988, 1995), lower Bay of Fundy (Murison and Gaskin 1989), Roseway Basin (Baumgartner et al. 2003a), and Jeffreys Ledge (M. Weinrich and M. Bessinger, pers. comm.). Most of these same studies indicate that right whales focus on the later juvenile stages (copepodites) and adults of *C. finmarchicus,* particularly stage 5 copepodites (hereafter referred to as *C. finmarchicus* C5) (Fig. 5.2). Payne et al. (1990) and Kenney (2001) documented anomalies in right whale occurrence in Massachusetts Bay and in the Great South Channel, respectively, that were strongly associated with changes in the occurrence of *C. finmarchicus.* There is even evidence to suggest that changes in the annual abundance of *C. finmarchicus* may influence right whale calving rates (Chapter 15).

The life history of *C. finmarchicus* in the North Atlantic is distinguished by a period just before adulthood when copepods cease development and enter a prolonged dormant phase called diapause (Fig. 5.2). A similar resting phase is common in insects and is somewhat analogous to hibernation in mammals. In the open ocean, *C. finmarchicus* emerge from diapause deep in the water column during the late winter and molt into adults (Marshall and Orr 1955). Males emerge first, followed later by females, and these adults mate as they migrate to the surface. Females feed in the surface waters during the early phase of the spring phytoplankton bloom and begin producing eggs at rates

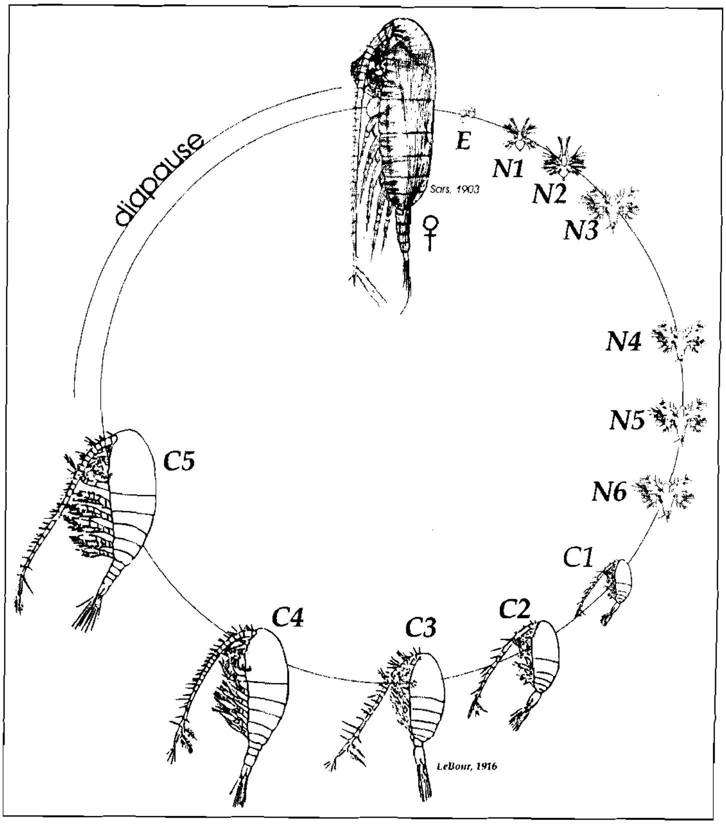

Figure 5.2. Life cycle of *Calanus finmarchicus* depicting the six naupliar stages, five copepodite stages, and the adult stage. The distance between stages represents the relative time between molts. Drawings adapted from Sars (1903) and LeBour (1916).

of up to 50–70 eggs per female per day (Campbell et al. 2001). After hatching, the early naupliar stages (N1–2) do not feed. The later naupliar stages (N3–6), all copepodite stages (C1–5), and adults feed primarily on phytoplankton. During the copepodite stages, *C. finmarchicus* develops an oil sac filled with wax esters, and by stage C5, this oil sac has reached its maximum size, comprising up to 50 percent of body volume (Miller et al. 2000) (color plate 6c). By this time, the phytoplankton bloom is nearly, if not already, over, and the longer and warmer days of late spring and early summer have begun to warm the surface waters of the North Atlantic. With no food left to eat, temperatures rising, and a significant risk of predation by visual hunters (e.g., fish) in the well-lit surface waters, *C. finmarchicus* migrates to depths greater than 200 m in oceanic waters or near the bottom over the continental shelf and enters diapause (Miller et al. 1991). *C. finmarchicus* does not actively feed during diapause but instead meets all of its nutritional needs during the summer, fall, and early winter by metabolizing the considerable energy stored in its oil sac.

In the Gulf of Maine and Nova Scotian Shelf, phytoplankton production is prolonged relative to oceanic production because of vertical mixing and stratification processes that are unique to the continental shelf (e.g., tidal mixing, fresh water influx from river runoff). This longer period of production allows *C. finmarchicus* to produce more than one generation in a single year. When each generation of copepodites reaches stage C5, it appears that some remain in the surface waters and molt into adults to continue production while others migrate to depth and enter diapause. The highest *C. finmarchicus* production appears to occur in association with the spring bloom, and most of the *C. finmarchicus* population can be found in diapause at depth in the summer and fall (Durbin et al. 2000; Baumgartner et al. 2003b).

When one considers this remarkable life history, particularly the development of an energy-rich oil sac, it is easier to understand why right whales prefer *C. finmarchicus. C. finmarchicus* is the dominant copepod in the North Atlantic and is therefore quite abundant. When compared to other copepods, *C. finmarchicus* has a much larger biomass and a higher caloric content. For example, *C. finmarchicus* females (for which there are published data) have a biomass that is nine times larger, a caloric content per unit weight that is 27 percent higher, and a caloric content per individual that is eleven times higher than *Pseudocalanus* spp. females. Hence, right whales would need to consume over an order of magnitude more *Pseudocalanus* than *C. finmarchicus* to obtain the same energy. Clearly, by focusing their foraging efforts on late-stage *C. finmarchicus,* right whales can maximize their energy intake.

Right whales do not feed exclusively on *C. finmarchicus,* however. In Cape Cod Bay, Mayo and Marx (1990) examined zooplankton abundance and community composition in proximity to surface skim-feeding right whales by towing zooplankton nets within 5 m of a whale's feeding path. *C. finmarchicus* dominated in most of the net samples; however, a few of the samples were dominated by *Pseudocalanus, Centropages typicus,* or barnacle larvae (in order of importance). Observers noted that feeding on barnacle larvae was quickly terminated, perhaps indicating that this prey was not suitable (Kenney et al. 2001). Watkins and Schevill (1976) also observed right whales surface skim-feeding on patches of juvenile euphausiids (krill) in Cape Cod Bay, and Collett

(1909) reported that right whales fed on euphausiids in the Hebrides and off Iceland in the northeastern Atlantic.

Reports of North Atlantic right whales feeding on euphausiids are very interesting because adult euphausiids are relatively large and may be capable of evading capture by these slow-moving whales. Estimating the contribution of euphausiids to the right whale diet is difficult for the same reason: adult euphausiids are adept at evading zooplankton nets (Brodie et al. 1978; Wiebe et al. 2004). Collett (1909) reported that right whales likely fed on *Thysanoessa inermis* in the northeastern Atlantic, a euphausiid that is ten times the size of *C. finmarchicus.* Although right whales may be able to capture juvenile euphausiids while slowly and continuously filter feeding, catching adult euphausiids may require a different strategy. Hamner et al. (1988) described a southern right whale surface skim-feeding on the very large and very mobile Antarctic krill during fifteen- to twenty-second feeding bouts at swimming speeds of 4–4.5 m/s. "During these powerful filter-feeding runs," wrote Hamner et al. (1988, 144), "enormous amounts of water were displaced, cascading beside and behind the right whale and producing a large wake." This feeding behavior is strikingly different from the continuous surface feeding observed for North Atlantic right whales characterized as four- to six-minute feeding bouts at swimming speeds of 1.5 m/s (Watkins and Schevill 1976; Mayo and Marx 1990), during which little or no bow wave is produced. The behavior of the southern right whale observed by Hamner et al. (1988) is undoubtedly a response to the size and mobility of *E. superba.* Adults of this euphausiid species can reach lengths of 6.5 cm (twenty-two times the size of *C. finmarchicus*). It is conceivable that North Atlantic right whales might also employ a similar, short-duration, high-speed feeding behavior to capture large and abundant euphausiids (e.g., the northern krill); however, this behavior has not yet been documented.

Studying Right Whale Food

Investigating Diet

Traditional field diet studies often involve some kind of manipulation of the subject animal, ranging from forced regurgitation to killing the animal, extracting the stomach, and examining the contents. For endangered animals, of course, this kind of manipulation is exceedingly undesirable. Before the international ban on harvesting right whales in the 1930s, stomach contents were available for examination, but published reports are anecdotal and lacking in taxonomic detail. Collett (1909, 97), for example, describes the diet of right whales harvested in the northeast Atlantic as "exclusively pelagic crustaceans (the "krill" of Norwegian whalers), a euphausiid about half an inch long, probably *Boreophausia inermis* [i.e., *Thysanoessa inermis*]." Collett's taxonomic identification sounds somewhat speculative, suggesting that perhaps he did not examine stomach contents himself but extrapolated from whalers' observations.

Current diet studies of endangered animals often rely on direct visual observations of feeding. Visual observation of right whale feeding is possible in habitats where surface skim-feeding occurs (e.g., Cape Cod Bay, the Great South Channel). Accounts from whaling days often mention right whales skim-feeding in patches of orange or red water similar to the modern accounts of right whales feeding on surface aggregations of *C. finmarchicus* (e.g., Beardsley et al. 1996). This coloring of the water is produced by the small areas of red pigment (notably at the posterior end of the oil sac) in the otherwise transparent *C. finmarchicus* (color plate 6). More recent and detailed accounts of skim-feeding have been published by Watkins and Schevill (1976, 1979), Wishner et al. (1988, 1995), Mayo and Marx (1990), Kenney et al. (1995), and Beardsley et al. (1996), and most of these reports include net sampling of zooplankton community composition.

Surface observations of feeding are clearly useful for identifying prey species, but most right whale feeding occurs below the surface well out of view. How, then, can researchers use observations to determine diet? Ingenious, animal-mounted video technology has facilitated underwater observations and identification of prey for other marine mammals, but in the turbid coastal environments in which right whales feed, it is impossible to use a back-mounted camera to see what is flowing into the whale's mouth several meters away. Moreover, it is impossible to identify zooplankton prey species that are likely smaller than the resolution of the camera. Instead of using this animal-mounted technology, right whale researchers have relied on both net- and instrument-based zooplankton sampling in proximity to whales to infer diet and prey concentrations during subsurface feeding. This technique is probably accurate for prey identification when sampling is conducted within tens to a few hundreds of meters of a foraging whale.

Qualitative diet analysis using fecal material has been used widely in terrestrial and pinniped research. Whale scat is difficult to collect, but recent advances in genetic and fecal hormone analyses have illustrated the value of fecal material for determining individual identification and reproductive status without any disturbance to the whale (Chapter 8). Microscopic examination of right whale fecal material in the lower Bay of Fundy (Kraus and Prescott 1982; Murison 1986) and in Roseway Basin (Stone et al. 1988) revealed the presence of many *C. finmarchicus* mandibles; body parts from other zooplankton taxa, such as chaetognaths and euphausiids, were found infrequently. These observations underscore the importance of *C. finmarchicus* in the diet of North Atlantic right whales. Sorting fecal material for undigested bits of crustaceans is tedious and may not reveal all of the prey present in the diet, particularly those that are more readily digested. Genetic analysis of prey DNA may represent a more reliable technique for determining diet composition from fecal material than microscopy. This promising method has been used to identify digested prey in stomach contents (Rosel and Kocher 2002) and in fecal material of other species (Jarman et al. 2002, 2004) but has yet to be applied to right whales.

Net Sampling

The most widely used method to sample zooplankton is the net tow. The size of the net's opening can vary from a few tens of centimeters to several meters wide and is chosen based on the size and motility of the zooplankton one intends to catch. Likewise, the net's mesh size is also chosen based on the size of the zooplankton. Net openings of less than 1 m^2 and mesh sizes of 0.150–0.333 mm are adequate for sampling zooplankton in the right whale's diet (although some larger and more mobile euphausiids may require larger net openings). To estimate zooplankton abundance, the net is outfitted with a flowmeter to measure how much seawater is filtered. Zooplankton are enumerated by identifying and counting organisms in an aliquot of the sample (i.e., in a subsample) using a dissecting stereomicroscope, and abundance is expressed as the number of individuals per cubic meter of filtered seawater.

Nets are typically deployed in two modes: vertical hauls and oblique tows. Vertical hauls consist of lowering the net to a particular depth and then slowly raising the net back to the surface. Oblique tows involve towing the net behind a moving vessel while paying out the tow cable until the net reaches the desired depth and then pulling the tow cable back in slowly to bring the net back to the surface (Fig. 5.3a). When lowered to the bottom, both vertical hauls and oblique tows of single nets provide estimates of average water column abundance. To estimate abundance in discrete strata, a depth-stratified sampler is re-

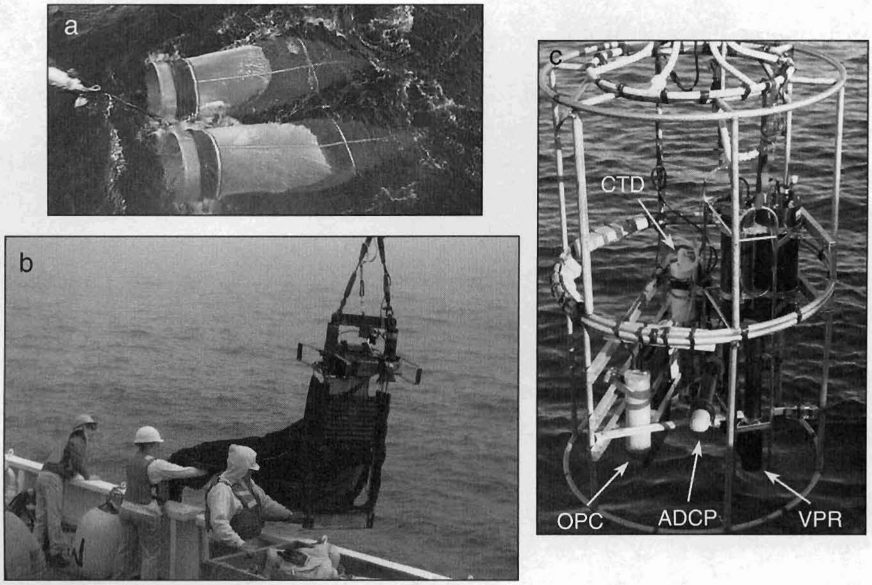

Figure 5.3. (a) Side-by-side 0.29-m^2 bongo nets being towed at the surface. (b) A 0.25-m^2 multiple opening and closing net and environmental sensing system that can accommodate up to nine nets. (c) A lowered instrument package consisting of an optical plankton counter (OPC), acoustic Doppler current profiler (ADCP), video plankton recorder (VPR), and a conductivity-temperature-depth (CTD) instrument. Mark Baumgartner / Woods Hole Oceanographic Institution.

quired, such as the multiple-opening-closing net and environmental sensing system (Wiebe et al. 1976, 1985) or the Bedford Institute of Oceanography net and environmental sensing system (Sameoto et al. 1980) (Fig. 5.3b). These sampling systems carry many nets that open sequentially on command from the ship and are typically used for characterizing the vertical distribution of zooplankton.

Net sampling remains the best method for identifying zooplankton species composition, but deployment and sample processing are time-consuming and require taxonomic expertise. Moreover, the spatial scales over which towed nets sample can be quite large compared to the spatial scales at which right whales forage. For example, a depth-stratified sampler that is towed over a kilometer while sampling several 30-m-thick depth strata from the bottom to the surface is not ideally suited for characterizing copepod abundance in patches that are only a few hundred meters wide and a few meters thick.

Instrument-Based Sampling

To observe fine-scale patches of zooplankton, some researchers have turned to instrument-based zooplankton samplers. For each of these instruments, precise taxonomic identification is sacrificed for sampling at smaller spatial scales and reducing deployment and processing time. Prudent use of these instrument-based samplers requires some knowledge of the zooplankton community in which they will be deployed; therefore, net sampling must remain an integral component of their use until the zooplankton community composition in the region of interest is sufficiently understood.

Two instruments, the optical plankton counter and the video plankton recorder, estimate zooplankton abundance in a small volume of water and must be towed or lowered through the water column. The optical plankton counter (Herman 1988, 1992) counts and estimates the size of particles as they pass through the middle of a sampling tunnel (Fig. 5.3c). A light source on one wall of the tunnel produces a beam of light directed across the middle of the tunnel and onto a photodetector on the opposite wall. A particle passing through the beam blocks this light and casts a shadow on the photodetector. The magnitude of the shadow is roughly proportional to the size of the particle in the beam. The optical plankton counter has no intrinsic ability to identify particles, but late-stage *C. finmarchicus* are readily detectable because there are no other abundant organisms in the North Atlantic that are similarly sized. The video plankton recorder (Davis et al. 1992) can be thought of simply as an underwater microscope consisting of a camera focused on a small volume of water illuminated by a strobe light (Fig. 5.3c). The camera records images of the organisms within this volume of water at a rate of thirty frames per second. Unlike the optical plankton counter, the video plankton recorder allows taxonomic discrimination because the organisms captured in the images can be examined and identified.

Acoustic instruments can obtain abundance estimates at distances of meters to hundreds of meters away by emitting a short pulse of sound that travels away from the instrument, echoes off particles or organisms in the water column, and then returns to the instrument. The intensity of the received echo is related to the size and the physical properties of the organism. Many acoustic systems exist (Chu and Wiebe 2003), and the processing and interpretation of the echo data require considerable expertise. Although acoustic methods have no intrinsic ability to identify zooplankton, they are capable of rapidly measuring echo intensity (also called acoustic backscatter) at high vertical and horizontal spatial resolutions over large areas. In regions where the zooplankton community is dominated by a single species (as is the case in many right whale habitats), acoustics offers a means to rapidly map the horizontal and vertical distribution of the dominant species at high resolution.

The Physics of Food Capture

The head and mouth morphology of the balaenids (right and bowhead whales) differs significantly from the rorqual whales (e.g., blue, fin, and humpback whales), and these differences are related to the foraging ecology of these two families. The rorquals feed primarily by engulfing enormous quantities of seawater and food in a single mouthful, and then sieving this seawater through their coarse baleen to trap prey inside the mouth. Pivorunas (1979) estimated that blue whales could engulf at least 60 m^3 (70 tons) of water in one mouthful. Rorquals have loose joints in their lower jaws that facilitate opening the mouth wide, ventral grooves that allow expansion of a unique interior space called the cavum ventrale to accommodate immense volumes of seawater, and a flaccid tongue that turns inside-out to line the cavum ventrale during engulfment (Lambertsen 1983; Orton and Brodie 1987). This feeding method, called lunge feeding, is likely a behavioral adaptation that serves to capture mobile schooling prey, such as euphausiids and small fish.

In contrast to the rorquals, balaenids feed by a method known as ram filter feeding, where the whale simply opens its mouth and swims forward. Right whales have been observed ram filter feeding for several hours without interruption; prey capture and filtering are continuous. To accommodate ram filter-feeding, right whales have very large heads (up to one-third of the body length), arching jaws, long (up to 2.7 m) and narrow baleen plates, and a very large muscular tongue (Fig. 5.1a). The baleen is organized in two racks on either side of the mouth, separated by a space at the front of the mouth called the subrostral gap (Fig. 5.4). This gap is unique to the balaenids, and it allows seawater to continuously enter the mouth as the whale swims forward. Right whale baleen fringes (the hairlike bristles that line the interior surface of the baleen) are finer and denser than rorqual baleen and can, therefore, retain much smaller particles (Nemoto 1959).

Despite the functional similarities, ram filtration by balaenids is not exactly equivalent to towing a plankton net through the water. By moving forward, both balaenids and plankton nets produce hydraulic forces that push zooplankton into the sieve. However, balaenid oral morphology is far more complex

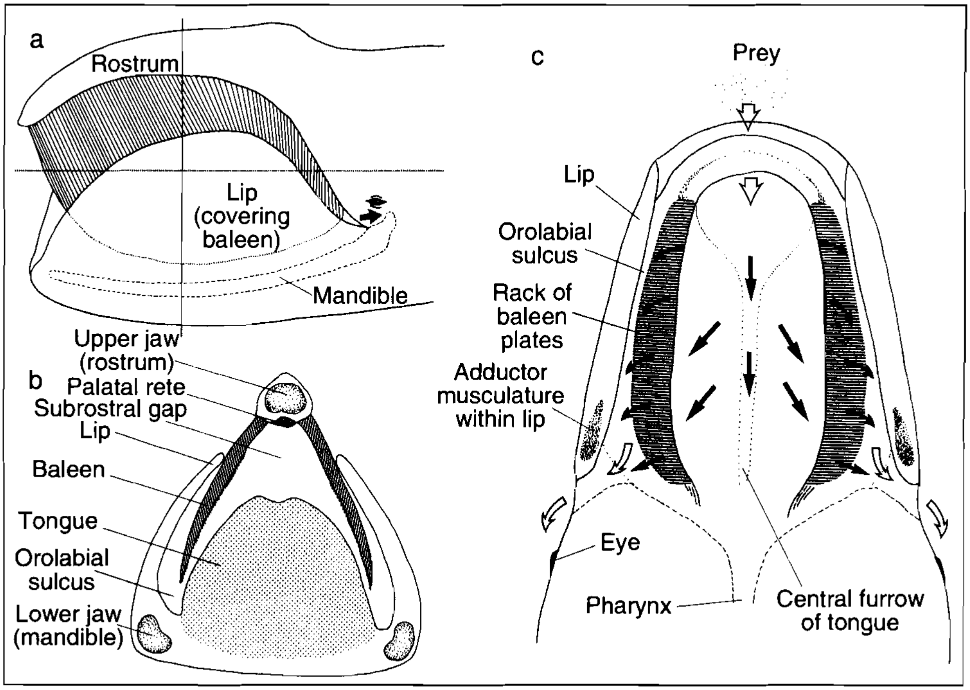

Figure 5.4. (a) Side view of a balaenid head. Arrow indicates where water exits the mouth at the rear end of the orolabial sulcus. Vertical and horizontal lines indicate the planes of sections shown in (b) and (c), respectively. (b) Front view of balaenid mouth depicting the positions of the tongue, baleen, lip, and orolabial sulcus. The subrostral gap is the space between the baleen racks. (c) Top view of balaenid mouth depicting the flow of water through the subrostral gap, through the baleen, and into the orolabial sulcus, exiting just in front of the eye. Drawings adapted from Werth (2004).

than a plankton net, and this complexity promotes hydrodynamic forces that improve filtration efficiency. When a right whale opens its mouth to feed, the lips of the lower jaw move downward away from the upper jaw (rostrum) and laterally away from the baleen (color plate 7). The lower jaw acts as a gigantic scoop, directing water into the mouth between the baleen racks (via the subrostral gap) and also along the outside of the baleen in the space between the baleen and the lips called the orolabial sulcus (Fig. 5.4c). Water entering the mouth through the subrostral gap passes over the tongue, through the baleen, and into the orolabial sulcus and then exits the mouth just in front of the eye. The water that enters the orolabial sulcus at the front and flows along the exterior margin of the baleen is not filtered, but it serves a critical function in the filtration process. The orolabial sulcus narrows from front to back, which accelerates flow along the outside of the baleen relative to the flow inside the mouth (via the Bernoulli effect; Werth 2004). Additionally, the front part of the baleen rack bulges outward toward the lower lip to create a hydrofoil that further accelerates water in the orolabial sulcus (Lambertsen et al. 2005). This acceleration creates a difference in pressure between the interior of the mouth and the orolabial sulcus (i.e., on either side of the baleen) that actually pulls water through the baleen (via the Venturi effect). Thus, filtration is not accomplished by hydraulic forcing alone (as in a plankton net) but is aided by this pressure differential and the associated through-baleen flow.

When a ship moves forward, it pushes water in front of it and produces a compressive bow wave (much to the delight of many dolphins). Although considerably more porous than a ship's bow, plankton nets can also push water. The resulting increase in pressure just in front of the net can alert zooplankton and elicit an escape reaction (Barkley 1964). Avoidance of nets and in situ instrumentation by zooplankton that are especially alert or mobile is a well-known problem in zooplankton sampling (Wiebe et al. 1982) and is presumably a challenge faced by right and bowhead whales as well. However, flow acceleration through the mouth may reduce or eliminate the pressure wave in front of the whale and significantly improve prey capture (Werth 2004; Lambertsen et al. 2005). Werth (2004) built an anatomically accurate, one-fifteenth-scale model of an adult bowhead whale head to examine the hydrodynamics of ram filter feeding. Both flow tank tests with the scale model and mathematical modeling suggested that flow into the mouth was laminar and that no compressive bow wave was formed. In fact, by seeding the water with particles, Werth (2004) was able to observe particles being "pulled" into the model's mouth. This evidence suggests that not only is there no compressive bow wave to alert zooplankton of the oncoming whale but that some mild suction is produced just forward of the mouth. When finally alerted to the presence of the whale, zooplankton are likely within the zone of accelerating water very near the whale's mouth, and escape may be nearly impossible.

Foraging Behavior

Right whale foraging behavior has traditionally been classified into two modes, surface skim-feeding and subsurface feeding, but it appears that the only real difference between the two is the vertical distribution of prey, not the whale's actual foraging behavior. Surface skim-feeding occurs when prey are within

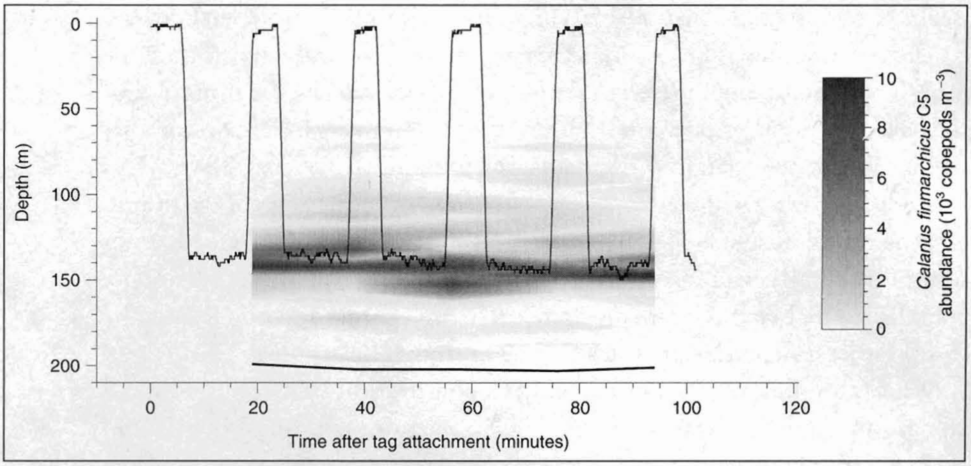

Figure 5.5. Foraging behavior of a right whale tagged with a time-depth recorder in the lower Bay of Fundy. Dive profiles (solid line) are shown over a contour plot depicting the vertical distribution of *Calanus finmarchicus* C5. The sea floor (ca. 200 m) is shown as a thick solid line. Adapted from Baumgartner and Mate (2003).

several tens of centimeters of the sea surface. The whale swims with the front portion of its upper jaw elevated above the sea surface and the rest of its body submerged (color plate 7). Right whales likely control the elevation of the upper jaw above the water based on the vertical distribution of prey. The subrostral gap is triangular in shape (Fig. 5.4b), so positioning the mouth such that the widest space between the baleen racks (i.e., near the floor of the mouth) coincides with the depth of the highest concentration of prey will maximize prey intake. In addition to finely adjusting their vertical position, right whales turn often in response to changing horizontal gradients in prey abundance to remain within the highest concentrations of zooplankton available (Mayo and Marx 1990). Watkins and Schevill (1979) observed sei and right whales feeding on zooplankton in proximity to one another, but the sei whales apparently lacked the right whales' ability to remain in the highest prey concentrations within the zooplankton aggregations. Instead, the sei whales moved completely outside of the aggregations before turning back into them. These differences in foraging efficiency highlight the right whale's extraordinary specialization for feeding on zooplankton.

Studying subsurface foraging behavior is challenging because visual observations are not possible; instead, researchers rely on instrumentation. In the

Great South Channel, Winn et al. (1995) monitored movements and surfacing and diving durations by attaching radio transmitters to right whales and also measured dive depths for some of the tagged whales using acoustic transmitters. Two whales equipped with acoustic transmitters spent the vast majority of their time (97 percent) within 20 m of the surface. In contrast, Goodyear (1993) and Baumgartner and Mate (2003) used acoustic transmitters and time-depth recorders, respectively, to observe right whales foraging well below 100 m and, in some cases, at the sea floor (ca. 200 m) in the Bay of Fundy (color plate 8). Right whales tagged in the Bay of Fundy spent most of their time foraging on discrete layers of diapausing *C. finmarchicus* C5 just above a turbulent bottom mixed layer (Fig. 5.5) (Baumgartner and Mate 2003).

Foraging Behavior and *Calanus* Life History

The habitats where surface feeding is most often observed, Cape Cod Bay and the Great South Channel, are late winter and spring habitats. Although subsurface feeding predominates in all habitats, it is most characteristic of the summer habitats in the lower Bay of Fundy and Roseway Basin. These seasonal differences in diving behavior may be directly related to the life history of *C. finmarchicus*. The year's first generation of *C. finmarchicus* spawned in December–January do not grow to late-stage copepodites until March–April (Durbin et al. 1997, 2000). Right whales cannot efficiently filter eggs, nauplii, or early copepodite stages of *C. finmarchicus*, so the first generation of *C. finmarchicus* is unavailable to right whales until late winter or early spring. Observations of right whales feeding on other copepods in Cape Cod Bay (Mayo and Marx 1990) occur primarily during this period of *C. finmarchicus* unavailability (Fig. 5.6).

When *C. finmarchicus* reaches the later copepodite stages in late winter and early spring, these copepodites remain in the upper water column to feed on phytoplankton that are restricted to well-lit surface waters. Right whales likely feed at or near the sea surface during this time because of the availability of late-stage *C. finmarchicus* in the upper water column. As the surface waters warm, and phytoplankton abundance decreases after the spring bloom in late spring, most late-stage *C. finmarchicus* copepodites (predominantly stage C5) begin to migrate downward to initiate diapause. By summer, the majority of *C. finmarchicus* can be found deep in the water column, and right whales engage in long subsurface dives to forage on these diapausing copepodites (Fig. 5.6). The transition period between *C. finmarchicus* occurrence in surface

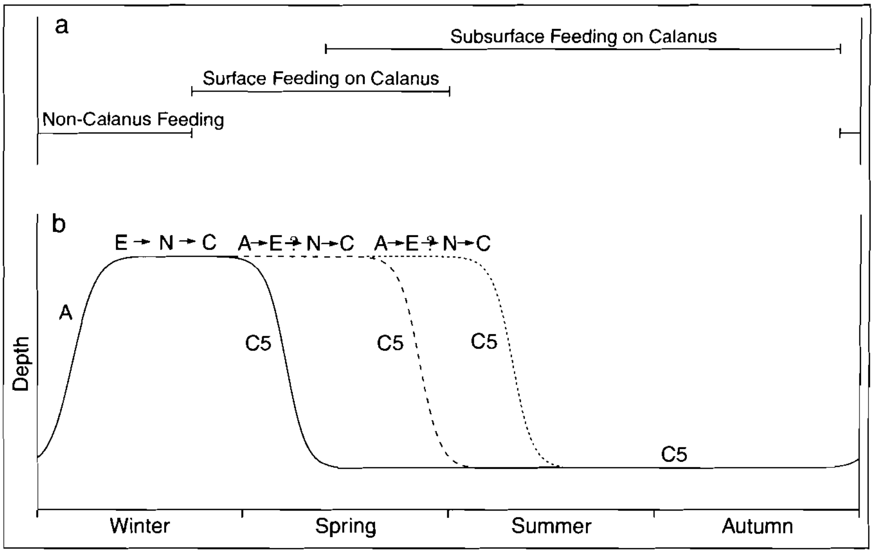

Figure 5.6. Conceptual relationship between right whale feeding and the life history of *Calanus finmarchicus*. (a) Timeline indicating periods when right whales feed on zooplankton other than *C. finmarchicus*, on *C. finmarchicus* near the surface, and on *C. finmarchicus* at depth. (b) Idealized depth distribution of *C. finmarchicus* indicating emergence from diapause, migration to the surface by adults (A), and progression of three generations (solid, dashed, and dotted lines) from eggs (E) to nauplii (N) to copepodites (C). After reaching stage 5 (C5), copepods either remain at the surface to molt into adults and spawn the next generation or they migrate downward and initiate diapause. By late summer and autumn, the entire population of *C. finmarchicus* is at stage C5 and is in diapause deep in the water column.

waters and deep waters spans the time when right whales visit the Great South Channel during April–June. Both surface and subsurface feeding have been observed in the Great South Channel, likely in response to the availability of active *C. finmarchicus* in the upper water column and diapausing *C. finmarchicus* deep in the water column.

Behavioral Implications of Prey Aggregation

At first glance, right whale foraging behavior appears to be profoundly boring when compared to that of the charismatic humpback whale. The humpback has a vast array of behaviors on which it can draw, including bubble-net, flick, lobtail, and cooperative feeding (Hain et al. 1982). Humpback whales use this repertoire primarily for the difficult task of organizing highly mobile prey into mouth-sized aggregations. In contrast, the right whale simply opens its mouth and swims forward, and there is no evidence to suggest that they actively organize zooplankton into exploitable aggregations. Instead, right whales rely wholly on the environment to organize their prey into aggregations suitable for feeding.

To appreciate these differences in feeding behavior, consider a humpback whale that encounters 200 1-kg fish distributed evenly throughout the water column. The humpback can employ a bubble net to corral these fish, push them to the surface, and engulf all of them. If a right whale encounters 200 million 1-mg copepods (200 kg of copepods) distributed evenly throughout the water column, it has no means to aggregate these prey and cannot consume them. The right whale must move on to another location where the environment has organized copepods into a vertically compressed, highly concentrated aggregation. When and where the environment produces these aggregations, they are likely to be pancake-shaped layers that are hundreds of meters wide but only tens of centimeters to a few meters thick. Right whales have no need for elaborate feeding behaviors that are designed to aggregate prey; an "open your mouth and drive" approach is sufficient for feeding on these compact zooplankton layers. This lack of exciting feeding behaviors, however, leads to much more intriguing questions. How does oceanography organize copepods into exploitable aggregations? And how do right whales find them?

Zooplankton Aggregation

Zooplankton are ubiquitous, yet zooplankton concentrations throughout most of the ocean are far too low for right whales to feed profitably. In particular areas, however, a variety of oceanographic processes operating at different spatial and temporal scales can lead to the formation of highly concentrated zooplankton patches. The right whales' survival depends on these oceanographic processes; therefore, it is vital to understand how these processes work.

Many studies have implicated ocean fronts in aggregating prey for top predators. Just as a weather front marks the location where two air masses abut in the atmosphere, ocean fronts demarcate the location where two water masses meet in the ocean. Prey can aggregate at these fronts through interactions between the organisms' vertical swimming behavior and the circulation at the front (Franks 1992). Although fronts provide a plausible mechanism for aggregating zooplankton, the extent to which right whales rely on them for feeding is unclear. Wishner et al. (1995) reported that late-stage *C. finmarchicus* aggregations in the Great South Channel were associated with a fresh water river-runoff plume and suggested that the front separating the river runoff water from the more salty oceanic water may have been responsible for aggregating *C. finmarchicus.* Epstein and Beardsley (2001) studied the structure of this same front and concluded that *C. finmarchicus* likely accumulated there because the copepods, in an effort to maintain a preferred depth, swam upward against the currents moving downward and away from the front. However, Beardsley et al. (1996) sampled intensively near a feeding right whale tagged with a radio transmitter in this area and found no evidence to suggest that a convergent ocean front was responsible for aggregating the copepods on which the whale fed. Right whales do not generally feed in areas with fronts in the Bay of Fundy, yet there is evidence to suggest that right whale occurrence in Roseway Basin on the southwestern Scotian Shelf may be related to the presence of fronts (Baumgartner et al. 2003a).

Aside from ocean fronts, few hypotheses exist to explain the formation of zooplankton aggregations. Yet there must be other mechanisms involved because right whales appear to also feed in areas devoid of fronts. Much work remains to be done to improve the presently poor understanding of the small-scale biological-physical interactions that form and maintain zooplankton aggregations.

Finding Food

Scientists' understanding of the conditions that aggregate zooplankton is exceedingly poor, but right whales must have a very good sense for when and where these aggregations form. But how do they do it? Because experimentation on right whales is not feasible, researchers are left largely with speculation and hypotheses that are difficult to test. Kenney et al. (2001) reviewed many hypotheses about how right whales locate prey over various spatial scales, and the following discussion draws heavily from their work.

At the largest spatial scales (thousands of kilometers), many hypotheses exist to explain right whale navigation during migration or extended excursions. It is likely that most long-distance movements are undertaken to find prey, with the exception of pregnant females migrating to the calving grounds. However, after birth, nursing cows are probably anxious to return to the feeding grounds after fasting during the winter calving season. Much longer trans-Atlantic excursions from the U.S. and Canadian continental shelves to the Labrador Basin, Iceland, and Norway have also been documented (Knowlton et al. 1992; Jacobsen et al. 2004). To navigate over large distances to find either feeding or calving grounds, right whales may rely on their memory, which is informed by topographic landmarks, bathymetric contours, or acoustic sources such as surf or seismic activity. Water masses or ocean currents may similarly act as environmental landmarks for navigation or may directly assist movements. Navigation by the sun has been observed in other taxa, so it is conceivable that right whales use the sun as a compass. A geomagnetic compass may also be available to right whales, as there is evidence of navigation by geomagnetic orientation in a variety of other marine taxa, including sea turtles (Lohmann and Lohmann 1996), and cetaceans (Walker et al. 1992).

At regional spatial scales (tens to hundreds of kilometers), right whales likely rely on learning and memory to locate and choose specific feeding habitats. Right whales preferentially visit habitats frequented by their mothers (Malik et al. 1999; Brown et al. 2001), which suggests that mothers teach calves where to find the best foraging conditions or areas. Mate et al. (1997) documented extensive movements of a tagged female and her accompanying calf throughout the Gulf of Maine and New England shelf and speculated that this mother was showing her calf potential feeding areas. Downstream physical and chemical cues might help right whales locate feeding grounds much the way American eels or Pacific salmon use organic compounds to find river inlets. For example, when returning from the calving grounds off the southeastern United States, right whales may locate the Gulf of Maine by tasting the fresh water plume spilling through the Great South Channel and onto the New England Shelf.

Once right whales locate and occupy a habitat at the regional spatial scale, they are unlikely to remain there long if prey resources are insufficient. Right whales tagged with satellite-monitored transmitters in the lower Bay of Fundy during the summer and early fall left the Bay and ranged widely throughout the Gulf of Maine, western and central Scotian Shelf, New England Shelf, and over the continental slope (Baumgartner and Mate 2005). Of the whales that left the Bay, several returned a few days or weeks later. These observations suggest that right whales are highly mobile and capable of adapting to variability in the regional-scale distribution of prey by visiting many potential feeding areas over a short period of time.

Over spatial scales of several kilometers, right whales probably rely less on long-range navigation abilities and more on their memory and immediate senses. A right whale's goal at this scale is to find super-abundant aggregations of zooplankton. It is difficult to imagine right whales randomly prospecting; instead, they likely have an intimate knowledge of the oceanographic conditions that form and maintain these aggregations. To improve their chances of finding exploitable patches of zooplankton, right whales may first locate the oceanographic features that are responsible for forming the patches, and then search within or near these features. For example, right whales may locate the leading edge of the fresh water plume present in the Great South Channel in the spring by tasting a strong change in salinity. Once the front is located, the whale can prospect back and forth across the front to find copepods that may be aggregated there.

Another possible method to detect prey patches at spatial scales of a few kilometers is cooperation among whales. Right whales are often highly aggregated on their feeding grounds, and in such a small population, it is quite unlikely that this occurs by chance. It is possible that right whales acoustically advertise the presence of abundant food resources (Lowry 1993; Winn et al. 1995), perhaps in an effort to attract other whales and, in particular, a potential mate. However, no evidence of this behavior in right whales has yet been reported.

At very small spatial scales (centimeters to tens of meters), right whales have a number of senses that may help them locate and remain within the highest zooplankton concentrations in an aggregation. Vision may play a significant role for whales that are feeding near the surface during the daytime. Despite having enhanced night vision (as in the bowhead whale; Zhu et al. 2001), vision is probably much less useful for subsurface and nighttime feeding. In the lower Bay of Fundy (a turbid coastal environment), Goodyear (1993) and Baumgartner and Mate (2003) observed whales diving to depths of up to 200 m where very little light penetrates. Kenney et al. (2001) suggested that perhaps the presence of bioluminescent zooplankton within prey aggregations might aid visual detection in the absence of ambient light. Chemical detection of prey might also be possible, but the persistence of this cue might be quite variable because of turbulence and diffusion. At point-blank range, the most reliable sense for directly measuring zooplankton abundance is probably tactile (Kenney et al. 2001). Cetaceans have sensory hairs or vibrissae that are richly enervated and are thus sensitive to deformation (Ling 1977). When zooplankton strike these vibrissae, the resulting bend in the hair may be sensed by the whale. Vibrissae in right whales are located around the mouth (Payne

1976), so they could be used to make fine-scale adjustments to the prey concentration immediately in front of the whale.

It is important to repeat that these hypotheses about sensory modalities are conjectural. Researchers simply do not know how right whales pull off the extraordinary trick of finding food in a vast ocean where most of the environment is unsuitable for feeding. Zooplankton prey resources can vary from year to year and from location to location, so a sophisticated suite of senses and an intimate knowledge of the environment are likely required to survive.

Making a Living on Zooplankton

Right whales need to consume an extraordinary amount of zooplankton virtually every day to survive, but females need even more food to support pregnancy and lactation. If the right whale population is failing to recover, perhaps there just isn't enough food in the ocean anymore to allow for successful reproduction. To determine if food resources are sufficient to sustain right whale population growth, researchers need to answer two seemingly simple questions: (1) how much do right whales need to eat, and (2) how much do right whales actually eat?

How Much Do Right Whales Need to Eat?

Look at the nutrition label printed on the back of just about any food container, and you'll find how much food (or, more accurately, energy) humans need to consume: roughly 2,000 calories per day. Kenney et al. (1986) used estimates for the filtering rate (based on mouth area and swimming speed), filtering efficiency, assimilation efficiency (i.e., how much ingested food is actually used by the body), time spent feeding per day, time spent feeding per year (to account for potential winter fasting), and metabolic rate based on body mass to calculate how much energy right whales need to consume: between 407,000 and 4,140,000 calories per day, which is equivalent to feeding on 0.25–2.6 billion *C. finmarchicus* C5 per day. This feeding rate is between 0.6 and 6.4 percent of right whale body weight per day, which brackets the 1.5–2.0 percent and 4 percent of body weight per day for other cetaceans estimated by Lockyer (1981) and Sergeant (1969), respectively. These calculations neglected the substantial energetic costs of pregnancy and lactation, so the resulting estimates should be considered as requirements for survival only, not reproduction.

The wide range of estimates by Kenney et al. (1986) reflects considerable uncertainties in most of the factors included in their calculations. Perhaps the greatest uncertainty is in the metabolic rate of right whales, which can be accurately measured only in whales that can be physically manipulated using respirometry or isotopic-labeling methods (Costa and Williams 1999). Adult baleen whales cannot be restrained, so direct measurements of metabolic rate are impossible to obtain. Although Kenney et al. (1986) argued that drag from a right whale's baleen might make ram filter feeding very costly in terms of metabolic rate, recent investigations of balaenid filter feeding suggest that a right whale's mouth morphology may reduce this drag (Werth 2004). Another uncertainty in these calculations is the time spent feeding per year. Right whales that visit the calving grounds in the winter do not feed for several months. Females killed in the Long Island fishery, presumably on their northward migration from a fasting period on the calving grounds, were not well nourished and were referred to as "dry skins" by the whalers because of their low oil content (Reeves and Mitchell 1986). However, the distribution, feeding behavior, and energetic needs of the rest of the population during winter are unknown.

How Much Do Right Whales Actually Eat?

Until recently, zooplankton sampling near whales has not matched the fine vertical and horizontal scales at which the whales forage. Prey concentrations exceeding those required by right whales have rarely been observed because typical zooplankton net sampling averages zooplankton abundance over the whole water column (i.e., it averages a dense copepod aggregation contained in a small volume of water with a much larger, empty volume of water). To improve on this sampling problem, Baumgartner and Mate (2003) used an optical plankton counter to measure the abundance of *C. finmarchicus* C5 over fine vertical spatial scales near right whales. They estimated that right whales encountered *C. finmarchicus* C5 concentrations of up to 15,000 copepods per cubic meter and ingested *C. finmarchicus* C5 at a rate of up to 66 million copepods per hour (1.6 billion copepods per day). If this feeding rate were sustainable, right whales could meet their daily metabolic needs in as little as three hours. A bucket sample taken in the Great South Channel near a feeding right whale yielded a late-stage *C. finmarchicus* abundance of 331,000 copepods per cubic meter, from which Beardsley et al. (1996) estimated that the whale was ingesting *C. finmarchicus* at a rate of 1.4 billion copepods per hour! At that rate, it could meet its daily metabolic energy requirement in less than 10 minutes.

Some right whales clearly encounter zooplankton aggregations that allow feeding rates that are sufficient to meet daily metabolic needs if feeding on those aggregations is sustained. However, the persistence of the aggregations (particularly in the face of intense right whale predation) and the frequency with which they are encountered are unknown, so it is unclear if right whales can keep feeding at these rates. Therefore, the instantaneous feeding rates estimated from short-term observations may not accurately estimate daily feeding rates. Over time scales as short as hours or days, right whales probably feed on an irregular boom-and-bust cycle by taking advantage of extremely high concentrations of copepods when they are encountered and then traveling through areas of suboptimal feeding conditions in search of more aggregations.

Is There Enough Food in the Ocean to Sustain Right Whales?

This turns out to be an extraordinarily difficult question because of the spatial scales at which zooplankton aggregate and right whales forage. Imagine assessing how much food is available to people in Florida by randomly sampling locations in the state. Unless you happened to sample a restaurant or a supermarket where most of the food is concentrated, you would grossly underestimate the amount of food available to people. If you followed people around, you would eventually find a restaurant and thereby know that they exist, but you wouldn't know how many restaurants are in the state. Right whale research is at exactly this stage. Long-term monitoring programs rarely detect the high concentrations of zooplankton required by right whales, yet when researchers find whales, they find superabundant zooplankton aggregations. This is almost certainly because the aggregations on which right whales feed are on the order of only a few hundreds of meters to a few kilometers in size.

It is critical to understand the processes that aggregate *C. finmarchicus* if large-scale prey abundance estimates (or proxies such as the North Atlantic Oscillation index; Chapter 15) are to be used to explain variability in right whale population growth. A frequent assumption in studies of right whale population dynamics is that annual *C. finmarchicus* abundance averaged over the Gulf of Maine and Scotian Shelf is proportional to the amount of food available to right whales and that variability in annual right whale birth rates can be directly compared with those large-scale *C. finmarchicus* abundance estimates. Yet, if aggregation mechanisms vary from year to year, then the food available to right whales will not be a function solely of the large-scale average *C. finmarchicus* abundance. A year in which *C. finmarchicus* average abundance is high may turn out to be a poor feeding year for right whales if the physical processes that aggregate *C. finmarchicus* are weak. Conversely, a poor year for *C. finmarchicus* production may mean a good year for right whale feeding if aggregation mechanisms can strongly concentrate the few *C. finmarchicus* available.

For example, both a large-scale *C. finmarchicus* abundance index for the Gulf of Maine and western Scotian Shelf (Greene and Pershing 2004) and in situ net and optical plankton counter sampling over the entire water column in the lower Bay of Fundy (Baumgartner et al. 2003a) suggested that *C. finmarchicus* was more abundant in 2001 than in 2000. However, *C. finmarchicus* sampled in the discrete layers within which right whales were feeding in the lower Bay of Fundy were nearly twice as abundant in 2000 as in 2001 (Baumgartner and Mate 2003). The concentration index (the ratio of peak water column abundance to the average water column abundance) measured near right whales was significantly higher in 2000 than in 2001, indicating that aggregation mechanisms were stronger in 2000 than in 2001. In this case, both the large-scale abundance index and the average water-column abundance of *C. finmarchicus* did not accurately reflect the concentration of prey available to right whales. Caution, therefore, is warranted in attempting to explain trends in right whale reproduction with prey abundances averaged over large spatial and temporal scales.

Feeding and Conservation Efforts

There is considerable interest in developing predictive models of right whale distribution in the conservation and management community (Chapter 16). Imagine a system that could describe where right whales are located at this very moment, or even where right whales will be in a few days or weeks hence. With such a capability, certain areas could be monitored closely, and regulation of human activities within those areas could be more proactive than is currently possible. Because the distribution of right whales throughout most of the year is governed primarily by feeding conditions, predictive models will need to incorporate our growing understanding of the factors that aggregate zooplankton and the whales' feeding response to those aggregations to achieve the accuracies required to effectively manage shipping or fishing activities (kilometers to tens of kilometers).

Fishing gear entanglements pose a serious risk of injury or mortality for right whales (Chapter 13). However, solving this problem has been hindered by a lack of information about where right whales spend their time in the water column and how their diving behavior may interact with fishing gear. Some evidence suggests that copepods in Cape Cod Bay, Bay of Fundy, and Great South Channel can aggregate very close to the sea floor at the same depths where ground lines (ropes connecting traps along the bottom) occur (C. Mayo, S. Kraus, and M. Baumgartner, pers. comm.). If right whales exploit these near-bottom resources, they may be at particular risk of entanglement. A better understanding of right whale diving and foraging behavior, and the environmental conditions that promote the formation of near-bottom copepod aggregations will inform conservation efforts.

Food and feeding also play a role in assessing the outcome of management actions. Without a better understanding of right whale feeding ecology and its relationship to reproduction (Chapter 15), it will be difficult to distinguish between fluctuations in population size that are caused by natural and anthropogenic factors. For example, a decline in calving rates might be the result of human-caused mortalities of reproductively active females or by depressed birth rates resulting from reduced food availability. In assessing the efficacy of management actions to reduce human-caused mortalities, a decline in calving rates might be interpreted as evidence that conservation efforts have failed, when, in fact, the decline is attributable to reduced food resources. In years when environmental conditions favor successful reproduction, management actions could be wrongly credited with increasing calving rates. The outcome of conservation efforts must therefore be evaluated within the context of environmentally induced changes in the population.

Conclusion

Although many other organisms filter feed exclusively on zooplankton in the ocean, only the right and bowhead whales do so to sustain an enormous body mass and a high mammalian metabolic rate. The challenges of eating roughly one billion flea-sized copepods per day are immense, and right whales possess two critical adaptations to meet these challenges: baleen and an extraordinary skill for finding zooplankton aggregations. Zooplankton are weak swimmers and therefore aggregate only where oceanographic conditions allow. Right whales probably use instinct, maternal teaching, memory, environmental cues, their immediate senses, and perhaps even help from conspecifics to find these aggregations from as far as thousands of kilometers to as close as tens of centimeters away. Elaborate feeding behaviors are not required to feed on zooplankton (right whales simply open their mouths and swim forward), but an elaborate feeding apparatus is essential. Right whales have evolved a large head, long baleen plates, fine baleen fringes, and an unusual mouth morphology to maximize both prey intake and filtering efficiency. These remarkable specializations are highly effective in times of zooplankton plenty, but when zooplankton populations decline, right whales are incapable of switching to an alternative food resource. Thus, boom-and-bust cycles in zooplankton abundance will likely affect right whale population dynamics and may ultimately govern the long-term survival of this endangered species.

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Acknowledgments

We are grateful to Regina Campbell-Malone, Marilyn Marx, Michael Moore, and Alex Werth for sharing photos and figures. Thanks also to Alex Werth and Michael Moore for fruitful discussions and Nancy Copley for creating the *Calanus finmarchicus* life history figure. Support for research was provided by the National Marine Fisheries Service, National Science Foundation, Office of Naval Research, National Aeronautics and Space Administration, and the Massachusetts Division of Marine Fisheries.