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ARE CETACEA ECOLOGICALLY IMPORTANT?

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ABSTRACT In undisturbed ecosystems, cetacean biomass is similar to that of other smaller size classes and cetaceans may be useful indicators of ecosystem health and productivity. Cetaceans are important in energy flux within marine and selected freshwater systems, but usually do not affect nutrient cycling to a significant degree. Cetacean carcasses provide important food sources for terrestrial and benthic scavengers. Feeding grey whales disturb local benthic environments on a scale equivalent to major geological forces. Living cetaceans are colonized by a diverse fauna of commensal and parasitic invertebrates. Seabirds and some fishes benefit from feeding associations with cetaceans. Cetacean sounds are prominent in the ocean and could be useful as cues to other animals. Fishes and invertebrates do not show noticeable adaptations to cetacean predators, but cetaceans themselves display defensive adaptations against killer whales. Whaling has altered ecosystem structure in Antarctica and perhaps other places, and the whaling industry caused profound ecological effects, especially on some oceanic islands. Cetacean entanglement in fishing gear can harm local fisheries, but there is no concrete evidence that they harm fisheries in other ways. In some cases they may benefit fishermen by removing species that could compete for commercially harvestable fish.

INTRODUCTION

Whales and dolphins live and feed in almost every part of the marine environment including the great rivers and their estuaries (Platanistidae), continental shelves (Mysticeti, Phocoenidae), deep ocean canyons (Physeteridae, Ziphiidae), tropical oceans (Delphinidae), and even amidst ice in the Arctic (Monodontidae, Balaenidae) or Antarctic (Mysticeti, Orcininae). Cetaceans clearly interact with many different organisms and marine systems (Ray, 1981; Viale, 1985). In this paper we review evidence and hypotheses as to whether any of these interactions are sufficiently significant or special to have important bearing on the normal operation of ecosystems or on the evolution or population dynamics of particular species.

Motivation for this review originally came from the conservation movement, whose laudable efforts to preserve whales left unanswered the question whether the animals are functionally 'important' in marine systems. In our presentation of an early draft of this discussion at the Conference on "Non-Consumptive Uses of Cetaceans" (Boston, June 1983) we phrased the question simplistically, asking whether the extinction of all cetaceans would create any noticeable difference in ecosystem function. Published results of recent investigations on cetacean biology and marine productivity have stimulated a more extensive review. For the purposes of this paper we consider certain interactions to be relatively unimportant. Mere lists of the prey species consumed by various cetaceans will not be given here. Readers are referred to Gaskin (1982) and Ray (1981) who classify cetaceans on the basis of food habits and social organization.

We recognize that the discussion below may do little more than suggest fruitful paths of further inquiry. More definitive conclusions are unlikely to appear soon because we are dealing with the intersection of three inexact sciences: cetacean biology, marine ecology, and fisheries biology. Knowledge of the first accumulates slowly, as our necessarily indirect methods reveal little of what the whales do underwater. Knowledge of the other two is bedevilled by their sheer complexity and dynamic nature. As noted by Kesteven (1972): "In its inability to predict, fisheries biology sits sadly and squarely beside ecology."

Donovan (1985) described two extreme types of cetologist who attend meetings of the Scientific Committee of the International Whaling Commission. They would have very different reactions to the question: "Are cetaceans ecologically important?" An exemplary preservationist might claim that all species present in an ecosystem are important for its proper and natural functioning. Often implicit in this view are the ideas that ecosystems are stable, self-correcting, and that species are all "optimally adapted" to each other when present in an undisturbed state (Goldsmith et al., 1972). On the other hand, a scientist with links to the whaling industry might take the utilitarian view that animals, like cetaceans, at the top of a food web can be heavily exploited with little or no effect on the entire ecosystem, except possibly increasing the availability of lower-level species, such as commercial fish, for harvesting. A central theme of this paper is that both positions are incomplete.

SIGNIFICANCE AT ECOSYSTEM LEVEL

BIOMASS

Despite being many times less numerous than most other sea creatures, cetaceans are large enough for their biomass to be significant on an ocean-wide scale. Sheldon, Prakash & Sutcliffe (1972) have argued that in ecologically stable ocean areas the standing stock is constant (within a factor of about 1.5) for organisms at all logarithmically equivalent size ranges, from phytoplankton to whales. Recent, more detailed, studies in the euphotic layer of the North Pacific Central Gyre indicated that the particle size spectrum of planktonic organisms is not as flat as Sheldon et al. (1972) supposed (Rodriguez & Mullin, 1986). Nevertheless, given the enormous variation in particle size, it is still remarkably level. Thus, in terms of biomass, the large whales appear to be as significant as any other set of marine organisms of a particular size class. The only other animals in this top class, a few large fish and squid, seem to be dominated in terms of standing stock by the whales.

Sheldon et al.'s (1972) rule of "constant biomass at all size ranges" means that, given that animals the size of whales can physiologically exist, their presence and approximate biomass could be predicted from a knowledge of the gross attributes of the marine system. Sheldon & Kerr (1972) have used a similar argument to estimate the population of monsters in Loch Ness, Scotland. Another consequence of the constant biomass rule is that, on a very broad ecological scale, all organisms in the pelagic system are in a very similar situation, sandwiched between comparable biomasses of larger and smaller organisms, often their predators and prey respectively; exceptions are the very small and very large: the phytoplankton and the whales. What is the significance of the cetaceans' special position?

There have been some theoretical investigations of energy flux between different size classes of organisms in pelagic ecosystems, culminating in Silvert & Platt's (1980) dynamic energy flow model. Unfortunately, this work has not given much consideration to the upper size bounds of the system, instead being concerned with its internal workings. At the least, we can say that if the whales did not occupy the upper class in the ocean another set of organisms would, but the implications of being the largest organisms in the ecosystem must await further investigation.

PRODUCTIVITY

Natural systems are more frequently valued by their productivity than their biomass, and here the whales' position is less prominent. Fenchel (1974) showed that productivity decreases at roughly the −0.275 power of body size. According to the relationships he derived, populations of homeotherms of the size of dolphins (100 kg) should have intrinsic rates of population increase of about 0.60 per year, and those the size of the large whales (100 000 kg) about 0.09 per year. Intrinsic rates of increase have rarely been accurately determined for cetaceans, but seem to be generally in the range of 0.02–0.08 per year (e.g. Perrin & Reilly, 1984; Reilly & Barlow, 1986). Thus, while the large whales have roughly the productivity levels suggested by Fenchel (1974), the smaller cetaceans are less productive than many similar sized terrestrial animals. On a broader scale, it is clear that the biomass of the whales is considerably less productive than similar biomasses of smaller organisms.

ECOSYSTEM DYNAMICS

The significance of particular sets of organisms in the dynamics of ecosystems is generally hard to determine (Ray, 1981), and cetaceans are no exception. Preliminary investigations, however, suggest that they are important. Kanwisher & Ridgway (1983) postulate that the cetaceans as a whole, and possibly the sperm whales (*Physeter macrocephalus*) alone, consume a greater quantity of prey than the entire world fishery. Several recent studies confirm that energy flow through the cetacean component of marine systems may indeed be potentially extremely important in particular situations.

Census counts obtained by aerial surveys indicated that 18 species of cetaceans comprising an estimated biomass of about 25 000 metric tons probably ate at least 46 000 and perhaps as much as 460 000 metric tons of prey annually in Georges Bank waters between 1979–1982 (Winn, Hain, Hyman & Scott, 1987). According to these authors, the average biomass of squid and fish on Georges Bank during those years was about 1 500 000 metric tons, and commercial fishermen took 112 000 to 250 000 metric tons. Hain, Hyman, Kenney & Winn (1985) made similar calculations, and came to similar conclusions, when considering the larger area of the shelf off the northeastern United States.

Viale (1985) estimated that the cetaceans in the northwestern Mediterranean eat about 229 000 tons of squid per year, about 2.3 times the predation by the "very teuthophagous" population of humans in the same area. In the Southern Ocean, Laws (1977b) estimated that before commercial whaling the baleen whales took about 190 million metric tons of krill (*Euphausia superba*) per year, about three times the total world catch of all species by marine fishermen (Kanwisher & Ridgway, 1983).

We look forward to future investigations that will evaluate the significance of predation by freshwater dolphins (Platanistidae), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) or other species that may have particularly important effects on their local environments where they are the only large predator.

If cetaceans are indeed significant elements in ecosystems, what are the effects of rapid changes in their biomass? Silvert & Platt (1980) have shown that under certain reasonable circumstances a sudden influx of biomass at small particle sizes, such as a phytoplankton bloom, can induce oscillations in the standing stock of larger organisms, which may take a long time to die out. Although simulations have not been performed, it is possible that sudden changes in the biomass of larger organisms might induce similar instability in other parts of the system. W. Silvert (pers. comm.) has suggested that if the baleen whales migrate to warmer waters for reasons unconnected with variations in the biomass of their prey, such as in response to temperature changes or their breeding cycle, then the sudden departure of their predatory biomass might induce instability at lower trophic levels. The depletion of baleen whales by twentieth-century whaling is less likely to have had such a destabilizing effect, because, although the reduction of standing stock was very rapid on the whales' own time scale, their prey have much shorter life cycles, and probably were able to adapt to the changing predation rate.

Evidence is accruing that marine ecosystems are not especially stable. For instance, capelin (*Mallotus villosus*), which live approximately four years and are a kingpin of the northwestern Atlantic pelagic ecosystem, show ten-fold variations in annual year-class strength (Carscadden, 1984). Thus, the many species which prey upon capelin have an exceedingly uncertain food source. What might be the effects of extremely long-lived top predators, like cetaceans, in such unstable systems? Much will depend on whether they react to scarcity of their primary prey by migration, fasting or switching to another food source. If they take none of these actions and continue to feed on the remnant primary prey, then, compared with more "*r*-selected" predators like squid, they will be less able to adapt to changes in the prey populations, and thus may tend to amplify "natural" troughs in abundance. S. Murawski (pers.

comm.) has suggested that, on Georges Bank, continued predation by finback whales (*Balaenoptera physalus*) upon young herring (*Clupea harengus*) following catastrophic overfishing during the 1960s and early 1970s may have pushed the fish to virtual extinction.

Ray (1981) classifies marine mammals on the degree to which they are obligate specialists in feeding, the degree to which they are *K*-selected, and the maturity of the ecosystems that they inhabit. He suggests that relatively obligate, *K*-selected species, inhabiting mature ecosystems, like blue whales (*Balaenoptera musculus*), are likely to have the greatest effect in structuring their ecosystems. On the other hand, more *r*-selected animals will probably have smaller effects. Many would, however, balk at calling any marine mammal *r*-selected, and recent theoretical research suggests that *r*- and *K*-selection should be viewed as a dichotomy rather than a continuum (Strebel, 1985).

BALEEN WHALES IN THE ANTARCTIC PELAGIC ECOSYSTEM

Large-scale removal of whales by hunting has provided a complementary perspective on their normal importance in marine systems. Few places in today's oceans are inhabited by original numbers of cetaceans, but nowhere have populations been so heavily impacted by whale hunting as in the Antarctic. In 1900, before the start of commercial whaling, baleen whales were almost certainly the major vertebrate group in the Southern Ocean both in terms of their biomass and effect on the Antarctic ecosystem (Laws, 1977a,b, 1985). Hunting during the twentieth century probably reduced their biomass by a factor of ten. Some conception of the importance of cetaceans in the Antarctic ecosystem can come from looking at the effects of this unparalleled over-exploitation.

Laws (1985) reviews the evidence for changes in the biomass of other Antarctic organisms. Populations of Antarctic seals and birds increased by approximately a factor of three following the destruction of the stocks of the large rorquals and sperm whales during the years 1904–1973. Evidence has also accumulated that some of the life history characteristics of the seals and whales changed in response to the decreased whale populations; pregnancy rates may have increased and age of sexual maturity may have decreased. These effects are not universally accepted; for example, Gaskin (1982) regards evidence for increase of Antarctic birds and seals as tenuous, and Mizroch & York (1984) argue that whale pregnancy rate increases are artifactual. Nevertheless, Laws (1977a, 1985) suggests that the entire "surplus" krill biomass released by the decimated whale populations may now have been taken up by other consumers, and concludes that the trophodynamics of the Antarctic marine ecosystem may have been altered so drastically that restoration of the putative original status might not be possible even with human management.

SURPLUS YIELD

The Antarctic experience has spawned a second generation 'experiment': harvesting of the presumed 150 million tons of surplus krill not being eaten by the vanished rorquals. Whether that surplus krill exists; whether it could be captured and utilized by humans; and what the effects might be, are subjects of modelling and debate (Roberts, 1977; May et al., 1979; Beddington & de la Mare, 1985; Laws, 1985).

The concept of surplus yield was recently put to the test in the northwestern Atlantic, where the quotas for the capelin fishery in the 1970s were based largely on Winters' (1975) estimate of the surplus yield of capelin left by the reduced stocks of whales, seabirds, seals, and cod (*Gadus morhua*). The fishery soon collapsed, but whether this was due to incorrect theory, unreliable assumptions, or other factors, is disputed (Brown & Nettleship, 1984; Carscadden, 1984).

Another challenge to surplus yield comes from historical records. Fish stocks generally appear to have been larger in the days before extensive commercial whaling, suggesting that depleted whale stocks are not a prerequisite for healthy fish populations.

RESOURCE PARTITIONING

Fishermen in many parts of the world see cetaceans as competitors for the resources on which they depend. Gaskin (1982) lists several examples of suspected competition including: the kill of dolphins by Japanese fishermen to release fish stocks for commercial harvest; the supposed consumption of capelin by finback and humpback (*Megaptera novăeangliae*) whales off eastern Canada; the dynamics of the krill population in the Antarctic; and the former bounty on beluga whales in the Gulf of St Lawrence. Calculations, such as those referred to in previous sections, suggest that cetaceans have a major trophic rôle in some marine systems which are commercially important to man, although Lavigne et al. (1986) show that cetacean metabolism, and therefore food consumption, has usually been over-estimated. But do man and cetacean compete? Are whales and dolphins indirectly taking dollars and jobs from fishermen?

Except in cases where dolphins actually steal fish from nets or whales blunder through them, there is no concrete evidence that cetaceans harm fisheries (Beverton, 1985). Similarly, except where cetaceans are themselves the target of fisheries, or are incidentally taken by them, there is no direct evidence that fisheries harm cetaceans (Beverton, 1985). The dynamics of marine systems are so complex that it is unlikely that evidence for either of these interactions will be found in the near future even if they exist (Bowen, 1985).

Interactions need not be harmful to one party. There are several ways in which cetaceans could be helping, rather than competing with, commercial fisheries. One particularly intriguing situation is discussed by Northridge (1982). He points out that the sperm whales in the North Pacific eat large quantities of squid, which is generally unexploited, and in the short term unexploitable, by man. In fact the sperm whales consume several times the tonnage of all the fisheries in the same area. The squid themselves eat commercially exploited species. The presence of the sperm whales may then lower the squid populations, and release more fish for commercial exploitation.

NUTRIENT CYCLING

Some of the most interesting speculation about the ecological significance of cetaceans concerns their possible rôle in promoting nutrient cycling. Kanwisher & Ridgway (1983) speculated that the faeces of some species of cetaceans, perhaps especially the sperm whale on account of its numbers, size, and deep-diving habits, may play an important part in promoting nutrient cycling if the whales eat at depth and then defaecate in the euphotic zone. Cetaceans are seen to defaecate and urinate at the surface, and there are physiological reasons for thinking that they may generally do so (Kooyman, Castellini & Davis, 1981).

In a steady state, with no lateral transference of nutrients, whales, or their prey and with no temporal changes in the trophic system, the importance (I) of whale faeces in the recycling of a particular nutrient Y can be given by:

$$I = \frac{\text{rate at which Y is excreted by whales per unit area}}{\text{rate at which Y is assimilated in primary production per unit area}}$$

But whales cannot excrete at a rate faster than the production of their food. Therefore:

$$I < \frac{\text{proportion of Y in food of whale} \times \text{productivity of food of whale}}{\text{proportion of Y in phytoplankton} \times \text{productivity of phytoplankton}}$$

$$= \frac{\text{proportion of Y in food of whale}}{\text{proportion of Y in phytoplankton}} \times E^t$$

where E is the ecological efficiency (Odum, 1971), and t is the number of trophic levels between the phytoplankton and the food of the whales. E is probably less than 0.2 and, for sperm whales, t is usually greater than 2—that is they usually eat at trophic level 3 or higher (Northridge, 1982). Therefore, E^t is less than 0.04, and unless a particular nutrient is especially concentrated in the whale's food, I cannot be greater than a few per cent. The concentration of nitrogen in oceanic squid is very approximately twice that in phytoplankton (Weyl, 1970; Clarke, Clarke, Holmes & Waters, 1985), so that, in a steady state, with no lateral transfer of nutrients or temporal variation, sperm whale faeces cannot provide more than about 8% of the nitrogen used in primary production. Generally the figure will be much less than this.

In order to examine the significance of sperm whale faeces as a medium for recycling nitrogen nutrients, we used data from the waters off the Galapagos Islands, Ecuador. The sperm whale density west of the islands of Isabela and Fernandina was estimated to be 0.015 whales·sq. km^{-1} in March 1985 (Whitehead, 1986). The whales were often seen to defaecate at the surface. Using Best's (1979) estimates for the food consumption of a sperm whale as 420 kg squid·day^{-1}, and Clarke et al.'s (1985) measurements of the nitrogen content of oceanic squid, we estimate that these sperm whales were ingesting nitrogen at a rate of 7.6×10^{-5} g N·m^{-2}·day^{-1}. This is a maximum for the rate at which they could excrete nitrogen. It is also only about 0.04% of the nitrogen content of the primary production west of the Galapagos (Weyl, 1970; Cowles, Barber & Guillen, 1977).

In special circumstances the nutrient cycling promoted by whale defaecations may, however, be important. For instance, if squid concentrate for breeding or other purposes in relatively nutrient-poor waters, then the whales that feed on them could induce considerable nutrient cycling through their faeces. Similarly, nutrients returned to the surface through faeces might allow the extension of a transitory phytoplankton bloom, or produce a secondary, smaller bloom some time after a major burst of productivity.

Sinking of the carcasses of cetaceans represents significant downward transport of nutrients, and probably provides occasional, but significant, windfalls for local populations of benthic scavengers. Jannasch (1978) includes a photograph of the half-eaten remains of a porpoise obtained from the research submersible ALVIN, but the overall magnitude of such events has not yet been estimated. A horizontal version of this form of nutrient cycling has been proposed by W. de la Mare (pers. comm.). The baleen whales do most of their feeding in cold, productive waters, but spend a considerable proportion of the year in nutrient-poor areas where they sometimes die. If these deaths occur over small barren areas substantial nutrient enrichment could result. This may be the case with the humpback whales which during winter form impressive concentrations with a substantial biomass in shallow, nutrient-poor areas, such as Silver Bank in the West Indies (Whitehead & Moore, 1982).

CO-EVOLUTION OF PREDATOR AND PREY

There is little question that terrestrial predators have shaped the morphology and behaviour of their prey. Who could doubt that gazelles (*Gazella* spp.), for example, would have evolved their wariness, speed and stamina without the selective pressure of cheetahs (*Acinonyx jubatus*), leopards (*Felis paradus*), hyenas (Hyenaenidae), lions (*Panthera leo*), and hunting dogs (*Lycaon pictus*) operating over evolutionary time?

Have cetaceans forced analogous adaptations in their prey? Answers are rarely simple in marine systems. Large, swift predators were chasing their prey long before cetaceans evolved. Included among them were various sharks, billfish such as swordfish (*Xiphias gladius*), marlin (*Makaira* and *Tetrapturus* spp.), sailfish (*Isiophorus* spp.), and the tunas (Scombroidea). Prey species probably evolved speed, streamlining, countershading, and schooling responses as defences against those pre-cetacean predators, and it seems likely that they would not grow slow and fat if the cetaceans suddenly disappeared.

Odontocete cetaceans, seem, however, to have brought a new hunting technique to the oceans—sonar. Although predation by groups of mackerel (*Scomber scombrus*) or echelon swimming of tunas may be interpreted as rudimentary co-operation, cetaceans have also refined hunting co-operation to a new marine peak (Conner & Norris, 1982).

Similarly, although basking sharks (*Cetorhinus maximus*) and whale sharks (*Rhincodon typhus*) filter-feed, the baleen whales have significantly increased the size-range of prey organisms that are subject to this kind of predation. For example, humpback and finback whales catch fast-moving schools of relatively large fish, such as mackerel and herring, which are otherwise only threatened by predators on individual animals.

Have these techniques shaped the behaviour of some prey species? One searches in vain to find a marine analogue to the anti-sonar defence used by noctuid moths to protect themselves from bats (Roeder, 1965). In view of the moths' achievements it is surprising that fish do not even come close to detecting sound frequencies used in most odontocete sonar (Hawkins, 1973; Popper, 1981). Prey species could perhaps hear the approach of a species such as the orca or killer whale (*Orcinus orca*), that uses lower frequency sonar pulses (Schevill & Watkins, 1966), but it appears that detection of higher frequencies had to await the evolution of an inner ear. No current information suggests that marine prey have any special defences against detection by echo-location or co-operative hunting.

Mysticetes, too, appear to have overwhelmed prey defences. Individual baitfish or krill theoretically minimize conventional predation, from sources such as seabirds or larger fishes, by forming tight schools (Brock & Riffenburgh, 1960). In contrast, when attacked by bulk-feeders like the whales, individuals would do better to scatter. There is some evidence that capelin schools may disperse when attacked by humpback and finback whales (Whitehead, 1981). Observations of whales feeding on dense fish schools are, however, so commonplace as to suggest that the fish do not always adopt this behaviour. The Mysticetes probably use the schooling response to their own advantage as they round up and engulf concentrated shoals of prey.

Apparent mutualism or commensalism between dolphins and baleen whales may at times prevent fishes from escaping engulfment by the whales. In Nova Scotian waters we observed white-sided dolphins (*Lagenorhynchus acutus*) herding herring (*Clupea harengus*, length about 25 cm) into balls (surface diameter 5 to 10 m) so dense that we scooped up 30 fish in a single dip of a five-gallon bucket. Humpback whales gently manoeuvered to eat these schools, after which the dolphins quickly circled the fishes to herd them close together again. The sequence was repeated at least ten times during the 1.5-h observation period. The fish schools appeared to offer a surfeit of food for the dolphins, and we consider it possible that the dolphins were playing and/or herding for the benefit of the whales. The whales could not easily have found schools of fish as closely packed as those the dolphins provided. We could not identify any immediate mutualistic benefit for the dolphins, although they swam with the whales throughout the observation period.

One curious example of possible adaptation by prey to odontocete hunting was recently proposed by Moynihan (1985). Moynihan cited Norris & Mohl's (1983) hypothesis that Odontocetes might be able to disorientate, stun or kill fishes using focused high-energy sonar pulses, then went on to explain deafness in coleoid cephalopods (squids, octopuses, and cuttlefish) as adaptation to odontocete attacks, arguing that the hearing apparatus would be severely damaged by such high-intensity sounds. This logic seems tenuous to us, and Taylor (1986) suggests that a phylogenetic explanation of coleoid deafness might be more reasonable.

The apparent general lack of prey defences to cetacean predation contrasts sharply with the defences that cetaceans have evolved against one of their own top predators, the killer whale or orca. Grey whales (*Eschrichtius robustus*) avoid orcas by swimming inshore to kelp beds and exhaling underwater (Cummings & Thompson, 1971); playback of recorded sounds of orcas have been used to drive belugas from salmon rivers (Fish & Vania, 1971).

Orca predation may have helped to select for a strong mother to calf bond in several large whale species that probably have few other predators.

There are a few cases in which we can hypothesize that cetaceans may have considerably affected the natural history of their prey. Has cetacean predation driven the large squid from the surface waters into the meso- and benthopelagic zones? Are oceanic dolphins partly responsible for the aerial skills of flying fish (Exocoetidae)? Or, has orca predation been a selective force in the evolution of the morphology or behaviour of penguins (Spheniscidae)? For now, these are speculations and, in general, we conclude that there is surprisingly little evidence that other animals in the ocean would appear or act differently had the cetaceans never evolved.

MUTUALISTIC AND COMMENSAL RELATIONSHIPS

Animals of several other groups form close associations with cetaceans. These may be mutualistic or commensal.

Evans (1982) reviewed a variety of associations between seabirds and cetaceans. Seabirds often follow dolphins or whales to feed on prey driven to the surface by the cetaceans. Both predators could benefit, as the birds may force fish back down to the cetaceans, or the cetaceans concentrate prey at the surface to the benefit of the seabirds. The behavioural interactions can be complex. As an example, we observed numerous repetitions of the following sequence while observing a humpback whale for several hours near Mount Desert Rock, Maine, on 13 August 1987. The whale exhaled underwater, creating a 10-m diameter patch of ascending bubbles. Krill (*Meganyctiphanes norvegica*) rose to the surface during the next 30 seconds, colouring the surface pink. During the following 30 seconds herring (*Clupea harengus*) appeared at the surface jumping so energetically in pursuit of krill that their splashing sounded like a heavy rainstorm. Herring gulls (*Larus argentatus*) and greater black-backed gulls (*L. marinus*) gathered and snatched herring. Apparently in response to the marauding fishes, the krill pressed together into tight, discrete schools up to two metres in diameter. The whale then surfaced, open-mouthed, to engulf krill from these tight schools, which were so thick that our dip net was packed full in one pass. It should be noted that seabirds form such associations not only with cetaceans, but also with schools of predatory fish, such as mackerel. The commensal relationship between seabirds and bottom-feeding grey whales, on the other hand, is unique. From their aerial vantage point, pelagic seabirds such as kittiwakes and various alcids can spot surfacing grey whales and can forage for benthic amphipods and other invertebrates in the plume of sediment which trails from the whale's baleen. Quantitative studies of the significance of grey whale plumes to seabirds in the Bering Sea region are being carried out by G. H. Hunt Jr. of the University of California at Irvine (pers. comm.). Similarly, Harris (1973) found beaks from mesopelagic squid in the faeces of the waved albatross (*Diomedea irrorata*) in the Galapagos, but albatrosses cannot dive to the depths where the squid live. Clarke & Trillmich (1980) have suggested that this may be due to sperm whales regurgitating these squid at the surface where they are then eaten by the albatrosses. Seabirds take part in another interesting, but less important, parasitic or commensal relationship with whales on some occasions when they scavenge sloughing skin or parasites from the whales' bodies (Thomas, 1985). Evans (1982) summarized our knowledge of the seabird-cetacean relationship: "It is not possible to say which derives benefit from the association, but on theoretical grounds it is most likely to be the seabird."

Tuna schools of several species, but particularly yellowfin tuna (*Thunnus albacares*), frequently form mixed-species aggregations with spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*) and sometimes common dolphins (*Delphinus delphis*) (Perrin, 1968). It is possible that the tuna are taking advantage of the cetaceans' increased ability to find food using echolocation. Studies of stomach contents show some dietary overlap, but also some differences in prey type (Perrin, Warner, Fiscus & Holts, 1973). Whether the dolphins normally gain any advantage from the relationship is not known. They have suffered from it since the mid-1960s when fishermen in the Pacific began setting purse seines around dolphin schools in order to catch the tuna (Perrin, 1968), a practice that has cost millions of dolphins their lives. Small yellowfin tuna have also been photographed swimming with a humpback whale (D. Glockner-Ferrari, pers. comm.). In this case, and possibly with the dolphins as well, the tuna can gain some protection against sharks or can benefit from visual orientation provided by their large swimming companions.

It is possible that communities of small fishes may at times gather beneath large whales as they often do under floating logs or other large objects, including sharks (Hunter & Mitchell, 1968). These authors suspected that floating objects function as a "schooling companion" or a "visual stimulus in an optical void". For such fishes a whale, a floating plank or a patch of *Sargassum* might be functionally equivalent. Perrin (1968) noted that fishes sometimes school under dead whales.

Of the eight known species of remoras (family Echeneididae), the whalesucker (*Remilegia australis*) is the only one to make extensive use of cetaceans, particularly blue whales (*Balaenoptera musculus*), according to Alling (1985). The relationship is at least commensal, with the remora possibly gaining transportation, protection from predators, a surface for meeting of males and females, and energy subsidy for respiration by taking advantage of increased water flow past the gills. In addition, Alling (1985) discusses the possibility that whale-suckers may supplement their diet by eating parasitic copepods or whale lice from the body surface, palate and baleen, in which case the relationship would be classified as facultatively mutualistic.

Finally, mention should be made of the parasites living on, or inside, the cetaceans. For some, cetaceans are only one of several possible hosts. Others, such as species of whale lice (Order Amphipoda, family Cyamidae), may be totally dependent on particular cetacean species (Leung, 1976). This class of interaction contains many relationships of great zoological interest (see Rowntree, 1983, for example), but their overall ecological significance must be considered very limited. Cetaceans, including pilot whales (*Globicephala melaena*), sperm whales, and others act as intermediate hosts for the nematode (*Anisakis* sp.), whose larvae infect northern Atlantic herring, cod, and other commercial fish (Platt, 1975) causing some financial loss and a small health threat.

PHYSICAL CHANGE OF THE ENVIRONMENT

Although it is unlikely that most cetaceans actually change the physical structure of their environment, grey whales apparently do so while suction-feeding for benthic infauna, their normal mode of feeding in the Bering Sea. Grey whales sucking up sediment while foraging for tube-building amphipods leave the bottom pock-marked with depressions up to 3 m long. Nerini (1984) estimated that grey whales annually turn over between 9 and 27% of the benthos of the northern Bering Sea, thereby creating a mosaic of clearings that help to maintain early colonizing species in higher abundance than would otherwise be the case. Even though the adult amphipods (*Ampelisca macrocephala*), which are normally the dominant benthic species and the primary food item of the grey whales, are not common in depressions, their larvae may require such cleared areas for settling. This system of cropping, and ploughing, albeit unconscious, bears some resemblance to human farming. Nelson & Johnson (1987) used side-scan sonar to estimate that grey whale feeding depressions cumulatively disturbed approximately 1200 sq km of Bering Sea bottom, resuspending at least 172 million metric tons of sediment per year, approximately three times the amount of suspended sediment discharged annually by the Yukon River into the northeastern Bering Sea. Prevailing northerly currents would tend to carry displaced clay and fine silt northward into the Chuckchi Sea, so the whales' activities probably remove accumulated mud, perhaps enhancing the ability of the feeding ground to maintain healthy amphipod populations.

Cetaceans have considerable effect on other aspects of the marine environment, for example sound. In almost any highly productive area the sounds of cetaceans are very prominent through a hydrophone. Sounds of different species are distinctive, as are the sounds emitted by a species engaged in different forms of behaviour (Herman & Tavolga, 1980). Sounds are excellent long-distance signals in the ocean, and convey considerable information about the marine environment. Cetacean "hot-spots", centred on oceanographic features (Leatherwood & Reeves, 1978), would be particularly prominent acoustically. It is possible that other marine animals can orientate to cetacean sounds, much as migrating birds have been postulated to use frog choruses and other terrestrial sounds for navigation (Griffin & Hopkins, 1974). Scattering, reflection or other acoustic effects could give another animal information about the organisms and environment between itself and a cetacean emitter.

SCAVENGING AND OTHER INDIRECT EFFECTS

Cetacean carcasses, and those of other marine mammals, are important in the diet of some terrestrial predators and scavengers, notably the polar bear (*Ursus maritima*) and Arctic fox (*Alopex lagopus*). Emslie (1986) has suggested that California condors (*Gymnogyps californianus*) survived in coastal regions after the disappearance of the Pleistocene megafauna by eating whale and seal carcasses. Humans have a long history of eating whale and seal carcasses.

Even if their importance in human evolution was not significant, these carcasses may have been particularly important for the survival and cultural evolution of coastal Indians and Inuit.

Transoceanic voyages to hunt whales hastened the spread of western culture through the northern Atlantic and the southern Pacific. On some oceanic islands, predation by whalers (such as that on the Galapagos tortoises, *Geochelone elephantopus*) and the introduction of rats, domestic cats, and other foreign predators, have caused profound ecological effects. The products and capital derived from the whaling industry fuelled the early stages of the industrial revolution that subsequently transformed almost all the world's ecosystems.

CETACEANS AS INDICATOR SPECIES

Cetaceans are extremely mobile. They must feed efficiently, and if small, often. Their distributions are far from regular or random—they are, almost always, where their food is. They are also visible and are thus excellent indicators of the health and nature of the subsurface ecosystem. In the days before spotter airplanes and echo-locating fish-finders, herring fishermen, for example, followed rorqual whales to locate fish schools (Brodie, 1975). The use of dolphin schools to find tuna (Perrin, 1968) has been discussed above (p. 563). Cetaceans are also long-lived top predators, and concentrate pollutants and other trace elements (Gaskin, 1982; Viale, 1978). Study of the tissues of living or dead cetaceans may be of use as pollution indicators.

CONCLUSION

It is possible that there would be no essential change in the nature of the marine environment if cetaceans were removed. It is unlikely that there would be a great alteration in either the primary productivity of the oceans, or the biomass available for commercial harvesting.

Cetaceans do, however, have important rôles in some parts of the system. The major contributors to the largest size class in the ocean, they have a biomass comparable with classes of smaller organisms; they make major changes to some marine environments; they may assist nutrient cycling in unproductive areas; and there are many species in whose lives cetaceans have a more or less important rôle.

Whether cetaceans have a positive or negative effect on fisheries is unclear, and will remain so for some time—there is little evidence either way.

The ecological importance of cetaceans is very difficult to determine, and depends greatly on what we consider important. There is, however, good reason to believe that the cetaceans have a considerable rôle in the ocean as man sees and uses it.

SUMMARY

(1) As the dynamics of ecosystems are extremely difficult to study, and there is no clear consensus about what is important in an ecosystem, the ecological importance of cetaceans cannot be definitively determined.

(2) If undisturbed ecosystems are considered important, cetaceans have value by their presence.

(3) The whales, the major component of the largest size class in the ocean, have a biomass similar to that of organisms in other, smaller, size classes, although their productivity is considerably less.

(4) Cetaceans seem to have important rôles in the energy flux of the oceans. In some cases, sudden changes in cetacean biomass, such as through seasonal migration, may induce instability in the populations of smaller organisms. There is evidence, especially from the Antarctic, that ecosystems have been affected by commercial whaling, but the concept of surplus yield should be used with extreme caution.

(5) There is no concrete evidence for cetaceans harming fisheries, except where they physically interact with the gear. In some cases they may help fishermen by removing species competing for commercially harvestable fish.

(6) In special circumstances, cetaceans, through their faeces or migrations, may contribute to nutrient cycling in the ocean, but this will not normally be the case.

(7) Grey whales disturb the benthic environment to their own advantage on a scale equivalent to major geological forces.

(8) The sounds of cetaceans are very prominent in the ocean and may be used as cues by other animals.

(9) Seabirds, tuna, and other fish probably benefit from feeding associations with cetaceans. Cetacean parasites certainly do.

(10) Fishes and invertebrates do not show marked adaptations to cetacean predators. In contrast, cetaceans themselves display defensive adaptations against orcas (killer whales).

(11) Cetacean carcasses may be significant food sources for some terrestrial animals.

(12) The development of the whaling industry had profound ecological effects especially on some oceanic islands.

(13) Cetaceans may be useful indicators of the health and productivity of the ecosystem.

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