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Cetacean Diet

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Definition

Cetacean diet refers to the types and amount of food taken by whales, dolphins, and porpoises, all of which belong to the mammalian order Cetacea.

Introduction

Cetaceans are typically top predators in marine (and in a few cases riverine) ecosystems, i.e., they are situated at the top of the marine food chain, and they may play an important role regulating the populations of their prey and contributing to the stability of the ecosystem. Cetaceans have few natural predators aside from sharks, although killer whales (*Orcinus orca*) take adults and juveniles of other cetacean species and the bottlenose dolphin (*Tursiops truncatus*) is known to attack and kill (but not eat) smaller cetacean species such as the harbor porpoise (*Phocoena phocoena*). Recent evidence indicates that gray seals also prey on harbor porpoises (e.g., Leopold et al. 2015).

Present-day cetaceans have evolved from an original common design to be able to exploit different kinds of prey. Their morphological adaptations to different diets form the primary basis for the division of the order Cetacea into two sub-orders: the Mysticeti (baleen or *mustached* whales), which feed on small organisms such as zooplankton and small fish, and the Odontoceti (toothed whales, odontocetes), which feed mainly on fish and cephalopods. The mysticete whales are characterized by the presence of baleen plates, made out of keratin, a protein that is also found in other mammals' hair and nails/claws. The baleen plates hang from the upper jaw of the whale and form a filtering mechanism by which it is able to trap shoals of the zooplankton and other small organisms (e.g., krill, copepods, amphipods, and even small fish) that constitute its food. The small size of these prey does not limit the size of the whale, and, in fact, the blue whale (*Balaenoptera musculus*), which belongs to this group of cetaceans, is the largest living animal. In addition to the baleen plates, Mysticeti have enlarged mouths, adapted for the filtering of huge amounts of food. Because of the nature of the filter-feeding process, baleen whales might not be expected to display cooperative hunting. However, some species (notably humpback whales) may cooperate in groups of up to 20 individuals, using *bubble netting* to concentrate prey. One whale in the group dives to locate prey and herds them to the surface,

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releasing air bubbles while spiraling toward the surface. The bubbles form a tubular *net* that *traps* the prey which the whales then take (see, e.g., Wiley et al. 2011).

As their name implies, most odontocetes have teeth, although the number and size vary greatly among species. Their prey ranges from small fish and crustaceans to the giant squid (*Architeuthis* spp.), remains of which have been found in the stomachs of sperm whales (*Physeter macrocephalus*). Those cetaceans feeding on squid (teuthophagous) tend to have fewer teeth or less visible teeth, while those feeding on fish (piscivorous) tend to have long jaws and numerous small teeth. Some odontocetes have developed echolocation, using the echoes returned when their emitted sound hits the target, to aid in the locating of food, and some also display cooperative hunting of prey.

In this brief overview, we draw examples largely from the Northeast Atlantic, but the general principles apply globally.

What Do Cetaceans Eat?

As already mentioned, cetaceans eat a wide range of prey, in terms of both the type and size of animal consumed. Baleen whales typically feed on small crustaceans, but the type depends on the species of whale and also on the area. For example, in the Antarctic, the main prey of rorquals (family Balaenopteridae) (and of many other species) is euphausiids (krill), of which only one species, *Euphausia superba*, makes up the bulk of the diet of all these predators. In other parts of the world, other euphausiid species are consumed by whales (e.g., *Meganyctiphanes norvegica* in the North Atlantic) together with other crustaceans, such as copepods. Small fish are also known to be eaten, notably by minke whales. Rorquals search for shoals of small prey, and, when they find them, the whales are able to expand their furrowed throats letting big volumes of water and prey into their mouths. Once maximum capacity is reached, the whale uses the muscles in the throat to force water out through the baleen plates – which are shorter and broader than those of the other families of baleen whales. The prey are retained by the baleen, and the whale then swallows the millions of small organisms that constitute its diet. Because of the way they feed and where their prey are found, rorquals are moderate to shallow divers and swimmers and show a coastal but also deep-ocean distribution.

Because the copepods and the other organisms on which they feed are relatively immobile, whales of the family Balaenidae are slow swimmers and shallow divers and tend to have a coastal distribution. They have long baleen plates but no furrows in the throat, and they feed by swimming with their mouths open, getting water in but making it pass through the baleen on its way out trapping the prey. Feeding can take place at the surface and in the water column, and when feeding at the surface, this type of feeding is called *skimming* or *skim feeding*. This family includes the right whales (*Eubalaena* spp.), so called because they were the *right whale* to hunt due to the ease with which they could be captured and the fact that they would float after being killed.

Gray whales (*Eschrichtius robustus*) (Eschrichtiidae) have specialized in taking benthic crustaceans such as amphipods and isopods at the seafloor.

Odontocetes have teeth developed to feed on fish and squid. Unlike most terrestrial mammals, these teeth are usually all the same shape (homodont), typically conical or spade-like, although male narwhals (*Monodon monoceros*) normally develop a single tusk (very rarely two tusks) that grows from one of the two teeth the species has retained. There are many species of odontocetes, which range widely in size from less than 2 m in length in the smaller porpoises to over 18 m in the sperm whale. Species feeding mainly on squid tend as a general rule to have fewer or less visible teeth, while those feeding on fish tend to have long jaws and numerous small teeth. It has been hypothesized (MacLeod et al. 2006) that the mode by which an odontocete captures its prey conditions the size of prey it can take, with those species that possess long jaws and many teeth able to capture a wide variety of relatively large prey (for the size of the predator) using their jaws as pincers and employing suction feeding.

Representatives of this group would include many small cetaceans such as the common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), and bottlenose (*Tursiops truncatus*) dolphins and porpoises (e.g., *Phocoena* spp.). Bigger toothed whales such as the killer whale would also belong to this group. The diet of all the smaller species mentioned above has been recorded as being mainly based on fish but with some cephalopods also being consumed (e.g., Santos et al. 2013). Crustacean remains have also been found in some stomachs but usually as a minor component of the diet.

In odontocete species with fewer teeth (e.g., the beaked whales, family Ziphiidae), the food consists mainly of cephalopods which are ingested using suction feeding. This method of feeding, however, restricts the size of the prey that can be consumed, and therefore a relatively narrow range of prey sizes is usually eaten (MacLeod et al. 2006). This group includes species that are able to perform dives that are among the deepest and longest known in cetaceans, presumably in search of their prey. Oceanic squid of several families (Histioteuthidae, Cranchiidae, Ommastrephidae, Gonatidae, etc.) has been reported as the main prey of most of these species (Cuvier's beaked whales, *Ziphius cavirostris*; northern bottlenose whales, *Hyperoodon ampullatus*; sperm whales, e.g., Santos et al. 1999). However, some beaked whales of the genus *Mesoplodon* have been found with only remains of fish in the stomachs.

The sperm whale could be considered an exception to the general rule, as a largely teuthophagous species in which the number of teeth has not been reduced (although teeth are only present in the lower jaw). It has been suggested (Clarke 1980) that teeth are only used to grasp prey, since fresh prey has been found generally intact in stomachs and because food has been found in the stomachs of young sperm whales in which the teeth had not yet erupted and in the stomachs of whales with deformed jaws (Rice 1989). Sperm whales have been found to feed on a wide range of cephalopod and fish species with a wide range of body sizes (see reviews by, e.g., Rice 1989; Whitehead 2003). The sperm whale is known to dive to more than 1,000 m, as revealed by animals found dead entangled in undersea cables and damage to cables that was attributed to sperm whales even when the carcass was not found.

Finally, earlier we mentioned the killer whale or orca. While some populations (ecotypes) do feed on marine mammals including cetaceans, seals, and sea otters, others specialize on fish. They may also eat penguins, squid, turtles, seabirds, and even moose.

Feeding Strategies

We have already touched on feeding mechanisms and feeding preferences in the previous sections without saying much about the behavioral processes involved. As noted, many cetaceans have apparently specialized in feeding on fish (piscivorous), while others specialize on cephalopods (teuthophagous). Some cetaceans take both kinds of prey.

It has been often asserted or assumed that, once a basic preference for (or adaptation to) feeding on fish or squid is taken into account, most cetaceans are opportunistic feeders, selecting their prey, in terms of species and sizes eaten, according to availability – the alternative being specialization, whereby a predator selects a *preferred* prey species and will only consume other prey types when the preferred prey is not available. These ideas about feeding strategies can be traced back through various paradigms, including optimal foraging theory (e.g., Hughes 1980) and functional responses (Holling 1959), but, as Dunnet (1996) pointed out, opportunism, selection, and availability are "in fact shorthand for very complex biological interactions about which we know only a little in quantitative terms," and the existence of these strategies in cetaceans is difficult to prove (Santos et al. 2013).

In predators that can be readily observed in captivity or indeed in the field, and in which the behavior of individuals can be followed, it is relatively straightforward to gain insights into prey selection behavior. However, with the current methods to study cetacean diet, regardless of whether dead or live animals are sampled, we normally have only a snapshot or average of diet choices. However, an approximation which has been explored is to analyze the relationship between prey abundance and their importance in stomach content samples. The rationale behind such analyses is that there would be a positive relationship between prey abundance and their importance in a cetacean stomach if the prey is a preferred prey. Because other prey would only be eaten only if preferred prey are not available, there would be a less clear relationship between abundance and importance in the stomach contents (and their importance in the diet would decrease as the abundance of preferred prey increases). However, direct comparisons between abundance of prey species and consumption by cetaceans are not always possible because of the different scales on which data on predator diet and prey abundance are usually available, and the spatial variability in occurrence of prey patches, such that environmental variables may be better predictors of prey occurrence than sampling the prey directly (Torres et al. 2008).

The selection pressures affecting diet selection may go beyond considerations of energetics and nutrients. Feeding on some prey can have lethal consequences, as evidenced by findings of dead cetaceans, which had apparently died from asphyxiation due to fish lodged in their throats. Interestingly, a recent study shows that bottlenose dolphins have learned to decapitate catfish, apparently to avoid ingesting spines which can cause fatal injury (Ronje et al. 2017).

Methods to Study Diet

There are several methods available to infer the diet of cetaceans, and we will mention some of their advantages and disadvantages. Knowledge of cetacean diet can provide a valuable insight into their biology and their role in the marine ecosystem in addition to helping answer questions about the potential effect of predation on prey populations and on threats to cetaceans, for example, arising from interactions with fisheries (Pierce and Boyle 1991).

Knowledge of cetacean diets has improved over the years with the establishment of systematic data collection (latterly from strandings and bycatches) that has allowed access to larger sample sizes, development of new prey identification methods, and new techniques to infer the diet of individuals over longer time scales and various numerical and statistical tools (e.g., quantitative fatty acid signature analysis, mixing models applied to stable isotope data). Several reviews of methodology have been published, including Pierce and Boyle (1991) and Tollit et al. (2010), so we will not attempt to cover all available methods here.

Stomach Content Analysis

When cetacean were hunted, information on diet was gathered by the examination of the stomach contents of recently killed individuals or observations of the food remains regurgitated by the whales after being harpooned. In some cases, the material observed led to mistaken assumptions, as can be seen from the following quote referring to baleen whales caught off Bermuda:

> "Their feeding on grass, growing at the bottom of the sea, appeared by cutting up the great bag of maw, in which was found two or three hogsheads of a greenish grassy matter." (Anon 1665)

Investigations on diet through the systematic identification and quantification of the prey remains found in the stomachs provided the first evidence about the prey species (and the sizes and amounts) consumed and allowed scientists to make inferences on the ecology of the whale and dolphins based on their diet. The late Malcolm Clarke pioneered the use of cephalopod mandibles (beaks) in whale stomachs to make inferences about diet, and, in some cases, cephalopod species new to science were first identified from remains found in the stomachs of deep-diving cetaceans such as the sperm whale and beaked whales (Clarke 1980).

Stomach content (and fecal and regurgitation) analysis is relatively straightforward in that it does not require specialized equipment. However, it is time-consuming, since it involves the identification, counting, and measurement of the hard prey remains (e.g., fish bones and otoliths, cephalopod mandibles, and crustacean exoskeletal remains) present to characterize and quantify diet and to back-calculate original prey size. Prey identification can be aided by the existence of reference material and the availability of reference guides (i.e., Clarke 1986; Härkönen 1986), but experience in identification is also important. The process may be simplified by using only otoliths to quantify fish in the diet, but this can result in incomplete and biased results. A major issue, especially in relation to (calcareous) fish otoliths, is the effect of acid digestion which can reduce size, remove key identification features, and ultimately entirely dissolve otoliths, to varying degrees depending on the species and size of fish. Some authors have *corrected* for effects of digestion, while others recommend using only undigested prey remains.

The advantages of, and possible biases in, dietary information derived from the analysis of stomach contents of stranded and/or bycaught animals have been discussed in detail in the literature (e.g., in the reviews by Pierce and Boyle (1991) and Tollit et al. (2010)). Biases can arise both from the source of samples, e.g., stranded animals may not be representative of the population because sick/injured animals or animals feeding near the coast are overrepresented. Concerns have also been raised when the origin of the samples is fishery interactions, because bycaught animals could have been feeding near the nets and species present in the nets could be overrepresented compared to the typical diet. Biases also arise from the samples themselves, for example, due to digestion or to secondary ingestion, whereby the remains found include prey remains from the stomachs of larger prey. Even with these potential biases, stomach content analysis remains the most widely used method to determine the diet of cetaceans, because it can provide fully quantitative information. Such data are needed for trophic models that can help determine the role of cetaceans in the ecosystem. Many other approaches either lack resolution (e.g., bulk stable isotope analysis), are not fully quantitative (e.g., DNA-based prey identification), or rely on availability of stomach content results to facilitate interpretation (e.g., fatty acid and stable isotope analyses).

Fatty Acid Analysis

Cetacean blubber (the vascularized layer of fat beneath the skin) can represent up to 50% of body weight and is used for energy storage, as an insulator, to aid in thermoregulation, and buoyancy, and gives a dolphin or whale its hydrodynamic shape. Blubber is mainly constituted by triacylglycerols consisting of three fatty acids each attached to one of the three carbons of a glycerol molecule with an ester bond through the oxygen atom. Although animals can synthesize fatty acids, these compounds are mainly incorporated through the diet (especially in the case of polyunsaturated fatty acids which are biosynthesized only by phytoplankton and macroalgae). Fatty acids from the prey are not degraded, but they accumulate in the blubber during the lifetime of the animal; thus, blubber fatty acid composition can reflect the diet over a period of days or months (Iverson et al. 1995).

Fatty acids have been used to infer the diet of predators following this principle, with the possibility to quantitatively determine the proportion of each prey type consumed by a predator using quantitative fatty acid signature analysis (QFASA) (Iverson et al. 2004), a numerical modeling approach that uses fatty acid signatures of putative prey species to estimate the most likely contribution of each prey species to the diet, based on the observed predator tissue composition.

Although, in comparison with stomach content analysis, analysis of fatty acids requires specialized equipment (e.g., a gas chromatograph), it has the potential advantage over the former that information on diet can be obtained from animals with empty stomachs, samples can be taken from live animals (using biopsies), and the technique provides dietary information integrated over a longer time period.

However, several issues need to be taken into account when interpreting fatty acid values: first, cetacean blubber is stratified, with differences between the fatty acid profiles of the inner blubber (which has a more recent dietary origin) and outer blubber (that has a more structural role); secondly, lipids break down during the decomposition of a dead animal, and fresh carcasses may be needed to obtain reliable fatty acid profiles. Thirdly, although most fatty acids are incorporated from the diet, others can be biosynthesized (mainly short-chain fatty acids), and it appears that amounts deposited may not be exactly proportional to amounts ingested. Therefore, *calibration coefficients* are needed that take into account predator lipid metabolism and deposition when estimating diet using the QFASA approach. For seals, these calibration coefficients were calculated using captive feeding experiments (Iverson et al. 2004), but to date there are still no calibration coefficients for cetaceans, although recent work on polar bears proposes that diet and calibration coefficients can be estimated simultaneously from the same data set (of predator plus prey fatty acid profiles) (Bromaghin et al. 2017). Finally, QFASA assumes that the fatty acid compositions of *all* potential prey are known and it is also clear that prey fatty acid profiles vary with age, season, sex, area, etc., of the prey – and of course also with the diet of the prey.

Although quantitative fatty acid analysis has been more successful when applied to invertebrate predators (e.g., squid, for which calibration coefficients are apparently unnecessary), useful semiquantitative results have been obtained in cetaceans, e.g., seasonal changes in fatty acid profiles of porpoises broadly matched expected changes based on stomach contents (Learmonth 2006).

Stable Isotope Analysis

Similar to fatty acid analysis, stable isotope analysis (SIA) follows the assumption that the isotopic composition in the tissues of a predator reflects the isotopic composition of its prey. Isotopes are different forms of atoms characterized by the same number of protons (the same atomic number) but different number of neutrons (hence different masses). The most commonly used isotopes are those of carbon (^{12}C and ^{13}C) and nitrogen (^{14}N and ^{15}N), although isotopes of sulfur and oxygen and strontium, among others, have also been used. These isotopes are all stable (non-decaying, hence nonradioactive) as opposed to, say, ^{14}C. Lighter isotopes are preferentially exhaled or excreted when food is metabolized producing an enrichment of the heavier isotopes in the tissues of the predator relative to its prey. This *fractionation* process takes place at each trophic level which means that the higher in the food web a predator is situated, the higher the enrichment of the heavier isotopes in its tissues and, in principle at least, this enrichment takes place in a predictable way. For carbon it has been estimated there is an enrichment in the ratio of ^{13}C to ^{12}C of approximately one part per thousand for each trophic level while for N, the increase is around 3% (Kelly 2000).

Having information on two isotope ratios in the predator provides very low-resolution evidence on diet composition, but stable isotope analysis is widely used to obtain data on the trophic position of individuals and populations and also to determine where the animal has been living, with C isotopes, for example, acting as chemical tracers of different sources of primary productivity (e.g., inshore versus offshore) and also varying with latitude. For these reasons, SIA has also been used to infer, or confirm, migration and population substructure of cetaceans (e.g., Fernández et al. 2011).

As is the case for fatty acids, SIA can provide information for animals with empty stomachs, and different tissues (with different turnover rates) can be used to provide information on diet integrated over different time periods (soft tissues, teeth, and bones can also be sampled). Another advantage of stable isotopes is that information can be obtained from specimens in museum collections, allowing us to reconstruct the past environment and trophic positions of individuals.

Again there are issues that need to be taken into consideration when interpreting the results from SIA. One of the most important is that the isotope fractionation, between the diet and the predator's tissues, can differ in different tissues (Tieszen et al. 1983). Captive feeding experiments in cetaceans suggest that the fractionation seen in C and N isotopes can be a long way from the *typical* values of 1 and 3% (e.g., Caut et al. 2011). In addition, isotopic fractionation can vary depending on food quality and the nutritional stress of the individual (Schmidt et al. 2004).

Finally, it is important to note that sample extraction methods and sample storage can affect the results obtained. In particular, the isotopic signatures of lipids differ from those of other body components.

Despite these issues, the advent of compound-specific SIA, in which isotope ratios are calculated separately for different amino acids, can greatly enhance the information obtained. The increased amount of data generated potentially provides much higher resolution of dietary composition (e.g., Matthews and Ferguson 2014; McMahon et al. 2016). Another relatively recent development is the calculation of isotope ratios in individual growth rings of *recording structures* such as teeth, such that dietary information can be obtained for each year of an animal's life (e.g., Borrell et al. 2013).

Other Methods

Several other methods have been used to obtain information on the diet of cetaceans. These include direct observations of animals feeding at the surface or using underwater cameras attached to the animals or to nets or other structures; the collection of feces and discarded prey remains from the water after detecting feeding behavior, for example, in the case of whales filter feeding baleen whales; and the identification of the soft tissues of prey in stomach contents. The latter approach has evolved from the use of electrophoresis to identify prey proteins, through raising antisera to detect proteins of specific prey, to identification of prey DNA. Molecular prey identification, for example, based on mitochondrial DNA, is increasingly the method of choice for a wide range of marine predators (e.g., Parsons et al. 2005) and has become relatively much less expensive than when first developed. Fully quantitative DNA-based diet analysis remains to be developed: the amount of DNA of a particular prey species amplified may bear little relation to the amount of the species in the stomach contents.

Conclusion

There are many reasons why knowledge of the diet and the feeding ecology of a cetacean species may be useful. Firstly, it provides insights into its biology and ecology, including habitat preferences, prey selection, competition and resource partitioning with other predators, energy transfer, population substructure, etc. In addition, understanding the effects of predators on the populations of their prey, and how predators cope with changes in prey abundance, is essential to predict responses of marine ecosystems to perturbation. Finally, diet analysis can provide important insights into threats including prey depletion and fishery bycatch. The diet is the main route by which various pollutants enter cetaceans, including toxic elements, persistent organic pollutants, and plastics. By understanding diet, we can gain a better understanding of these various threats and therefore contribute the conservation of these species.

Cross-References

- ▶ Amino Acid
- ▶ Cetacean Morphology
- ▶ Cooperative Hunting
- ▶ DNA
- ▶ DNA Marker
- ▶ Ecological Niche
- ▶ Optimal Foraging Theory
- ▶ Predator
- ▶ Prey

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