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## Abstract

Pelagic predators (larger elasmobranchs, teleost fishes, squid, sea turtles, seabirds, and marine mammals) congregate in the photic zone, often in regions of increased primary production such as ocean current divergences or convergences, regions of localized upwelling, fronts, or eddies. They are generally large in body size compared to other marine predators with relatively high metabolic rates. The combination of these factors leads to relatively high average daily prey requirements. Because primary production is relatively low in pelagic ecosystems, these predators must adapt to a nutritionally dilute three-dimensional system where prey resources are patchy and ephemeral. Thus, most species range long distances in search of patchy and ephemeral concentrations of prey. Compared to other pelagic predators, squid tend to be short-lived with rapid growth and population turnover rates and thus they are capable of responding rapidly to ecosystem change, and some have speculated that squid populations may rapidly exploit prey resources made available by the removal of other predators. Many species are directly targeted or incidentally taken in fisheries, and several species have declined precipitously or have been driven to extinction. Some researchers have speculated that they play an important top-down role in pelagic ecosystems, leading to concerns regarding their recent declines. Given their dependence upon ocean processes that serve to enhance productivity and concentrate prey, climate change may have important direct and indirect impacts on these predators including changes in movement patterns, species ranges, food web interactions, trophic status, and life-history traits.

a0005 # Pelagic Predators

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Further Reading

p0005 Pelagic ecosystems are characterized by two major groups of animals: zooplankton and nekton. Pelagic predators are larger nektonic species including elasmobranchs (e.g., pelagic sharks and rays), teleost fishes (e.g., tuna and billfishes), large squid, and marine tetrapods (e.g., sea turtles, marine mammals, and seabirds). The majority of pelagic predators congregate in the photic zone, often in regions of increased primary production such as ocean current divergences or convergences, regions of localized upwelling, fronts, or eddies. Such regions, or 'hot spots', serve to enhance primary production rates or concentrate prey resources at higher densities.

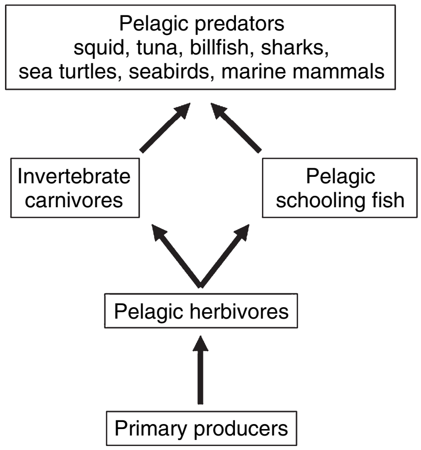
p0010 Compared to terrestrial and many near-shore systems, net primary production is low in pelagic ecosystems. Thus, these predators must adapt to a food web that is a nutritionally dilute three-dimensional system where prey resources are patchy and ephemeral (**Figure 1**). Pelagic primary producers (e.g., diatoms) constitute a relatively small proportion of total pelagic biomass, but they have high turnover rates – able to respond rapidly to increases in nutrient availability. The prey of pelagic predators similarly has relatively high turnover rates. This results in a situation where the biomass density of the primary producers and prey of pelagic predators may be similar to that of the predators themselves.

p0015 Pelagic predators are generally large in body size compared to other marine predators (e.g., geometric mean body size of pelagic predators is 4.7 vs. 0.19 kg in coastal predators) with relatively high metabolic rates. The combination of these factors leads to relatively high average daily prey requirements, and most species range long distances in search of patchy and ephemeral concentrations of prey. Likewise, they may range long distances in search of mates or breed and forage in widely separated locations (**Figure 2**). As a result, most are streamlined, efficient swimmers, with low costs of transport. Many species utilize efficient lift-based locomotion strategies (e.g., tuna, billfish, sea turtles, seabirds, and cetaceans such as whales and dolphins). Elasmobranchs and teleosts have evolved rigid bodies with small scales, reduced fins, and keels. In addition, many of these predatory fishes have adaptations to increase the efficiency of aerobic swimming with high proportions of red muscle with complex rete systems to maintain elevated body temperatures. Pelagic seabirds are efficient flyers able to take advantage of global and localized wind patterns (e.g., albatrosses, shearwaters) that significantly reduce their cost of transport. In comparison to other pelagic predators, squid utilize a relatively inefficient jet propulsion-based mode of locomotion that, while less efficient than vertebrates, is relatively efficient in comparison to other invertebrates.

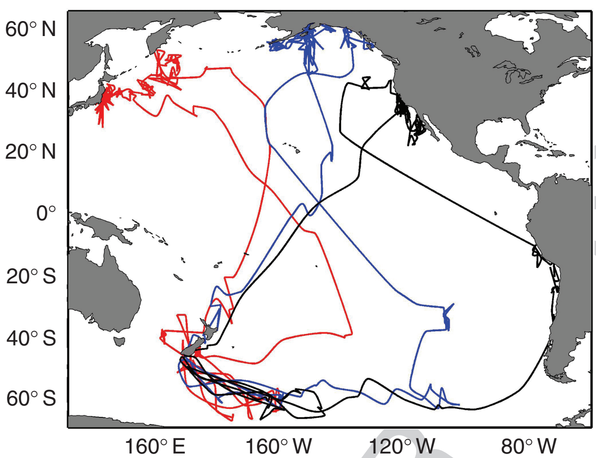
Successful feeding of most pelagic predators depends p0020
upon schooling prey or, less commonly, other top predators (e.g., white sharks, killer whales). Pelagic schooling likely evolved as a predator defense strategy and the large body size and generally low cost of transport in pelagic predators allows them to fast for extended periods while ranging long distances in search of prey schools. Large body size is also advantageous in allowing pelagic predators to consume and process larger quantities of prey in a single feeding event. As a means to further increase the efficiency of processing schooling prey, filter feeding has evolved independently in four groups of pelagic predators (seals, whales, sharks, and rays). This allows them to engulf and process many individual prey at once – further increasing the rate at which energy may be ingested when encountered.

As large, conspicuous components of pelagic ecosys- p0025
tems, many pelagic predators are economically or culturally important. Because they are a large and high-quality food resource, many species are directly targeted in fisheries, and the exploitation of pelagic predators was arguably one of the first major impacts of humans on marine ecosystems. Recently, several authors have argued that stocks of pelagic predatory fishes have declined precipitously due to exploitation. For many species it has been estimated that large predatory fish have declined to 10% of unfished levels in the last 50–100 years. For elasmobranchs and marine tetrapods which tend to be long-lived with low fecundity, direct exploitation likely had greater impacts.

Direct exploitation of many marine tetrapod species p0030
has led to catastrophic declines (e.g., pinnipeds, cetaceans, sea turtles) and, in some cases, extinction (e.g., Steller's sea cow, great auk). More recently, indirect exploitation via by-catch in commercial fisheries has further added to population declines, particularly in sea turtles and seabirds (e.g., albatrosses). Declines of colonially breeding tetrapods due to direct and indirect exploitation at sea have been further exacerbated by the introduction of




f0005 **Figure 1** Simplified pelagic predator food web.




f0010 **Figure 2** Basinwide migrations of three sooty shearwaters equipped with archival geolocation loggers. Although each bird bred at a colony in New Zealand (see multiple foraging trips to Antarctic waters), shearwaters experience a pan-Pacific distribution during the postbreeding migration (May–Sep.). For complete details of the study, see Shaffer SA, Tremblay Y, Weimerskirch H, *et al*. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America* 103: 12799–12802.

non-native predators (e.g., rats, cats, dogs, pigs, mongooses) at breeding colonies.

p0035 Compared to other pelagic predators, squid are unique. They tend to be short-lived with rapid growth and population turnover rates. Thus, unlike other pelagic predators, they are capable of responding rapidly to ecosystem change, and some have speculated that squid populations may rapidly exploit prey resources made available by the removal of other predators. In addition, squid are important as both predators in pelagic ecosystems as well as prey to larger predatory fish and marine tetrapods.

While pelagic predators are conspicuous, important harvest species, the foci of popular attention, and rallying species for environmentalists, our understanding of their role in pelagic ecology is limited. Some have speculated that the removal of these predators may have had significant effects on marine community structure. Given their rapid growth rates and likely high population numbers, the role of squid in top-down regulation of pelagic ecosystems may be significantly underestimated. For whales, it has been debated that declines of large whale biomass in northeast Pacific triggered significant increases in herring and walleye pollock stocks. Because pelagic predators may be relatively abundant, have large body sizes, high metabolic rates, and high trophic status, a significant proportion of ocean primary production indirectly passes through them. Thus, there is the possibility for them to exert strong top-down control in pelagic ecosystems. This may be particularly true for squid given their likely high abundances, metabolic rates, and growth rates. However, evidence for such control is limited, and their top-down impacts may be ameliorated by mismatches in turnover rates of primary producers, consumers, and pelagic predators or the structure of pelagic food webs. p0040

Given their dependence upon ocean processes that serve to enhance productivity and concentrate prey, climate change may have important direct and indirect impacts on these predators including changes in movement patterns, species ranges, food web interactions, trophic status, and life history traits. p0045

*See also:* 00533; 00534.

## Further Reading

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