migrate over the upper 100 m, rising to the surface at dawn and dusk. The adults, in contrast, remain below 100 m, with no distinct vertical migration pattern until summer, when they migrate to the surface at dawn and dusk. The optimal depth position was calculated in their model as a balance between feeding opportunity and risk of mortality from predation, which correctly predicted the dawn and dusk migration and feeding pattern. The observed differences in vertical migratory behaviors of this species, as an example, depend on individual differences in age, size, energetic state, variations in the seasonal environment, and an optimization between minimizing predation losses, maximizing food intake, and minimizing metabolic losses that may depend on different life history requirements.

Conclusions

Diel vertical migrations of marine fish are relatively common phenomena that occur in many species and at different life history stages. The relative constancy of their diel periods is consistent with the notion of an underlying circadian rhythmicity. The process of vertical migration also appears to be a facultative one in many cases, as the pattern of vertical migration can be changed by a number of factors. An example of a hypothetical system of multiple controls on diel vertical migrations is shown in **Figure 5**. In this model, an endogenous rhythm of vertical migration is determined initially by photoperiod. Under certain circumstances, the vertical migration pattern of the fish switches from being entrained by a light–dark cycle to entrainment by the tidal cycle, for example, with the result that the period of vertical migration activity is modified. Likewise, events such as a full moon on a cloudless night might act to modify the rhythm by suppressing the amplitude of the vertical migration.

Such variations in vertical migration pose profound difficulties for surveys of the abundance of fish. To reduce these problems, researchers may study different life history stages or use different sampling techniques that include the range of vertical migration, when this is known.

See also

Demersal Fishes. Fish Feeding and Foraging. Fish Larvae. Fish Locomotion. Fish Migration, Horizontal. Intertidal Fishes.

Further Reading

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FISH PREDATION AND MORTALITY

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Overview

Not only do fish prey on one another, but almost every other type of animal in the sea from jellyfish to whales and seabirds eat enormous quantities of fish. Apart from some less usual conditions (such as outbreaks of disease, mass starvations, harmful algal blooms, or extreme over-fishing) predation by other animals is the largest source of mortality of fishes in the sea. Among the most voracious of these predator groups, other fishes consume the lion's share, but in some seas marine mammals also consume large amounts (**Figure 1**). Predation mortality is generally highest on juvenile fishes, but fishing mortality

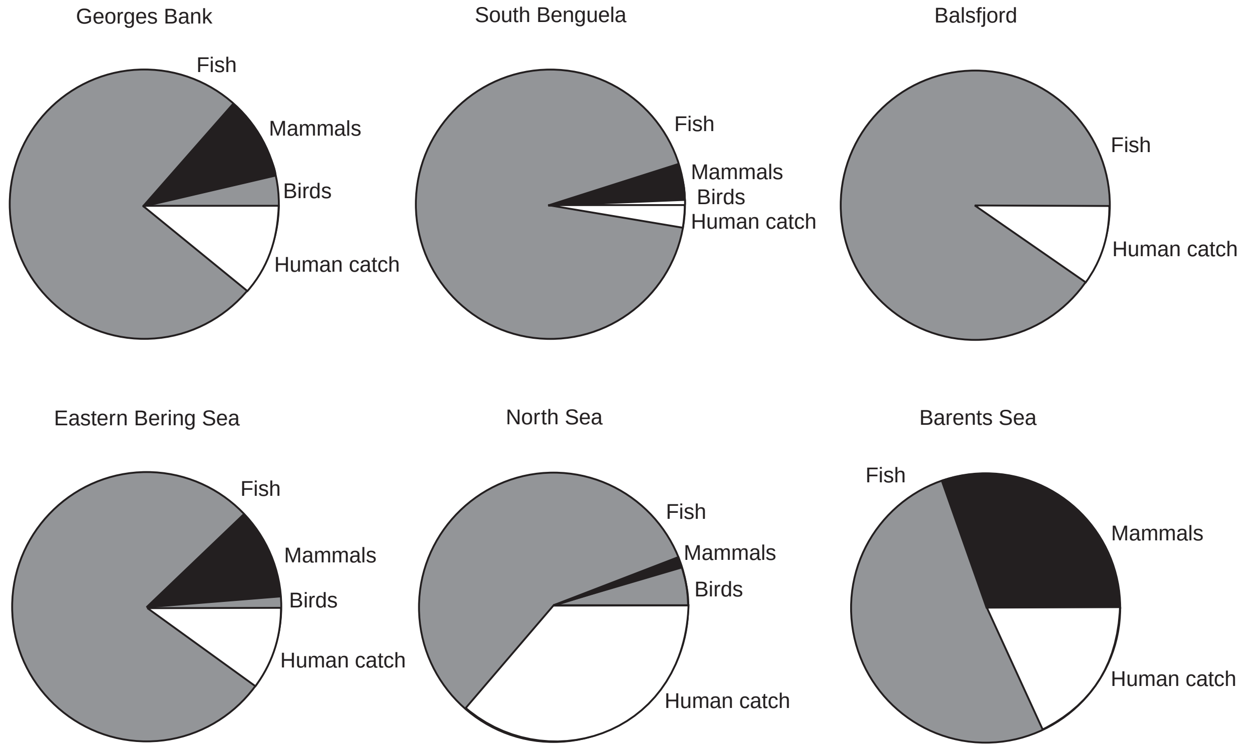

Figure 1 The relative annual biomass removal of fish by humans, mammals, birds, and other fishes in six commercially important marine ecosystems. (Adapted with permission; from Bax NJ (1991). A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. *ICES Journal of Marine Science* 193: 217–224. As noted by that author, these estimates of relative biomass removals can be regarded as gross approximations.)

increases as fish mature and grow, so in some areas commercial harvesting is the greatest source of mortality of the adult stage.

As opposed to fishing mortality, natural mortality rates (which include predation) of most marine fishes decline throughout their life span, resulting from a narrowing scope of the field of potential predators. For example, in the case of walleye pollock, the source of one of the world's most important commercial fisheries, mortality rates for eggs and larvae decline from an average of about 10% loss per day to 1% loss per day for 6-month-old juveniles to 0.05% loss per day for adults. However, because fish are increasing in size with age, the loss of biomass due to mortality peaks during the juvenile stage (**Figure 2**). As a consequence, it is juvenile fish that are most important as prey for providing energy to higher trophic levels.

The Diversity of Predators

A broad variety of predator types and sizes feed on marine fishes. These predators vary from near-microscopic organisms such as *Noctiluca* which feed on fish eggs, to invertebrates such as jellyfish which feed on fish larvae, to whales which feed on juvenile and adult fishes. Fish as prey may be attacked from above by birds or from below by benthic crabs, shrimp, and bottom fishes.

Invertebrate predators employ diverse ways to detect and secure their prey (**Table 1**). Ambush raptorial invertebrates include ctenophores and chaetognaths. Siphonophores may use lures to attract and attack their larval fish prey. Many invertebrate predators such as copepods and chaetognaths detect their prey by mechanoreception of larval fish swimming activity. Jellyfish may depend on random encounters with fish larvae, ensnare them with mucus, and/or then immobilize them with stinging nematocysts. Euphausiids are actively cruising-contact predators, which probably sweep fish eggs and larvae into their mouth parts with feeding currents generated by thoracic legs. Other crustacean predators may use their chemosensory abilities to detect prey, and some may use vision.

Fish also use a variety of methods to capture prey (**Table 1**). Herring either filter-feed or actively bite individual prey, depending on the prey's size and relative density. Other fishes are obligate filter (e.g. menhaden) or raptorial feeders (e.g. walleye pollock). Filter-feeding fishes generally feed on small,

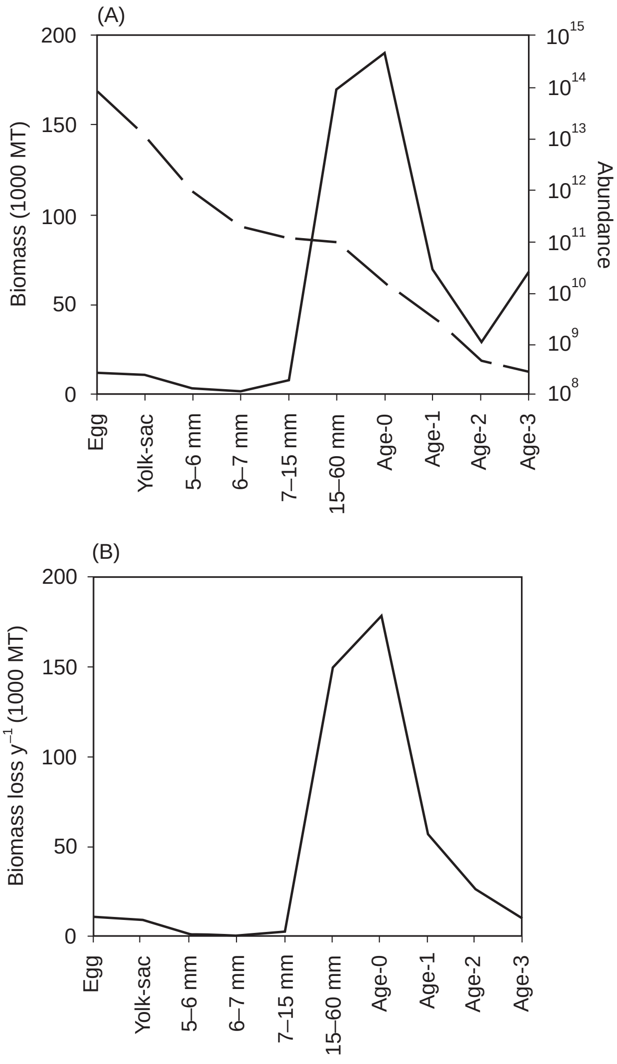

Figure 2 (A) Trends in abundance (dashed line) and biomass (solid line) of different life stages of a typical cohort of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. Numerical abundances of eggs and larvae are much higher than juveniles (note log scale), but total cohort biomass peaks during the juvenile period due to rapid growth in weight. (Adapted with permission from Brodeur RD and Wilson MT (1996). A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography* 5 (suppl. 1): 148–166.) (B) Annual loss of biomass due to natural mortality. Assuming that most of the loss is due to predation, the annual removal of biomass by predators peaks in the early juvenile stages due to the longer stage durations of juveniles.

abundant particles, while raptorial feeding fish generally pursue larger, less abundant prey.

How to Study Predation

There are several methods (**Table 2**) and steps to assessing the impact of predation on marine fishes. First, is the identification of their predators and prey. This has been done by direct observation of predator stomach contents, either looking at whole prey or parts of prey (for example, otoliths or scales), using immunochemical techniques, or looking at the presence of prey DNA in predator stomachs. After prey are identified, and their relative presence is determined, then the amount eaten is estimated from models that utilize the quantity of prey in guts and prey digestion rates to calculate predator daily rations. Alternatively, daily rations are calculated from energetic-demand models and then the amounts of specific prey consumed are estimated from their percent composition in gut contents. The amount of prey consumed by the overall predator population is extrapolated from the abundance of the predators. Predation is sometimes inferred from inverse oscillations in predator and prey populations, although other factors may also be involved, such as competition for resources or distribution shifts.

The dynamics and impacts of who is eating how much of what were examined by ecosystem modeling in the late 1970s. Ecosystem models range from simple to complex. In the past few years, partly due to enhanced computing power, ecosystem modeling has made a comeback. More complex models require that a large number of parameters be estimated. For example, in such models it is assumed that the input data are representative (i.e. that a relatively small sample of stomachs collected over a limited temporal and spatial scale represents what the whole population is eating annually), and that they include the correct terms that account for both seasonal movements and interactions between predators and prey. Another approach is to incorporate predation as a component in catch-at-age fisheries models – so-called multispecies virtual population analyses. These models share many of the same data problems and assumptions as ecosystem models.

The Predation Equation

The act of predation consists of a sequence of events that either lead to a successful feeding bout or failure (**Figure 3**). An encounter begins when the prey enters the volume within which a predator can detect it. The rate of encounter is a function of population densities and swimming speeds. Detection occurs when a predator locates the prey and is a function of prey 'visibility' and predator acuity, which depends on the sensory system utilized. Encounter and detection are followed, or perhaps not, by pursuit, strike, and capture.

Table 1 The diversity of fish predators, prey capture strategies, methods of detection, life stages consumed, and predation rates

Predator type	*Hunting strategy*	*Modes of detection*	*Manner of capture*	*Stages consumed*	*Predation rates* (*from various sources*)
Ctenophores	Cruising	Contact	Entanglement	Eggs, larvae	0.4–8% d^{-1}
Jellyfish	Cruising	Contact	Entanglement	Eggs, larvae	2–5% d^{-1}
Chaetognaths	Ambush	Mechanoreception	Raptorial	Larvae	Negligible
Copepods	Ambush	Mechanoreception	Raptorial	Larvae	6–100% d^{-1}
Amphipods	Cruising, ambush	Vision, chemoreception	Grasping	Eggs, larvae	0.1–45% d^{-1}
Euphausiids	Cruising	Contact	Raptorial	Eggs, larvae	1.7–2.8% d^{-1}
Shrimp	Ambush	Chemoreception, mechanoreception	Raptorial	Larvae	16% d^{-1}
Filter-feeding fishes	Cruising	Vision	Filtering	Eggs, larvae	0.15–42% d^{-1}
Biting fishes	Ambush	Vision, mechanoreception	Biting	Juveniles, adults	20–80% d^{-1}
Birds	Ambush	Vision	Biting	Juveniles, adults	10% $month^{-1}$
Otarids	Cruising	Vision	Biting	Juveniles, adults	10–20% y^{-1}
Baleen whales	Cruising	Sonar	Filtering	Juveniles, adults	0.3–2.6% $month^{-1}$

Predation rates on fish are size-, age-, stage-, and species-specific. It is known that on a gross-scale, size is the most important characteristic of individuals that determines predation rates, as it is associated with escape abilities, swimming speeds, and encounter rates. In particular, jellyfish and crustaceans show decreasing rates of predation on fish larvae of increasing size. In the case of raptorial fishes, predation rates may increase with larval prey sizes due to increased visibility and encounter rates, and then decrease when a critical predator size to prey size ratio is attained.

Often the young stages of marine fishes are located in patches or schools, and predators that forage in such aggregations display definite changes in behavior. Swimming speeds change, predominant directions of swimming shift, and changes in the number of turns have been demonstrated for predators encountering high concentrations of prey. All of these behaviors may serve to increase encounters and/or keep predators within prey patches.

From the prey's perspective, once it has been encountered it may detect the oncoming predator (although the sensory systems to detect oncoming predators are poorly developed in the early larval stage of most species), or it may escape after contact with the predator. The success of a larva's escape response depends on its development, startle response, burst swimming performance, and the capture tactics and capability of the pursuing predator.

The Changing Predator Field

As fish grow and develop, their vulnerability to specific predators changes, as does the suite of predators that may consume them (**Figure 4**). Predators

Table 2 Methods of studying predation

Approach	*Advantages*	*Disadvantages*
Direct counts from stomach contents	Widely available application; little technical skill required	Fish larvae are digested rapidly, predation rates may be underestimated
DNA analyses	Provide conclusive identification to the species level	Difficult to quantify; time-consuming
Immunochemistry	Results can be obtained rapidly	Time-consuming development of antibodies, non-specific reactivity
Laboratory studies of predator–prey behavior	Provide fine control of multiple variables	True field dynamics are not well represented
Mesocosm studies	Simulate physical and chemical characteristics of water column	Container effects may elevate contact rates between predator and prey
Predator/prey abundance estimates	Provide estimates of mortality due to specific predators	Correlations in predator–prey abundances are not equivalent to causation
Models	Provide a systematic approach to testing system function	Estimation of mathematical function is limited by biological data

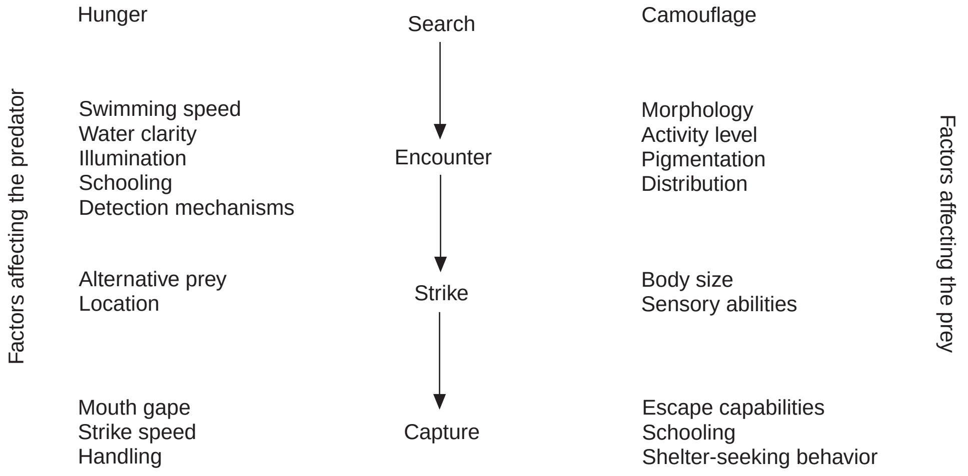

Figure 3 A simplistic conceptual model of the predation process. Left: factors affecting the predator at each stage; right: factors affecting the prey. More complex versions of the model include other steps such as detection, pursuit, contact, satiation, and digestive pause.

of fish eggs include many types of invertebrates and other fishes. Generally, egg loss by invertebrate predation may result in predation mortalities ranging from 1 to 10% loss of the population per day. These are high but not devastating mortalities. Pelagic fishes may also be important egg predators. It has been calculated that herring and sprat could theoretically consume the total standing crop of cod eggs in regions of the Baltic Sea.

Predators on fish larvae include most species that feed on eggs, as well as numerous others that are either not able to detect eggs because of transparency and immobility, or cannot grasp them and puncture them. Fish larvae are quickly digested, so it has proven difficult to get reliable estimates of predation rates from stomach content analyses.

As fish reach the juvenile stage, many of the smaller invertebrate predators and fishes are no longer able to consume fish of a larger size, but they are replaced by a new array of predators including larger raptorial fishes, birds, and marine mammals. Predation by benthic crustaceans such as shrimp may be particularly important for demersal fishes that undergo a transition from planktonic larva to benthic juvenile.

Adult fishes are prey to other larger fishes, seabirds and marine mammals. Natural mortality rates of adults probably fluctuate with the abundance of predators, and may be influenced by migrations. Adult forage fishes can be severely impacted by migrations of predators, examples being capelin which are consumed by migratory cod in the Barents Sea, and sandlance being eaten by migrating schools of mackerel on Georges Bank (northwestern Atlantic Ocean).

Life Transitions and Predation

Predation seems to be highest during or immediately after important life history transitions. For example, newly hatched larvae are vulnerable to a variety of new predator types. Newly hatched larvae are no longer protected by an egg shell and they now attract predators with their swimming motion. In addition, they have yet to learn predator avoidance and escape responses (or their innate abilities are still poorly developed).

Metamorphosis from the larval to juvenile stage has also been described as a period of high predation. For many species, metamorphosis represents a shift in habitat. The transition of flatfish larvae (such as plaice and Japanese flounder) as they settle from the plankton to the epibenthos has been found to be a period of high mortality that may modify recruitment levels. Likewise for coral reef fishes, the transition from freely floating planktonic larvae to their association with reef structures is a period of high mortality. This period of high mortality associated with a change in habitat may result from a lack of recognition of potential predators, or delays in acquiring camouflage, finding refugia, or learning behaviors that may protect them from predators (such as burying and hiding). In addition, competition for refugia or shelter may leave the losers exposed.

Predation and Recruitment

Recruitment is the abundance of an annual cohort at an age just prior to their joining the adult or harvestable population. At this age, the cohort

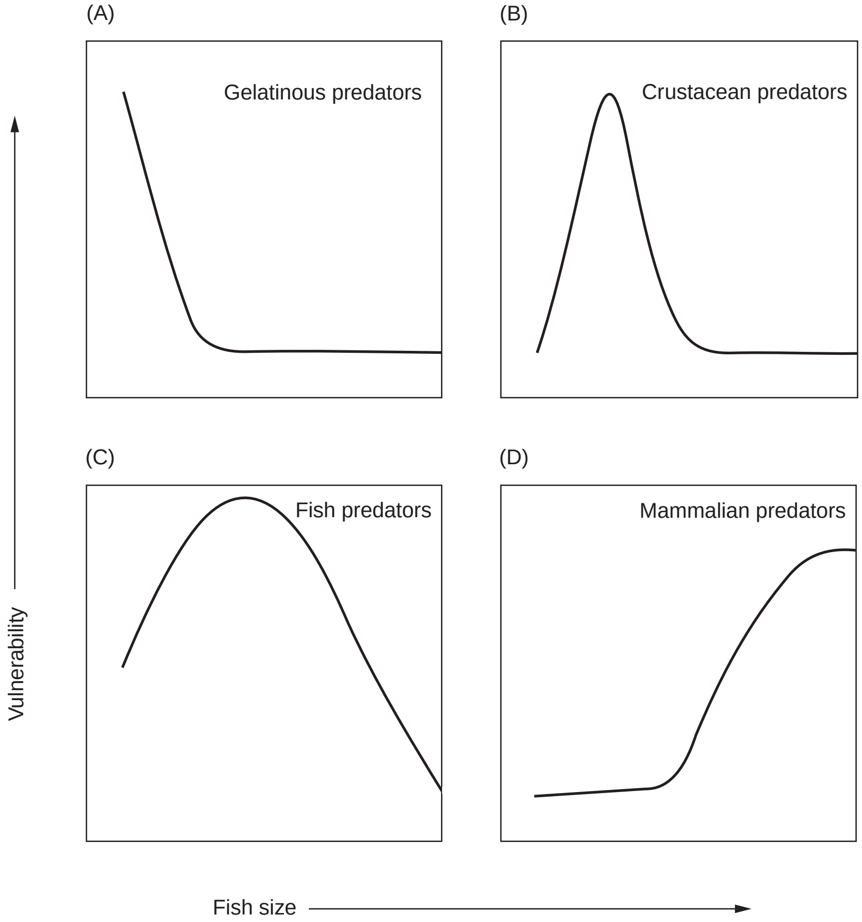

Figure 4 Schematic representation of changes in the relative vulnerability of fishes to different types of predators with increasing fish size. Vulnerability is the product of encounter rates and susceptibility or capture success, as determined by the prey's ability to detect and respond to a predator's presence or attack. (A) Very small fish are most vulnerable to cruising gelatinous predators because they have a poorly developed escape response and encounter rates between predator and prey are high. (B) Vulnerability to some ambush crustacean predators might be dome-shaped because encounter rates increase as developing fish increase their swimming speeds, but vulnerability declines as larger fishes become more adept at escaping. (C) Visual fish predators may not see very small fish prey and larger fish prey have improving escape and avoidance abilities that eventually reduce their vulnerability to fish predators. (D) Mammals may select larger fish.

strength has been determined, but it has not been impacted by the fishery. In marine fishes, the level of recruitment is highly variable but is critical in establishing population levels. For many species, there is ample evidence that recruitment is established by the end of the larval period (e.g. Arctic cod and Pacific hake). For other species, heavy predation on juveniles can influence relative recruitment levels (e.g. northern anchovy and walleye pollock); this is very likely to be the case for many forage fish species or in geographic areas where predators of juveniles are typically abundant. Predation on early stages is one factor that is believed, in some cases, to increase recruitment variability, and in other cases to dampen variability.

The abundance of predators on eggs and larvae, and in some cases juvenile fishes, has been correlated with poor recruitment success of a number of species. For example, large numbers of adult herring are believed to consume vast quantities of cod and plaice eggs in the North Sea, thus depressing recruitment of these species. The variability in recruitment caused by predation is probably associated with the abundance of predators and the degree of their spatial and temporal overlap with prey, which can be related to environmental conditions. In particular, there are several studies demonstrating the deleterious impact of high consumption rates of gelatinous predators of fish eggs and larvae (see **Table 1**). The heavy predation of pelagic fishes on fish eggs is also well documented. Anchovies are known consumers of fish eggs, and in fact, several studies indicate that cannibalism by anchovies on their own eggs accounts for a large proportion of the total anchovy egg mortality. When pelagic predators are very abundant, they may consume a large portion of a year class. A strong year class can occur when predators decline or conditions dissociate the distribution of predators and prey in time or space, causing a release from predation pressure. Alternatively, a strong year class can result when larval production is so high that it swamps the predatory capacity of the ecosystem. There is also an interplay between growth and predation, such that the longer that fish remain in stages vulnerable to heavy predation pressure, the higher the cumulative mortality.

Density-dependent predation mortality has been shown to occur for juvenile fishes, but not for larvae. Density-dependent mortality can result from individual predators feeding disproportionately on prey of increasing abundance, so-called switch-feeding, and from predator swarming on abundant prey. In theory, other mechanisms include density-dependent growth interacting with size-dependent mortality, density-dependent condition of prey, and limited refugia from predators that become filled at a threshold density (leaving the excess unprotected from predation).

Predation and Community Structure

The effects of predation on structuring marine rocky intertidal and freshwater communities is well known, but more recently, predation has become more widely recognized as a force that shapes the structure of marine communities. This is especially the case for coral reef communities where fish densities are high, predators are varied and abundant, and prey refuges are limited. Ecological disturbances such as hurricanes, El Niño events and long-term climate changes may shift conditions that favor certain species and thus reorganize community structure. For example, a climate shift in the late 1970s in the North Pacific Ocean favored increasing abundances of long-lived piscivorous flatfish species, which has altered the pattern of recruitment of their prey species. Trophic cascades are important indirect forces that play a role in the organization of marine communities. These cascades describe the repercussions of predator–prey interactions throughout the food web. In the Baltic Sea, for example, the mortality of sprat and herring has declined as the biomass of its major predator, cod, has decreased. Since, as mentioned above, herring and sprat also consume large quantities of cod eggs, different interactions between predators and prey at different life stages may reinforce (or sometimes counteract) shifts in community structure.

Predation and Evolution

Evolution is driven, in part, by the ability to survive long enough to contribute to the gene pool. As such, predation is a strong determinant of natural selection and fish have evolved an amazing variety of tactics in nearly all aspects of their life history to avoid predation mortality. For example, many tropical species, such as sciaenids and engraulids, demonstrate crepuscular or night-time spawning activity that minimizes the proficiency of visually foraging predators to locate newly spawned eggs, potentially reducing total egg mortality. Moreover, reproduction during periods of reduced light intensity may also minimize the vulnerability of spawning adults to predation by larger animals, leaving iteroparous spawners an opportunity to spawn again. Live-bearing strategies, such as viviparity and ovoviviparity, are common among elasmobranchs and may minimize predation on early life stages. Gross changes in fish distribution are also evolutionary adaptations to predation pressure. Current hypotheses suggest that diel vertical migrations are an adaptive behavior to avoid daytime predation by visual predators and permit feeding at night when predation risks are presumably reduced (**Figure 5**). Studies of fish aggregations, particularly of small-sized fish, indicate that synchronized schooling is an important 'safety in numbers' evolutionary strategy to confuse and evade a pursuing attacker.

Feeding in fish is often a trade-off between foraging success and predator avoidance. A variety of studies have demonstrated that fishes can assess predation risk and modify their behavior to maximize fitness. This ability provides a strong, selective advantage to fishes that in the long run, increases their likelihood of reproducing. As a final example, predation has had profound impacts on fish morphology, ranging from adaptations that aid in disguising the fish from its predators to those that make the fish highly conspicuous. In the former case, fishes have evolved to resemble seaweeds, sponges, sticks, detritus, and sand. These cryptic strategies are common in blennies, pipefish, seahorses, and flatfishes. Fishes also have evolved patterns that disrupt their outlines, including silvery sides, lateral bands, and countershading. These strategies are common among silversides, killifish, and a variety of pelagic species. In the case of increased conspicuousness, fishes have evolved elaborate spines, bright warning colours, distinct eyespots, and mimicry of inedible species. An interesting example of mimicry has been observed in coral reef systems around Florida, USA.

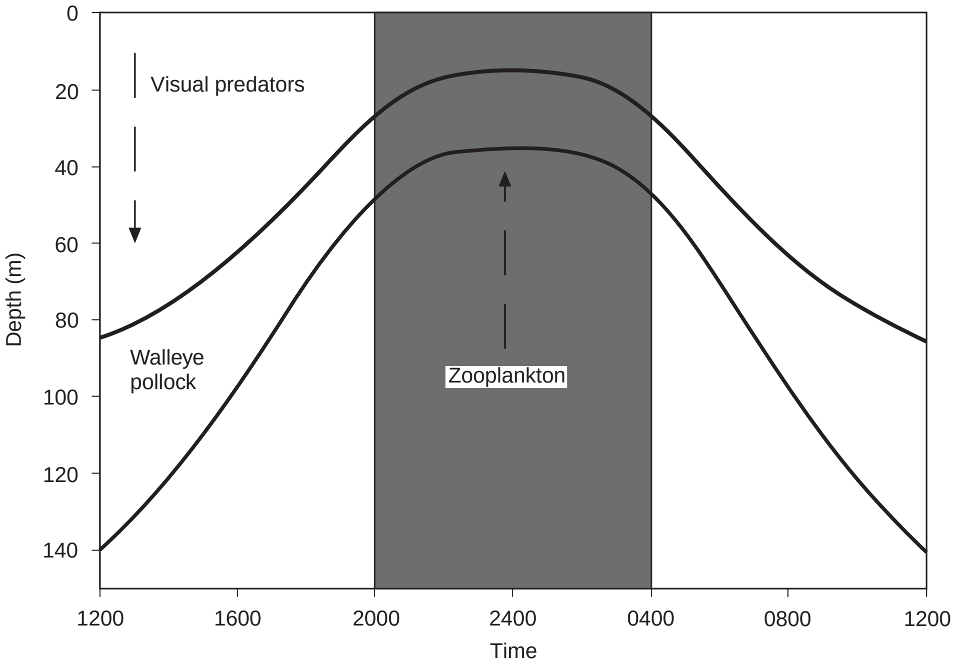

Figure 5 Spatial–temporal variations of young-of-the-year walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Walleye pollock occur at depth during daylight hours when visual predators in the surface waters are most active. At night (shaded area) when the risk of attack from visual predators is reduced, walleye pollock move to the upper water column to feed on available zooplankton.

The blenny, *Hemiemblemaria simulus*, is very similar in both appearance and behavior to the cleaner wrasse, *Thalassoma bifasciatum*. The mimic blenny has a comparable body shape and color pattern to the wrasse and it adopts a similar swimming strategy. The blenny apparently benefits not only from the protection from predation the cleaner wrasse receives from other fishes, but also by consuming ectoparasites on host fishes that come to be groomed by the wrasse.

Conclusions

Predation plays a significant role in the recruitment and population dynamics of marine fishes. The broad variety of predators that consume fishes, coupled with the potential for the removal of large portions of the available population, make it likely that predation is an important part of observed fluctuations of fish populations. Integrated studies of the physical and biological processes that influence predation, and especially the spatial overlap of predators and prey, coupled with long-term observations of the consequences, can provide useful information for evaluating the role of predation to overall recruitment success.

See also

Dynamics of Exploited Marine Fish Populations. Fish Feeding and Foraging. Fish Larvae. Fisheries: Multispecies Dynamics. Fisheries and Climate. Seabird Foraging Ecology. Seabirds and Fisheries Interactions.

Further Reading

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