DEMERSAL FISHES

O. A. Bergstad, Institute of Marine Research,
His, Norway

doi:10.1006/rwos.2001.0013

Introduction

Fishes of many families, shapes, and sizes obtain their food in the near-bottom zone and show morphological and behavioral adaptations for life on or near the seabed. These are the demersal fishes, comprising both benthic and benthopelagic species, the latter usually performing vertical migrations to feed.

Demersal fishes occur at all depths and in all near-bottom habitats of the oceans. In this chapter the emphasis will be on species inhabiting the continental shelves, i.e., mainly waters shallower than about 200 m but deeper than the littoral and shallower part of the sublittoral. Some 7.5% of the marine environment belongs to this category, very little compared with oceanic waters (91.9%), but considerably more than estuaries, algal beds, and reefs that together cover only 0.6%. More emphasis will be placed on fishes living in offshore waters than those inhabiting typical shallow coastal environments, although it is recognized that very shallow habitats may constitute highly significant nursery areas for many shelf species.

Worldwide about 85% of the total continental shelf area has sandy or muddy substrate. Only about 6% is rocky or gravelly, and the remaining areas are coral reefs or shellbeds (e.g., mollusc shells). However, there are both latitudinal and depth-related patterns. Corals are almost entirely confined to low latitudes where organically enriched muddy areas are also most extensive, particularly near the mouths of major rivers or below highly productive upwelling areas. Sandy, rocky, and gravelly sediments are more common at high latitudes. Regional and local modification of the distribution and character of soft sediments is common, e.g., due to water currents flushing the shelves.

In addition to offering a range of physical habitats to fishes, continental shelves are usually highly productive, and especially in temperate and boreal regions, demersal species of the shelf waters are very abundant and support some of the world's major fisheries. Of the approximately 13 500 marine fish species, 1000–2000 inhabit continental shelf water of temperate and boreal zones. The majority of these are demersal species. In the subtropical and tropical zones, the richness and diversity is much greater.

Taxonomic Diversity, Geographical Patterns, and Assemblages

A wide range of families, including both cartilaginous and bony fishes, has demersal representatives in shelf waters. There are some rather consistent geographical patterns, however, both on a worldwide and regional scale. The taxonomical diversity tends to be higher at low than at high latitudes. Both species richness and evenness is normally highest in tropical and subtropical waters. An example is the Gulf of Thailand, a rather shallow soft-substrate shelf sea, where 850–900 fish species from around 125 families occur, of which at least 300 demersal species are commercially important. By comparison, the number of species in the boreal North Sea is only 160–170, belonging to about 70 families. Of these roughly 70 may be caught regularly in bottom trawl surveys offshore and only 10–15 are commercially important demersal species. These numbers decline even further in subArctic shelf waters.

However, the abundance and biomass of demersal fish is considerably higher at high latitudes, i.e., in temperate and boreal waters. The latter is normally due to high abundances of a few species, especially gadiform fishes such as hakes (Merluccidae) and cod-like fishes (Gadidae), but also flatfishes (Pleuronectiformes) and rockfishes (Scorpaenidae) (**Figure 1**). Moreover, consistent differences between the oceans have evolved, e.g., gadiform fishes being more diverse on temperate Atlantic shelves than on North Pacific shelves where scorpaenids are very diverse and few gadiforms occur. The evolutionary history forms the background for present-day species composition patterns that are maintained by the rather strong structuring influence of regional and local environmental conditions, including the patterns of biological production in the surface layers.

Upwelling areas, well-mixed shallow shelf seas or shoals, and hydrographical frontal zones along the shelf-break are typical highly productive areas. Each of these environments is inhabited by subsets of the fish species found in the zoogeographical province to which they belong. Also, within such environments there may be a range of demersal habitats characterized by their hydrographical regime, currents, substrate quality, depth range, demersal

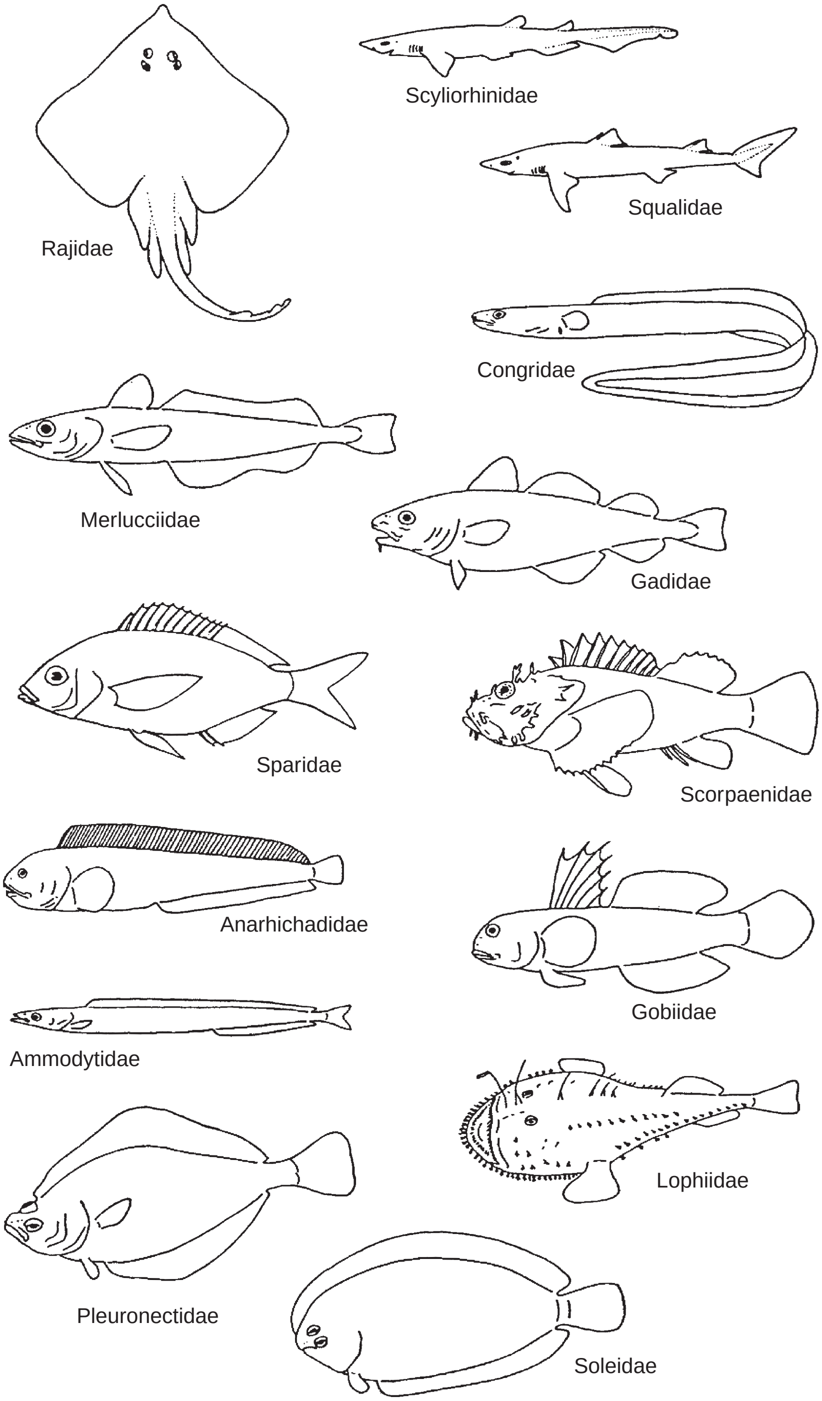

Figure 1 Body shapes of fish from selected demersal families.

invertebrate fauna, etc., each favoring particular assemblages of fish species. Underlying this structuring is each species' preference for certain environmental conditions, e.g., limited ranges of depth, temperature, sediment type, prey type, and size, etc., but also biotic processes among the fishes such as predator–prey relationships and competition. Such assemblage patterns have been found in a variety of coastal and shelf regions. The distribution of such assemblages on and around the Georges Bank off the east coast of North America is an example (**Figure 2**).

Narrow shelves tend to have fewer demersal species than wide shelves and shelf seas. The highly

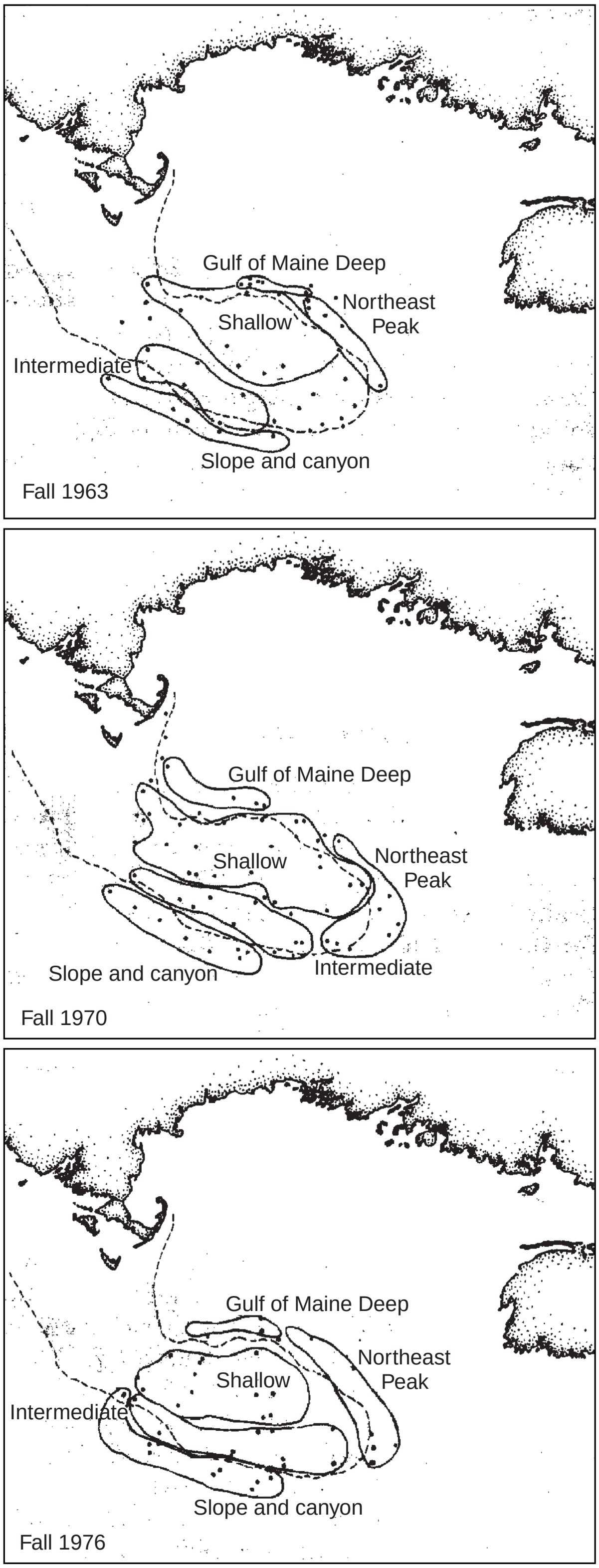

Figure 2 The geographical distribution of demersal fish assemblages on the Georges Bank of the Northwest Atlantic in 1963, 1970, and 1976. Each of the encircled areas has a distinctive assemblage of fishes characterized by the relative abundance or biomass structure of its member species. Broken line is the 100 m isobath. (Reproduced with permission from Overholtz and Tyler, 1985.)

productive upwelling areas associated with eastern boundary currents have few demersal species, and most are benthopelagic. Hakes (Merluccidae) are very well adapted to these environments and live both demersally and pelagically, mainly feeding on other fish. In contrast, demersal assemblages in major shelf seas and on offshore shoals have tens to hundreds of species with a wide range of adaptations. Even in the subArctic shelf seas, such as the Barents Sea and Bering Sea, there are high numbers of demersal species, yet only a few are very abundant.

Appearance and Behavior

In contrast with the slender and often torpedo-shaped pelagic fishes, typical demersal fishes are not so well adapted in terms or body shape or physiology for endured fast swimming. However, many shapes have proven successful (**Figure 1**), ranging from the eel-shaped (e.g., Congridae, Ammodytidae) through the more classical fish shapes of the cods (Gadidae), sparids (Sparidae), and rockfishes (Scorpaenidae), to the laterally compressed flatfishes (Pleuronectiformes) and dorso-ventrally compressed rays (Rajiformes). Eels and other elongated fishes swim by undulating the trunk and do not, as fishes of more classical shapes, use the caudal fin as their main means of propulsion. Pleuronectids and rays use the rather enlarged dorsal-anal or pectoral fins, respectively, for propulsion, but some flatfishes may also undulate the trunk to achieve higher speed or thrust when leaving the seabed or capturing prey. Regulating buoyancy may not be as important to demersal fish as to pelagic organisms. Pleuronectiform fishes, rays, and sharks lack gas-bladders, and in many groups the gas-bladder serves other purposes such as sound detection, as well as providing buoyancy.

Demersal fishes come in all sizes from small gobies with adult sizes of a few centimeters to the Atlantic halibut (*Hippoglossus hippoglossus*) and Greenland shark (*Somniosus microcephalus*) that may reach 2 and 6.5 m, respectively. The general rule is that abundance declines roughly exponentially with body size. In most demersal shelf assemblages, however, the overall size distribution tends to be log-normal, i.e., bell-shaped but skewed towards low sizes. The very smallest fishes may be rare, distributed in other areas, or undersampled, while intermediate sizes are very abundant. Beyond a certain size there is an exponential decline in numbers with increasing size. The shape of the size frequency distribution seems to be a characteristic feature of a given assemblage.

Many modes of life are possible in the demersal environment. Some fishes are sluggish and have evolved a typical 'lie-and-wait' strategy. Examples are the conger eel (*Conger conger*) which hides in crevices, and the monkfish (*Lophius piscatorius*) which utilizes elaborate camouflage to remain inconspicuous to potential prey animals while swaying its modified first dorsal fin ray as a lure. Other species are very active, and some almost behave as pelagic species, forming aggregations and even schools. Flatfishes and several rays spend part of their time buried in the sand and may only emerge for certain times of the day or tidal cycle to feed. An extreme adaptation is seen for the 5–30 cm sand eels (Ammodytidae) which alternate between a pelagic life style when feeding on zooplankton, to a benthic mode of life during the night and during the winter months when they bury in the sand. Cyclic activity patterns are commonly observed in demersal fish, but may vary seasonally. Most species are more active during the night or at dusk and dawn. Others have rhythms corresponding with tidal cycles. For relatively small demersal fishes these activity patterns tend to reflect a compromise between the need to feed efficiently while not being overly vulnerable to predation from bigger predators.

Camouflage may be attained in many ways, i.e., through body shape, skin coloration, and modification of the skin into appendages resembling algae or debris, and may serve two main purposes, either to avoid predators or to remain inconspicuous to prey passing by. Many species can adjust their body coloration to their environment almost continuously (e.g., many flatfishes), others have different persistent color varieties depending on the habitat in which they grow up and live. An example of the latter is all the different varieties of grey, brown, golden, and even dark red Atlantic cod (*Gadus morhua*) found in different parts of the range of this species across the North Atlantic.

Despite sharing some fundamental common features, many morphological adaptations have occurred within fish families, enabling closely related species to utilize a variety of resources in a given habitat. Among the gadid fishes of the North Atlantic, the size range is great, e.g., from <20 cm Norway pout (*Trisopterus esmarki*) to Atlantic cod (*G. morhua*) and ling (*Molva molva*) that may reach 190–200 cm and weigh 40–50 kg. The Norway pout, saithe (*Pollachius virens*), and blue whiting (*Micromesistius poutassou*) share morphological characters with pelagic fishes, i.e., dark or silvery backs, white bellies, big eyes, and almost toothless mouths, and they also form fast-swimming shoals when feeding benthopelagically on plankton or micronekton. Others are particularly well adapted for feeding on epi- and infauna, e.g., the haddock (*Melanogrammus aeglefinus*). A typical piscivore with a large gape and well developed dentition is the whiting (*Merlangius merlangus*), which may become piscivorous even as 10–15 cm juveniles. Other much bigger piscivores are the ling and blue ling (*Molva dipterygia*), which have elongated bodies and probably mostly behave as crepuscular ambush predators. The cod and pollack (*Pollachius pollachius*) appear more as generalists, feeding on benthopelagic and benthic crustaceans, pelagic and demersal fish, and even large pelagic crustaceans such as hyperid amphipods. Similar variations are found in many other fish families that are predominantly demersal.

Migration

As noted above, diurnal migrations, either vertical or horizontal, are common in demersal fishes. More fascinating, however, are the long-distance seasonal migrations associated with reproduction, feeding, and sometimes overwintering. Many examples were already well described several decades ago, based on traditional tagging data. However, the application of modern electronic tagging techniques, whereby positional information can be derived after retrieval of the tag, has revealed that, e.g., plaice may make extensive migrations much more frequently than previously thought. For some species, e.g., cod, saithe, halibut, and Greenland halibut (*Reinhardtius hippoglossoides*), traditional tagging experiments have provided evidence of migrations across deep-sea areas. Even trans-Atlantic crossing has been recorded for the cod. Although such basin-wide migrations may not occur regularly, they certainly show that demersal fishes are quite capable of considerable movements over long distances.

An example of regular seasonal migrations is offered by the north-east Arctic cod stock which has its main nursery and feeding area in the Barents Sea and along the shelf off Svalbard (**Figure 3**). Within this area, seasonal feeding migrations occur, typically in response to the distribution and migration of one of its principal prey, the small pelagic capelin (*Mallotus mallotus*). However, more spectacular are the several hundred kilometer spawning migrations of the adult cod. In the middle of the Arctic winter, cod from the northern feeding areas migrate southwards along the shelf edge off Norway, mostly against the prevailing currents. In February and March they aggregate in some primary coastal spawning areas such as the Lofoten grounds, and the banks and fiords of Møre. Spawning in the

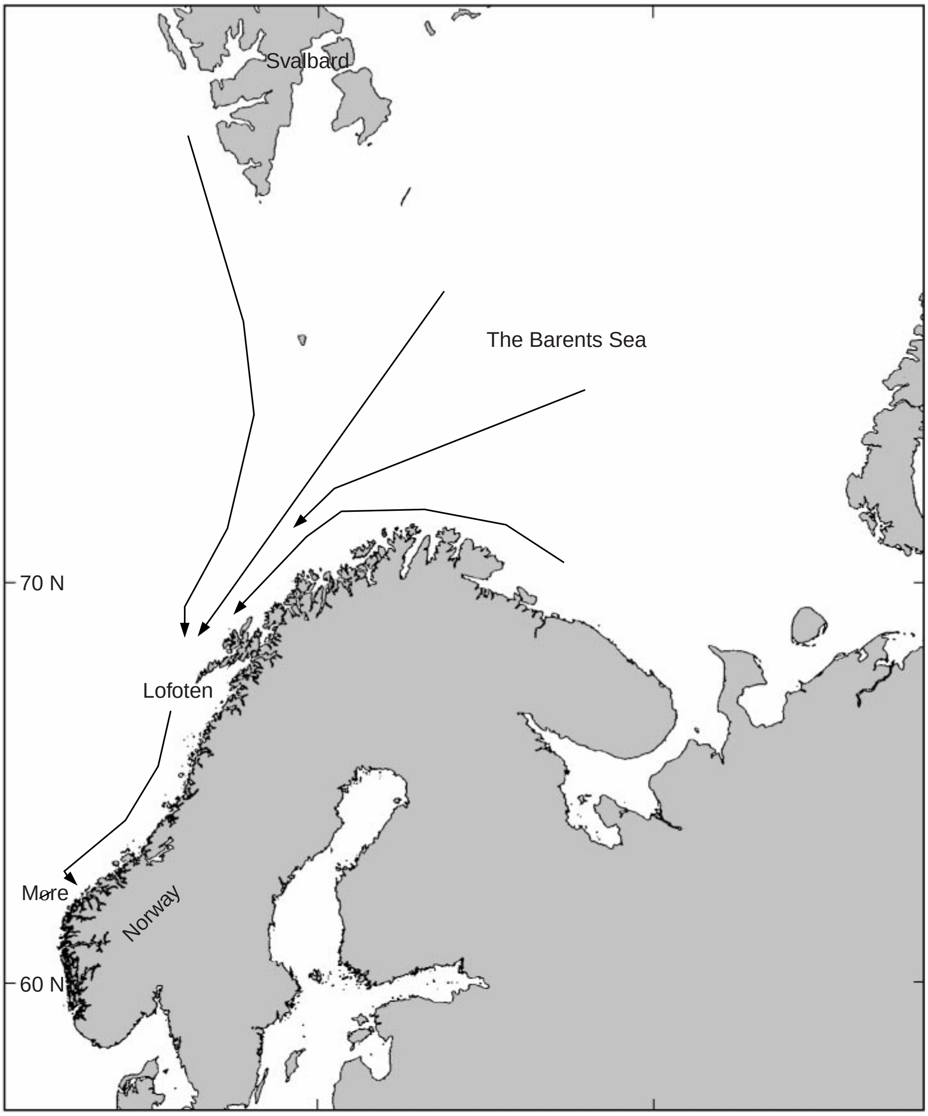

Figure 3 The pre-spawning migration of the north-east Arctic cod stock from its Barents Sea feeding areas to the spawning grounds on the coast of Norway.

right place at the right time is apparently essential to cod and many other demersal fishes.

Feeding and Diets

Most demersal fish are carnivores, customarily grouped into three categories: piscivores, benthophages, and zooplanktivores that predominantly eat fish, benthos, and zooplankton, respectively. In many areas, the production of benthic food is low or slow compared with the pelagic production, and in a range of demersal fish communities, there are actually surprisingly few entirely benthophagous fishes, i.e., feeding on epi- or infauna. A lot of demersal species depend on pelagic production by feeding on vertically migrating nekton and zooplankton entering or living in the near-bottom layer.

Piscivores usually have the capacity to deal with live prey that are large compared with their own body size, hence they tend to have big gapes. Some swallow their prey whole, others tear and bite the prey into smaller pieces. However, the techniques vary widely between species within the demersal fish group. Piscivores may either be active hunters, stealthers, or ambush predators. The latter two are often well camouflaged and obtain their prey by slowly approaching the prey or by a 'lie-and-wait' strategy. Stealthers rush forward to attack and grip the prey, whereas 'lie-and-wait' strategists may suddenly open their big mouth and ingest the prey by suction (e.g., the monkfish). Piscivores generally have several rows of conical backwardly pointing teeth both on the jaws and within the mouth and pharynx. These primarily prevent the prey from escaping and help in swallowing.

Benthophagous fishes also have several prey capture methods. Some apply suction after detecting prey on the surface of the sediment or within the sediment (e.g., many flatfishes, haddock), others bite off the siphons of buried bivalves or the arms of brittle stars, for example. Others feed on shelled animals and have very muscular jaws, and both jaw and pharyngeal dentition are adapted to crushing bivalve molluscs, coral, and sea urchins. Examples of the latter are the wolffishes (Anarichadidae) of boreal waters, and the parrotfishes (Sparidae) of warmer regions, but also many flatfishes that feed on bivalves or other animals with hard exoskeletons.

Zooplanktivores often lack dentition on the jaws, and rely on suction for ingesting their rather small prey whole. Most species probably pick their prey one at a time rather than filter-feed as clupeids and mackerels do at high prey densities. A most spectacular adaptation is seen among the sand eels (Ammodytidae) where the jaw is protrusible to the extent that the mouth size at prey capture becomes surprisingly big compared with the small head of the fish.

Co-existing species may have to divide resources amongst themselves in a way which reduces competition but enhances growth and survival. Partitioning of food resources among co-occurring species is regarded as a very significant structuring process within demersal fish communities. Many species may occupy the same space at the same time, but their diets tend to differ. However, the patterns observed today reflect both current processes and evolutionary adaptations (co-evolution). The resource partitioning among flatfishes is an example of the latter. Careful consideration of species-specific characters involved in the feeding process (e.g., mouth size and morphology, dentition, capability to detect and capture different prey taxa, etc.), reveals that the co-occurring species are actually different in many important ways.However, it is often found that juveniles have greater diet overlap than the adults. The potential for competition for food would therefore seem greater in areas where juveniles are abundant and co-occur.

In most demersal species there are significant ontogenetic, i.e., essentially size-related, changes in diet and feeding ranges. At metamorphosis, when larval characters are lost and most demersal fish take up a demersal life style, pronounced diet changes from feeding on planktonic crustaceans to feeding on benthic or benthopelagic prey may occur. As the fish grows larger, bigger or more energy-rich prey are needed to satisfy its energy requirements. Many species therefore go through a succession of feeding modes during their lifetime, usually starting as planktivores and ending as piscivores or benthofages. For a given species, pronounced diet shifts tend to happen at rather fixed sizes, but habitat shifts may happen concurrently, and it is sometimes difficult to determine which is more significant. Many species are also quite opportunistic, and their diet varies greatly between habitats and seasons, often depending on the food availability. In other more specialized species the character and extent of diet changes may be more constrained by their morphological adaptations.

Extensive studies of many co-occurring species were conducted in a demersal fish community on the North Sea coast off southern Norway, revealing rather pronounced species-specific diets and also ontogentic diet shifts. Benthofages, piscivores, and planktivores were represented in the area. For the piscivores, sand eels were the most common prey and several species fed on this prey, also the cod. The small cod had significant proportions of other prey, i.e., crustaceans, in its diet, but from about 30 cm onwards the sand eel dominated greatly (**Figure 4**). This pattern was observed in all seasons except for a short period in March–April when another prey, the herring, became very abundant and seemingly easily available. The herring visits this particular site to deposit its demersal eggs for a 4–6 week period every year. The cod showed a pronounced diet shift in this period, and the response was size-dependent. Only the larger individuals, 50–60 cm and more, fed on adult herring. Smaller cod may not be capable of capturing the 30–35 cm herring, but evidently feed heavily on herring eggs. Only the smallest cod continued to eat crustaceans even though they should be well adapted to locate and ingest herring eggs. Similar responses were observed for many of the demersal fishes in this community, even for planktivores that temporarily became benthofages when turning to egg feeding. In this case, diet overlap appeared to increase significantly both between and within species and this was probably possible because the herring and herring eggs were temporarily extremely abundant compared with the demand from the demersal fishes. The dietary flexibility observed in this area may be very advantageous, especially when living in strongly seasonal environments where the prey abundance varies quickly and perhaps unpredictably.

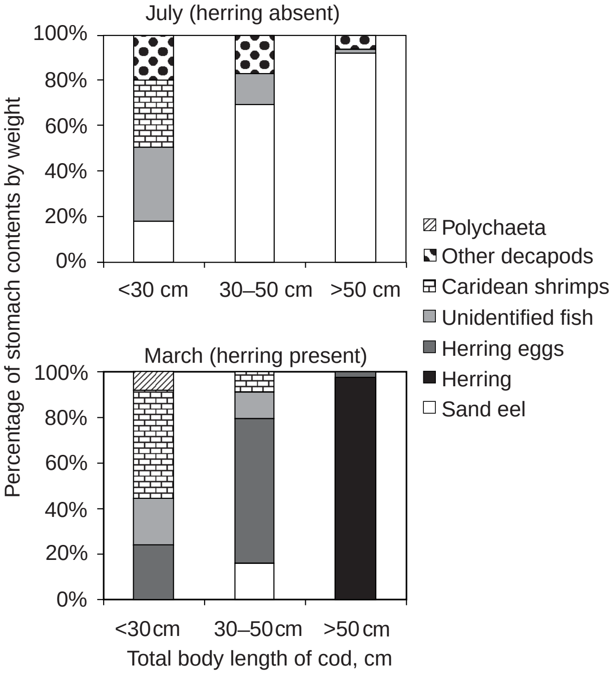

Figure 4 The diet of cod (*Gadus morhua*) on a coastal bank off south-west Norway, illustrating size-related and seasonal variation. Based on data given by Høines *et al.* (1995).

Sensory Systems

The shelf environment is generally well-lit and most demersal fishes have well-developed vision. In addition demersal fish may use mechanoreceptors (sense of pressure, motion, and sound), chemosensory (e.g., olfaction, gustation), and electrosensory (i.e., ability to detect electric fields) systems. Different systems may play essential roles during different stages of important processes such as prey detection, capture and handling, predator avoidance or reproduction. In general, mechanoreception by the acoustico-lateralis system (lateral line organ and ear) tends to be most important for the detection of predators, conspecifics, and other physical disturbances in the environment. Olfaction is very important to benthofages that have to search the substrate for food, whereas planktivores and piscivores tend to rely more heavily on vision. Gustation is most important after capturing prey. Benthofages may have elaborate adaptations of their olfactory system. In addition to a well-developed nose, they may have barbels on the snout (e.g., gadids, zoarcids) and modified and extended first rays of their pectoral fins (e.g., Triglidae) densely packed with olfactory sensory cells.

The electrosensory system is particularly well developed in some sharks and rays, and they may primarily use this system for prey location, but also for orientation and navigation. Some classical studies of the spotted dogfish (*Scyliorhinus canicula*) showed that this species was able to detect weak electric fields produced by an electrode buried in the sand. Indeed, the dogfish attacked the electrode in preference to a readily available piece of fish flesh, suggesting that electric cues were more important than visual and chemical cues in this case. Live prey, such as a buried flatfish favored by dogfish, produce weak electric fields that are modified by muscle activity, e.g., during ventilation.

Reproduction and Life History

The majority of demersal teleosts (bony fishes) are oviparous and produce free-floating eggs. Mating and spawning happen at the same time, often in mid-water. Some notable exceptions are the viviparous redfish (*Sebastes*) that release numerous pelagic larvae, and the wolffish (Anarhichadidae) which deposits a cluster of large eggs that is guarded until hatching. Sand eels (Ammodytidae) also have demersal eggs but do not protect the eggs. Most teleosts have no parental care other than making sure that they mate and spawn in an area and habitat that enhances the survival probability of their eggs, larvae, and pelagic juveniles. Most pelagic teleost eggs are small, i.e., a few millimeters in diameter, and the fecundity is high, i.e., thousands to millions of eggs per female. Batch spawning is common in the highly fecund species, e.g., the cod may spawn 10–13 batches of its very small eggs within a spawning season.

Demersal sharks are either ovoviviparous or viviparous, whereas rays and chimaeroids are oviparous, attaching their few large encapsulated eggs to debris or macroalgae. All species produce rather few young in each batch, i.e., from a couple to a few tens of eggs/juveniles, and the lifetime production is very low compared with most teleosts. Upon hatching or birth, the young resemble the adults, i.e., there is no definite larval stage such as in teleosts.

Spawning seasons vary in duration, and the general rule is that the more seasonal the production cycle, the more fixed and limited is the spawning season. High latitude fishes and those living in monsoonal or upwelling regions have comparatively short spawning seasons, whereas tropical and subtropical fishes have protracted seasons or year-round reproduction.

Larvae hatched from small pelagic eggs have a yolksac that may provide sufficient nutrition for a few days or weeks, after which they depend on exogenous feeding, usually on small crustacea such as copepod nauplii. The mortality in this period is very high indeed, and only a minute fraction of the total number of eggs spawned will eventually result in a surviving demersal juvenile.

The teleost postlarvae pass through a metamorphosis upon reaching a certain size. Characters such as fins and juvenile pigmentation develop, and sense organs also become fully developed. In flatfishes, the eye migration occurs. In general, the larva is transformed into a fish morphologically and behaviorally adapted for demersal life. Associated with this change is the settling on the seabed, at least for parts of the diurnal cycle. Settling areas are often, but not always, separated from the feeding areas of the older fish. This reflects the different habitat and food requirements of juveniles and adults, but may also reduce cannibalism. In the majority of teleost species, the demersal nursery areas are shallower than feeding grounds of older conspecifics. Estuaries and offshore shoals are typical nursery areas, also rocky shores where the substrate and macroalgae offer protection and a variety of prey. Tidal flats and sandy beaches are typical habitats of juvenile flatfish. A gradual ontogenetic shift in depth distribution happens as the juveniles grow larger.

The expected longevity of demersal species varies greatly. A general pattern is that longevity increases with increasing adult size, but there are many exceptions to this rule. Some species, e.g., redfishes (*Sebastes*), can probably live for at least 30–40 years, but this is unusual for shelf species. Small species such as Norway pout (*Trisopterus esmarki*) may live for 5–6 years at most, but in exploited areas this seldom happens. In most shelf waters, the fisheries have influenced age distributions to the extent that life expectancy is significantly reduced.

Somatic growth patterns also vary widely among demersal fishes. In fast-growing species living in strongly seasonal environments, the overall growth trajectory may show seasonality either because food supply and feeding rates vary, or because the somatic growth is influenced by reproductive activity/gonad growth. Growth rate usually declines significantly when the fish becomes mature, but never ceases entirely. Attempts have been made to classify species into *r*- and *K*-selected types (*r* and *K* are coefficients expressing rate of reproduction and somatic growth, respectively). The *r*-selected types are those with short life spans but fast growth and rather small adult size. They mature at a small size and low age, and can rapidly take advantage of short and unpredictable favorable environmental conditions by increasing their numbers. The *K*-species, however, tend to invest more energy in somatic growth by growing more slowly and maturing later in life, when they are capable of producing many young. The populations of such species comprise many age groups, and they are not, as the *r*-species, so vulnerable to repeated recruitment failures due to low survival of young over a range of years. There are many species that do not readily fit into these classes, and it is unusual for demersal shelf fishes to have the extreme *r*- or *K*-strategies as seen among epipelagic fishes and demersal deep-sea fishes, respectively.

See also

Antarctic Fish. Coral Reef Fishes. Deep-sea Fishes. Demersal Species Fisheries. Fish Feeding and Foraging. Fish Hearing, Lateral Lines. Fish Larvae. Fish Locomotion. Fish Migration, Horizontal. Fish Predation and Mortality. Fish Reproduction. Fish Vision. Intertidal Fishes.

Further Reading

Alexander RM (1967) *Functional Design in Fishes.* London: Hutchinson University Library.

Gerking SD (1994) *Feeding Ecology of Fish.* San Diego: Academic Press.

Gomes MC (1993) *Predictions under Uncertainty. Fish Assemblages and Food Webs on the Grand Banks of Newfoundland.* St John's, Canada: ISER, Memorial University of Newfoundland.

Høines Å, Bergstad OA and Albert OT (1995) The food web of a coastal spawning ground of the herring (*Clupea harengus* L.). In: Skjoldal HR, Hopkins C, Erikstad KE and Leinaas HP (eds.) *Ecology of Fjords and Coastal Waters,* Amsterdam: Elsevier Science BV.

Jobling M (1995) *Environmental Biology of Fishes.* London: Chapman and Hall.

Laevastu T (1996) *Exploitable Marine Ecosystems: Their Behaviour and Management.* Oxford: Fishing News Books.

Nelson JS (1976) *Fishes of the World.* New York: John Wiley & Sons.

Overholtz WJ and Tyler AV (1985) Long-term responses of the demersal fish assemblages of Georges Bank. *Fishery Bulletin US* 83: 507–520.

Pitcher TJ (ed.) (1993) *The Behaviour of Teleost Fishes*, 2nd edn. London: Chapman & Hall.

Postma H and Zijlstra JJ (1988) *Ecosystems of the World 27. Continental Shelves.* Amsterdam: Elsevier Science Publishers BV.

Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* 2: 352–388.