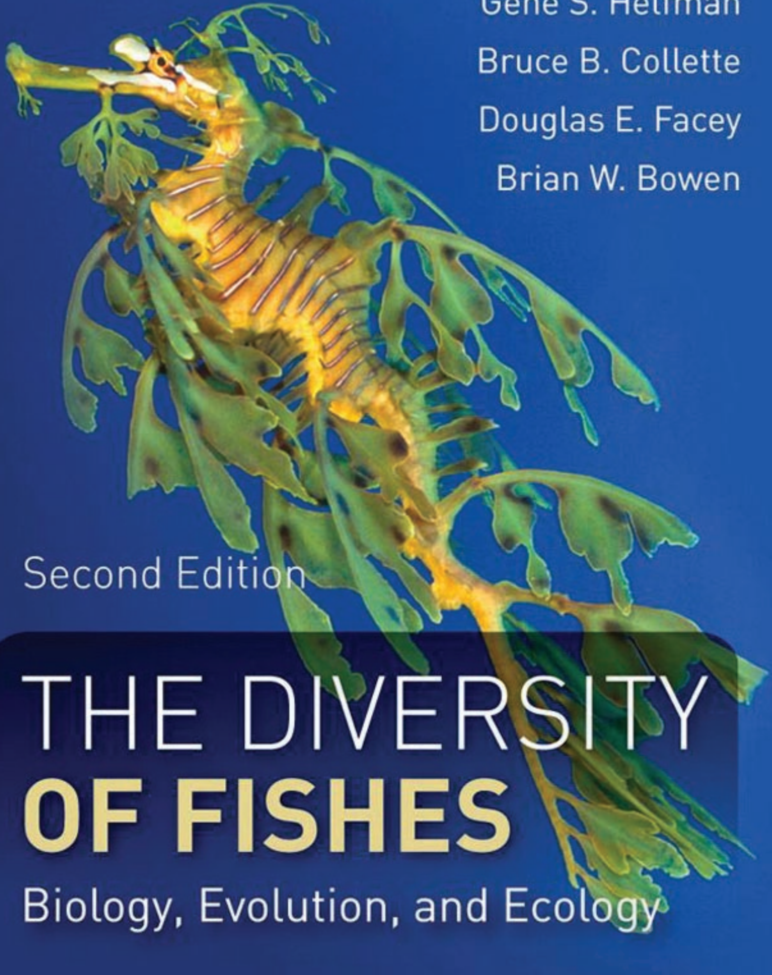

Gene S. Helfman
Bruce B. Collette
Douglas E. Facey
Brian W. Bowen

Second Edition

THE DIVERSITY OF FISHES

Biology, Evolution, and Ecology

WILEY-BLACKWELL

THE DIVERSITY
OF FISHES

Dedications:

To our parents, for their encouragement of our nascent interest in things biological;

To our wives – Judy, Sara, Janice, and RuthEllen – for their patience and understanding during the production of this volume;

And to students and lovers of fishes for their efforts toward preserving biodiversity for future generations.

Front cover photo:

A Leafy Sea Dragon, *Phycodurus eques*, South Australia. Well camouflaged in their natural, heavily vegetated habitat, Leafy Sea Dragons are closely related to seahorses (Gasterosteiformes: Syngnathidae). “Leafies” are protected by Australian and international law because of their limited distribution, rarity, and popularity in the aquarium trade. Legal collection is highly regulated, limited to one “pregnant” male per year. See Chapters 15, 21, and 26. Photo by D. Hall, www.seaphotos.com.

Back cover photos (from top to bottom):

A school of Blackfin Barracuda, *Sphyraena qenie* (Perciformes, Sphyraenidae). Most of the 21 species of barracuda occur in schools, highlighting the observation that predatory as well as prey fishes form aggregations (Chapters 19, 20, 22). Blackfins grow to about 1 m length, display the silvery coloration typical of water column dwellers, and are frequently encountered by divers around Indo-Pacific reefs. Barracudas are fast-start predators (Chapter 8), and the pan-tropical Great Barracuda, *Sphyraena barracuda*, frequently causes ciguatera fish poisoning among humans (Chapter 25).

Longhorn Cowfish, *Lactoria cornuta* (Tetraodontiformes: Ostraciidae), Papua New Guinea. Slow moving and seemingly awkwardly shaped, the pattern of flattened, curved, and angular trunk areas made possible by the rigid dermal covering provides remarkable lift and stability (Chapter 8).

A Silvertip Shark, *Carcharhinus albimarginatus* (Carcharhiniformes: Carcharhinidae), with a Sharksucker (*Echeneis naucrates*, Perciformes: Echeneidae) attached. This symbiotic relationship between an elasmobranch (Chapter 12) and an advanced acanthopterygian teleost (Chapter 15) probably benefits both, the Sharksucker scavenging scraps from the shark’s meals and in turn picking parasitic copepods off the shark. Remoras also attach to whales, turtles, billfishes, rays, and an occasional diver. Remoras generate sufficient suction to hang on even at high speeds via a highly modified first dorsal fin.

A recently discovered 10 cm long Indonesian antennariid, nicknamed the Psychedelic Frogfish (Lophiiformes: Antennariidae) (Chapters 14, 18). Among its atypical traits are its shallow water habitat, a lack of an illicial lure, jet propulsion, and a bouncing method of movement, and its practice of hiding in holes, not to mention the spectacular head and body coloration.

A mating pair of Mandarinfish, *Synchiropus splendidus* (Perciformes: Callionymidae), Indonesia. These small (6 cm), secretive dragonets live among coral branches or rubble, and usually emerge just after sunset to mate. Recently extruded eggs can be seen just below the pair.

Lionfish, *Pterois volitans* (Scorpaeniformes: Pteroidae), are native to the Indo-Pacific region. They have been introduced along the southeastern coast of the USA and the Bahamas, apparently due to aquarium releases. In their native habitats they seldom reach high densities but have undergone a population explosion on Bahamian reefs. Atlantic reef fishes are naive to lionfish predatory tactics, and predation rates by lionfish are high.

Photos by D. Hall, www.seaphotos.com.

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Chapter 18

Special habitats and special adaptations

Chapter contents

CHAPTER CONTENTS

Given our themes of diversity and adaptation, it seems appropriate to explore habitats and geographic regions that have led to spectacular evolutionary events among fishes. Certain climatic regimes and regions appear unusually harsh for successful invasion by complex vertebrate life forms. But fishes have been able to occupy almost all naturally occurring aquatic ecosystems that have any degree of permanence or at least predictability. It is often quite easy to determine the major selective pressures impinging on fishes in these habitats, and it is also often obvious what physiological, anatomical, and ecological adaptations have evolved in response to specific environmental pressures. An axiom of evolutionary biology is that animals exposed to similar selection pressures are likely to evolve similar adaptations. This axiom, formalized as the **Principle of Convergence**, states that the stronger the selection pressures, the more similar unrelated animals will appear. In other words, where selection pressures are particularly extreme, animals will converge in morphology, physiology, behavior, and ecology, approaching an optimal design for that particular set of environmental forces. The special habitats discussed below – the deep sea, the open sea, polar regions, deserts, turbulent water habitats, and caves – show this principle in operation.

The deep sea

The most diverse deepsea fish assemblages occur between 40°N and 40°S latitudes, roughly between San Francisco and Melbourne, Australia in the Pacific Basin and between New York City and the Cape of Good Hope in the Atlantic Basin. Separation of deepsea fishes occurs more on a vertical than on a latitudinal basis (Fig. 18.1). The three major regions of open water are **mesopelagic** (200–1000 m), **bathypelagic** (1000–4000 m), and **abyssal** (4000–6000 m); deepsea regions below 6000 m are referred to as **hadal** depths. A second group of **benthal** or bottom-associated species swims just above the bottom (= **benthopelagic**) or lives in contact with it (= **benthic**), usually along the upper continental slope at depths of less than 1000 m; corresponding ecological zones of benthal species are referred to as bathyal, abyssal, and hadal. The upper 200 m of the open sea, termed the **epipelagic** or **euphotic zone**, has its own distinctive subset of fishes (see below). This is the region where the photosynthetic activity of phytoplankton exceeds the respiration of the plants and animals living there, i.e., where production/respiration >1. The euphotic zone is the energy source for the deeper waters (Marshall 1971; Wheeler 1975; Nelson 1994; Castro & Huber 1997, Neighbors & Wilson 2006).

The deepsea fishes of the mesopelagic and bathypelagic regions are readily recognized by just about anyone with a passing interest in fishes or marine biology. Deepsea fishes often have light-emitting organs, termed **photophores**;

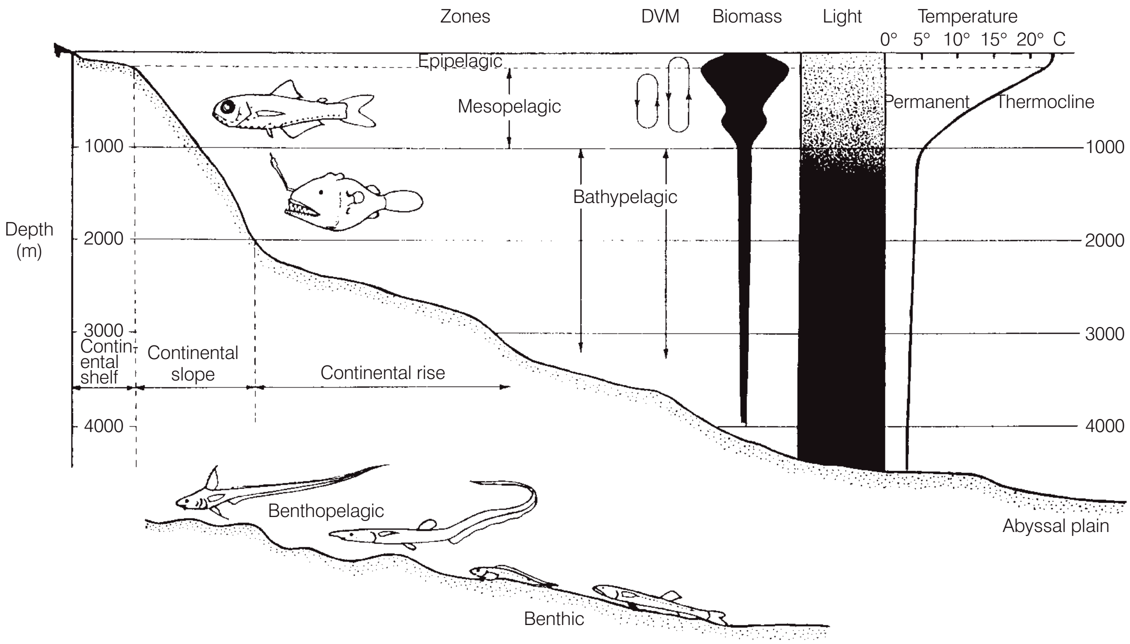


Figure 18.1

Regions and physical features of the deepsea environment relative to depth. Representative species are a mesopelagic lanternfish, bathypelagic ceratioid anglerfish, benthopelagic rattail and halosaur, and benthic snailfish and greeneye. Many mesopelagic species undergo a diurnal vertical migration (DVM) to shallower waters at dusk, returning to deeper water at dawn. Total biomass of living organisms, available light, and temperature all decline with depth in the deep sea. From Marshall (1971), used with permission.

large or long mouths studded with daggerlike teeth; chin barbels or dorsal fin rays modified as lures; long, thin bones; and greatly enlarged, tubular eyes or greatly reduced eyes (Marshall 1954, 1971). Such familiar appearances could result from a relative scarcity of forms. For example, widespread familiarity with deepsea fishes could occur if we were exposed to many illustrations of the same strange animals. As the taxonomic listing in Table 18.1 reveals, the recognizability of deepsea fishes is not a function of scarcity or a depauperate fauna. More than 1000 species of fishes inhabit the open waters of the deep sea and another 1000 species are benthal, with good representation across orders of cartilaginous fishes and superorders of bony fishes. Similarities among unrelated fishes are therefore not due to phylogenetic relations but to convergent adaptations.

Deepsea fishes look alike because different ancestors invaded the deep sea from shallow regions and evolved similar anatomical and physiological solutions to an extreme environment. Understanding the convergent adaptations of deepsea fishes requires that we first understand the physical environment of the deep sea and its influences on biota. Five physical factors contrast markedly between the surface and the deep sea and appear to have been strong selective forces on fishes (Marshall 1971; Hochachka & Somero 1984).

Physical factors affecting the deep sea

Pressure

The weight of the overlying column of water, measured in atmospheres, increases constantly with depth at a rate of 1 atm/10 m of descent (1 atm = 1.03 kg/cm^2 or 14.7 lbs/in^2). Thus between the top of the mesopelagic region at 200 m and the lower bathypelagic region at 4000 m, pressure increases 20-fold, from 20 to 400 atm. The deepest living fishes, the neobythitine cusk-eels, *Bassogigas profundissimus* and *Abyssobrotula galatheae*, have been collected at 7160 and 8370 m, respectively, where they would experience pressures of 700–800 atm, or *c*. 12,000 lbs/in^2 (Nielsen & Munk 1964; Nielsen 1977). Below the surface, pressure at any given depth is constant and predictable, whereas at the surface it can change rapidly and significantly with each passing wave.

The tremendous pressures of the deep sea do not create problems for most biological structures because fishes are made up primarily of water and dissolved minerals, which are relatively incompressible. However, pressure has an influence on the volume of water molecules, water-containing compounds, and proteins, which affects the rates of chemical reactions. Several deep mesopelagic and bathypelagic species have evolved proteins that are much less sensi-

Table 18.1

Representative teleostean taxa from the three major deepsea habitat types. The approximate number of deepsea families is given in parentheses the first time a group is listed. Based on Marshall (1971, 1980); Wheeler (1975); Gage and Tyler (1991); Nelson (2006). Figures from Marshall (1971), used with permission.

Mesopelagic (750 spp.)

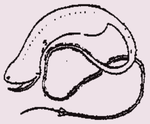
- Superorder Elopomorpha
  - Albuliformes (3): Notacanthidae – spiny eels
  - Anguilliformes (6): Nemichthyidae – snipe eels; Synaphobranchidae – cutthroat eels
- Superorder Protacanthopterygii
  - Argentiniformes (5): Microstomatidae – deepsea smelts; Opisthoproctidae – barreleyes; Alepocephalidae – slickheads; Platytroctidae – tubeshoulders
- Superorder Stenopterygii
  - Stomiiformes (5): Gonostomatidae – bristlemouths; Sternoptychidae – hatchetfishes; Stomiidae – barbeled dragonfishes
- Superorder Cyclosquamata
  - Aulopiformes (11): Evermannellidae – sabertooth fishes; Alepisauridae – lancetfishes; Paralepididae – barracudinas; Giganturidae – telescopefishes
- Superorder Scopelomorpha
  - Myctophiformes (2): Neoscopelidae – blackchins; Myctophidae – lanternfishes
- Superorder Lampriomorpha
  - Lampriformes (4): Stylephoridae – tube-eyes
- Superorder Acanthopterygii
  - Stephanoberyciformes: Mirapinnidae – hairyfish
  - Perciformes: Chiasmodontidae – swallowers; Gempylidae – snake mackerels

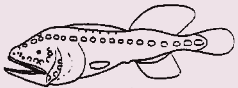

hachetfish


giganturid

Bathypelagic (200 spp.)

- Superorder Elopomorpha
  - Anguilliformes: Nemichthyidae – snipe eels; Serrivomeridae – sawtooth eels
  - Saccopharyngiformes: Saccopharyngidae – swallower and gulpers; Eurypharyngidae – pelican eels
- Superorder Protacanthopterygii
  - Argentiniformes: Alepocephalidae – slickheads
- Superorder Stenopterygii
  - Stomiiformes: Gonostomatidae – bristlemouths
- Superorder Paracanthopterygii
  - Gadiformes: Melanonidae – pelagic cods; Macrouridae – grenadiers and rattails
  - Ophidiiformes: Ophidiidae – cusk-eels; Bythitidae – viviparous brotulas
  - Lophiiformes (12): Ceratioidei – deepsea anglerfishes, seadevils (11)
- Superorder Acanthopterygii
  - Stephanoberyciformes: Melamphaidae – bigscale fishes; Stephanoberycidae – pricklefishes; Cetomimoidea – whalefishes (3)
  - Beryciformes (9): Anoplogastridae – fangtooths
  - Perciformes: Chiasmodontidae – swallowers


gulper


whalefish

Benthal[a] (1000 benthopelagic and benthic spp.)

- Superorder Elopomorpha
  - Albuliformes: Halosauridae – halosaurs; Notacanthidae – spiny eels
  - Anguilliformes: Synaphobranchidae – cutthroat eels
- Superorder Cyclosquamata
  - Aulopiformes: Synodontidae – lizardfishes; Chlorophthalmidae – greeneyes; Ipnopidae – spiderfishes and tripodfishes
- Superorder Paracanthopterygii
  - Gadiformes: Macrouridae – grenadiers; Moridae – morid cods; Merlucciidae – merlucciid hakes
  - Ophidiiformes: Ophidiidae – cusk-eels; Bythitidae – viviparous brotulas; Aphyonidae – aphyonids
  - Lophiiformes: Ogcocephalidae – batfishes
- Superorder Acanthopterygii
  - Scorpaeniformes: Liparidae – snailfishes
  - Perciformes: Zoarcidae – eel-pouts; Bathydraconidae – Antarctic dragonfishes; Caproidae – boarfishes


brotula

[a] Chimaeras and many squaloid sharks are benthopelagic. Most benthal fishes live above 1000 m, although some grenadiers and rattails live between 1000 and 4000 m, macruronid southern hakes live somewhat deeper, tripodfish live to 6000 m, snailfishes to 7000 m, and neobythitine cusk-eels live down to 8000 m.

tive to the effects of pressure than are their shallow water relatives (Hochachka & Somero 1984; Somero et al. 1991). Gas-containing structures are particularly affected because both volume relationships and gas solubility are sensitive to pressure. The organ most affected is the gas bladder because it is difficult to secrete gas into a gas-filled bladder under high pressure. Three trends occur in the gas bladders of deepsea fishes that reflect the constraints of pressure:

1. The efficiency of gas secretion depends on the interchange surface of the capillaries of the **rete mirabile**, the main gas-secreting organ (see Chapter 5, Buoyancy regulation). Whereas the retes of epipelagic fishes are usually less than 1 mm long, retes of upper mesopelagic fishes are 1–2 mm long, those of lower mesopelagic fishes are 3–7 mm long, and those of some bathypelagic fishes are 15–20 mm long.
2. Although mesopelagic fishes have large gas-filled bladders, most bathypelagic fishes have lost their gas bladders. Flotation might therefore be a problem for these fishes, but their body musculature and skeletons are reduced as energy saving mechanisms and they consequently approach neutral buoyancy. As long as a fish remains at relatively constant depths, it has minimal need for buoyancy control. However, many mesopelagic fishes undergo **diurnal vertical migrations**, have a greater need to adjust their buoyancy, and have retained their gas bladders. Deep benthopelagic fishes are able to hover just above the bottom with minimal energy expenditure via a different mechanism. Instead of trying to secrete gases against incredible pressure gradients, they have evolved **lipid-filled** gas bladders. Lipids are relatively incompressible and are lighter than sea water and thus provide flotation. Interestingly, the larvae of these fishes have gas-filled bladders, but these larvae, and the larvae of nearly all deepsea fishes, are epipelagic, where the costs of gas secretion and buoyancy adjustment are much less. Benthopelagic squaloid sharks such as *Centroscymnus* and *Etmopterus* show parallel evolution. These deepsea sharks have exceptionally large livers that account for 25% of their total body mass. Their livers contain large quantities of the low-density lipid **squalene**. Deepwater holocephalans also achieve neutral buoyancy via squalene and by reduced calcification of their cartilaginous skeletons (Bone et al. 1995).
3. Most deepsea fishes belong to the relatively primitive teleostean superorders Protacanthopterygii, Stenopterygii, Cyclosquamata, and Scopelomorpha. These taxa typically have a direct, physostomous connection between the gas bladder and the gut. Deepsea fishes are, however, “secondarily” physoclistous, having closed the pneumatic duct, thus preventing gas from escaping out the mouth.

Temperature

At the surface, temperature is highly discontinuous, changing markedly both seasonally and daily. In the deep sea, temperature is a predictable function of depth. Surface waters are warmer than deeper waters. Water temperature declines with depth through the mesopelagic region across a **permanent thermocline** until one reaches the bathypelagic region, where temperature remains a relatively constant 2–5°C, depending on depth.

Temperature is a strong predictor of distribution for different taxa of deepsea fishes. Ceratioid anglerfishes and darkly colored species of the bristlemouths (*Cyclothone*) are restricted to the deeper region. Even within the mesopelagic zone, species sort out by temperature. Hatchetfishes, pale *Cyclothone*, and malacosteine loosejaws are restricted to the lower half at temperatures between 5 and 10°C, whereas lanternfishes and astronesthine and melanostomiatine stomiiforms occur in the upper half at 10–20°C. Latitudinal differences in temperature–depth relationships lead to distributional differences within species. Some species such as ceratioid anglers that are mesopelagic at high latitudes occur in bathypelagic waters at lower latitudes, a phenomenon known as **tropical submergence** that results from the warmer surface temperatures in the tropics.

Since temperature remains fairly constant at any given depth, absolute temperature is a minimal constraint on a fish that does not move vertically. But vertically migrating mesopelagic species must swim through and function across a temperature range of as much as 20°C (see Fig. 18.1). Lanternfish species that migrate vertically have larger amounts of DNA per cell than do species that are non-migratory. Increased DNA could potentially allow for multiple enzyme systems that function at the different temperatures encountered by the fishes (Ebeling et al. 1971).

Space

The volume occupied by the deep sea is immense. Approximately 70% of the earth’s surface is covered by ocean, and 90% of the surface of the ocean overlies water deeper than 1000 m. The bathypelagic region, which makes up 75% of the ocean, is therefore the largest habitat type on earth. This large volume creates problems of finding food, conspecifics, and mates because bathypelagic fishes are never abundant. Life in the bathypelagos is extremely dilute. For example, female ceratioid anglerfishes are distributed at a density of about one per 800,000 m^3, which means a male anglerfish is searching for an object the size of a football in a space about the size of a large, totally darkened football stadium.

Deepsea fishes show numerous adaptations that reflect the difficulties of finding potential mates that are widely distributed in a dark expanse. Unlike most shallow water forms, many deepsea fishes are **sexually dimorphic** in ways directly associated with mate localization. Mesopelagic fishes, such as lanternfishes and stomiiforms, have species-specific and sex-specific patterns and sizes of light organs, structures that first assure that individuals associate with the right species and then that the sexes can tell one another apart. Among benthopelagic taxa, such as macrourids, brotulids, and morids, males often have larger muscles attached to their gas bladders that are likely used to vibrate the bladder and produce sounds that can attract females from a considerable distance.

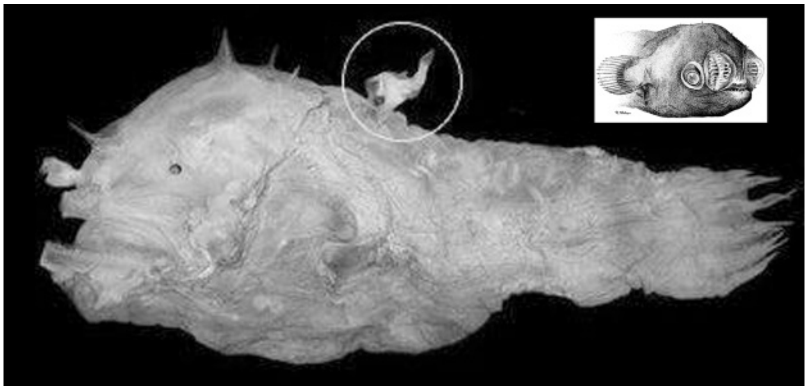


Figure 18.2

Size differences in male versus female anglerfishes. A 6.2 mm parasitic male *Photocorynus spiniceps* (Linophrynidae) (circled) attached to the dorsal area of a 46 mm female. Inset: a free-living, 18 mm male of *Linophryne arborifera* (Linophrynidae), showing the greatly enlarged eyes and olfactory lamellae apparently used in finding females. From Pietsch (2005), used with permission; photos courtesy of T. W. Pietsch.

Some of the most bizarre sexual dimorphisms occur among bathypelagic species, where problems of mate localization are acute. The most speciose group of bathypelagic fishes is the ceratioid anglerfishes, of which there are 11 families and about 162 species (Bertelsen 1951; Pietsch 1976, 2005; Nelson 2006; Pietsch & Orr 2007; see Fig. 14.28). In several families, the males are dwarfed, reaching only 20–40 mm long, whereas females attain lengths 10 or more times that size, up to 1.2 m in one species. In five families, males attach temporarily to females, spawning occurs, and the males swim free (Pietsch 2005). In five other families, the males are entirely and permanently **parasitic** on the females, and males in these taxa may be as small as 6.2 mm, making them the smallest known sexually mature vertebrate (Fig. 18.2). Males attach most frequently to the ventral midline of the belly of the female, but may be attached on the sides, backs, head, and even the fishing lure of a female; as many as eight males have been found attached to a single female (including some species mismatches). In parasitic species, males attach by the mouth, his mouth tissue fuses with her skin, and he becomes parasitically dependent on her for nutrition. Many of his internal organs degenerate, with the exception of his testes, which can take up more than half of his coelom. Females do not mature sexually until a male attaches to them (Pietsch 2005).

The premium placed on locating a female is reflected throughout the anatomy and physiology of searching males. During this phase, males have highly lamellated olfactory organs and well-developed olfactory tracts, bulbs, and forebrains, whereas females have almost entirely degenerate olfactory systems. Males also have extensive red muscle fibers, the kind used for sustained swimming. Females have predominantly white muscle fibers, which usually function for short bursts of swimming. Males of some species possess enlarged, tubular eyes that are extremely sensitive to light (see below), whereas females have small, relatively insensitive eyes. Males also have high lipid reserves in their livers, which they need because their jaw teeth become replaced by beaklike denticles that are useless for feeding but are apparently specialized for holding onto a female (the denticular jaws are derived embryologically from the same structures that in females develop into the fishing lure, discussed below; Munk 2000). All this comparative evidence indicates that males are adapted for swimming over large expanses of ocean, searching for the luminescent glow and some olfactory cue emitted by females. Females in contrast are floating relatively passively, using their bioluminescent lures to attract prey at which they make sudden lunges, and trailing pheromones through the still waters. The coevolved nature of these traits is evident from the dependence of both sexes on locating each other. Neither sex matures until the male attaches to the female.

Convergence occurs in the unrelated bathypelagic bristlemouths, which are probably the most abundant vertebrates on earth. Again, males are smaller than females, have a well-developed olfactory apparatus, extensive red muscle fibers, and larger livers and fat reserves. Although the males are not parasitic on the females, they are unusual in that they are **protandrous hermaphrodites**, meaning that an individual matures first as a male and then later switches sex and becomes a female. Sex change theory predicts just such a switch because relative fitness favors being a male when small and a female when large (see Chapter 10, Determination, differentiation, and maturation; Chapter 21, Gender roles in fishes). Cetomimid whalefishes – one of the few percomorph groups to occupy the bathypelagic region and second only to oneirodid anglerfishes in diversity there – have also converged on having dwarf males, although male whalefishes are not known to be parasitic on the larger females (Nelson 2006).

Light

Below the euphotic zone, light is insufficiently strong to promote significant plant growth. Visible light to the human eye is extinguished by 200–800 m depth, even in the uniformly clear water of the mesopelagic and bathypelagic regions. Deepsea fishes are 15–30 times more sensitive to light and can detect light down to between 700 and 1300 m, depending on surface clarity. The mesopelagic region is often termed the **twilight zone**, whereas the bathypelagic region is continually dark. What little light that passes into the mesopelagic region has been differentially absorbed and scattered by water molecules and turbidity and is limited to relatively short, blue-green wavelengths centered on 470 nm.

The greatly reduced illumination of the mesopelagic region, and the missing light of the bathypelagic region, have produced obvious adaptations among both the eyes and photophores of fishes living there. Bathypelagic fishes live in permanent darkness and, with the exception of male ceratioid anglers, have greatly reduced eyes that probably function primarily for detecting nearby bioluminescence. Mesopelagic fishes have modifications to their eyes that generally increase their ability to capture what little ambient light is available, although different species appear to have emphasized capturing dim ambient spacelight versus brighter point sources from bioluminescence (Warrant & Locket 2004). Mesopelagic fishes have very large eyes, often measuring 50% of head length; most North American freshwater fishes have eye diameters that are only 10–20% of head length.

Mesopelagic fishes also have comparatively large pupils and lenses and lengthened eyes. Elongation results either from a space between the pupil and lens, termed the **aphakic** or **lensless space**, or from lengthening of the retina-containing portion of the eye posterior to the lens. Aphakic spaces have evolved convergently in protacanthopterygian platytroctids and bathylagine deepsea smelts, stenopterygian loosejaws (Malacosteinae), cyclosquamate waryfishes, and scopelomorph lanternfishes, most of which live in the upper region of the mesopelagic zone. Tubular eyes, more characteristic of deeper mesopelagic species, have evolved convergently in four superorders and five orders of mesopelagic fishes, including protacanthopterygian barreleyes, stenopterygian hatchetfishes, paracanthopterygian anglerfishes, and acanthopterygian whalefishes. Eye elongation provides two visual benefits, increasing the sensitivity of the eye to light by about 10% and also increasing binocular overlap, which aids depth perception (Marshall 1971; Lockett 1977).

Mesopelagic fishes have pure rod retinae with visual pigments that are maximally sensitive at about 470 nm, which is a good match to the light environment at mesopelagic depths and also matches the light output from photophores, structures that are much more common among mesopelagic than bathypelagic fishes. **Bioluminescence** has evolved independently in at least five superorders of deepsea teleosts – protacanthopterygians, stenopterygians, scopelomorphs, paracanthopterygians, and acanthopterygians – as well as in dogfish sharks, squids, crustaceans, and other invertebrates. Light organs, in addition to identifying the species and sex of the emitter, may also illuminate nearby prey. The structures that bioluminesce may be a simple luminescent gland backed by black skin that emits on its own or contains bioluminescent bacteria. More complex circular photophores may be backed by silvery reflective material with a lens through which light passes. In highly derived photophores, the lens may be pigmented and hence the light transmitted is of a different wavelength, as in the malacosteine loosejaws which have a red filter over the subocular photophores and also have retinal reflectors and receptors sensitive to red wavelengths (e.g., Herring & Cope 2005). This unique combination of luminescent emission and spectral sensitivity could give loosejaws a private channel over which they can communicate without being detected by potential predators or prey. It could also serve to maximize illumination of red mesopelagic crustaceans (Lockett 1977; Denton et al. 1985; Sutton 2005). Photophores tend to flash on for 0.2–4 s, depending on species. Different species of lanternfishes may have similar photophore patterns but different flash rates, suggesting a convergence in communication tactics between deepsea fishes and fireflies (Meinsinger & Case 1990).

Food

Limited light and huge volume mean that food is extremely scarce in the deep sea. All marine food chains, except at **thermal vents**, originate in the euphotic zone, which makes up only 3% of the ocean. Food for bathypelagic fishes must therefore first pass through the filter of vertebrates, invertebrates, and bacteria in the mesopelagic zone; much of this food rains down weakly, unpredictably, and patchily in the form of carcasses, sinking sargassum weed, detritus, and feces. All deepsea fishes are carnivorous, feeding either on zooplankton, larger invertebrates, or other fishes. Zooplankton biomass at the top of the bathypelagos is only about 1% of what it is at the surface, and densities of benthic invertebrates decrease with depth and distance from continental shores. High densities, diversities, and productivity of invertebrates at thermal vents on the deepsea floor do not support a similar abundance or diversity of fishes. Only three species – a bythitid brotula and two zoarcid eel-pouts – are endemic to and frequent vent areas (Grassle 1986; Cohen et al. 1990). A general scarcity of food in the deep sea puts a premium on both saving and obtaining energy. Convergent traits in both categories are readily apparent.

Foraging adaptations

Deepsea fishes show a number of convergent foraging traits (Gartner et al. 1997). In general, zooplanktivores have small mouths and numerous, relatively fine gill rakers, whereas predators on larger animals have larger mouths and fewer, coarser gill rakers. **Daggerlike teeth** or some other form of long, sharp dentition is so characteristic of deepsea forms that their family names often refer directly or indirectly to this trait, including such colorfully named groups as dragonfishes, daggertooths, bristlemouths, snaggletooths, viperfishes, sabretooths, and fangtooths. Large, expandable mouths, hinged jaws, or distensible stomachs are also reflected in such names as gulpers, swallowers, and loosejaws. Saccopharyngoid gulper and swallower eels have enormous mouths that can expand to > 10 times the volume of the animal's entire body, the largest mouth : body volume of any known vertebrate (Nielsen et al. 1989). Black dragonfishes, viperfishes, ceratioid anglerfishes, and sabertooth fishes can swallow prey larger than themselves (Fig. 18.3), as much as three times so in the case of the anglerfishes. Their swallowing abilities are increased because the pectoral girdle is disconnected from the skull, enlarging the intercleithral space of the throat (see Chapter 8, Pharyngeal jaws). All of these anatomical specializations point to a strategy of taking advantage of any feeding opportunity that may come along, despite the size of the prey.

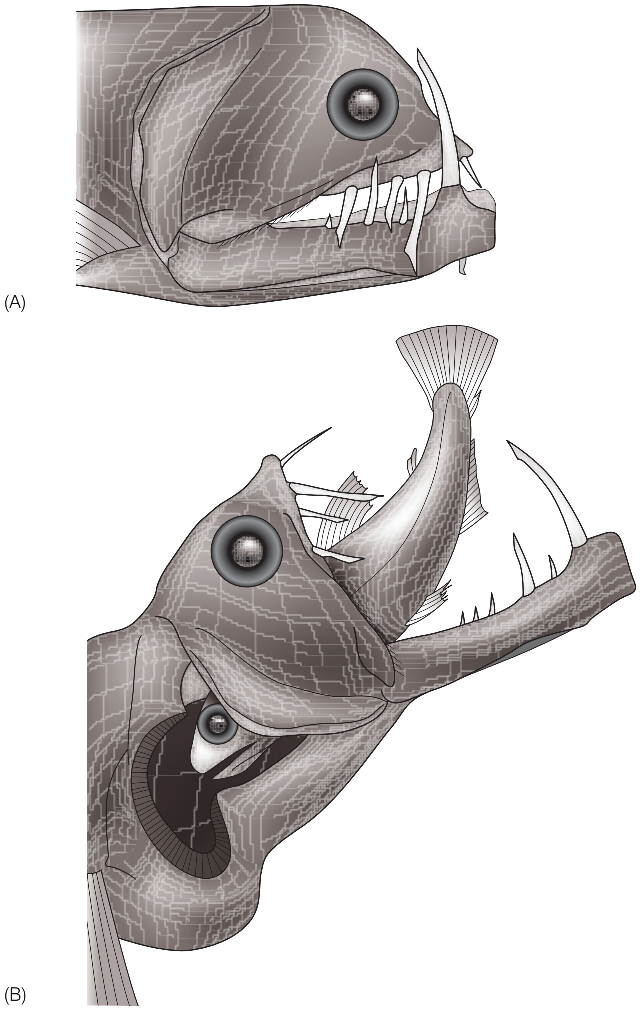


Figure 18.3

Extreme movements of the head and mouth during swallowing in the viperfish, *Chauliodus sloani*. (A) Mouth at rest, showing the premaxillary and mandibular teeth that sit outside the jaw when the mouth is closed. The maxillary and palatine teeth are small and slant backward. (B) Mouth opened maximally as prey is captured and impaled on the palatine teeth prior to swallowing. The anterior vertebrae and neurocranium are raised, the mandibuloquadrate joint at the back corner of the mouth is pushed forward, and the gill covers are pushed forward and separated from the gills and gill arches. The heart, ventral aorta, and branchial arteries are also displaced backward and downward. Such wide expansion of the mouth accommodates very large prey and is in part necessary for prey to pass between the large fangs. After Tchernavin (1953).

A small number of shallow water paracanthopterygian species, notably the goosefishes, frogfishes, batfishes, and anglerfishes, possess modified dorsal spines that are waved in front of prey species to lure them within striking distance. Such lures reach their greatest and most diverse development among mesopelagic and bathypelagic fishes, where they occur on viperfishes, various dragonfishes, astronesthine snaggletooths, most ceratioid anglerfishes, and arguably as luminescent organs in the mouths of hatchetfishes, lanternfishes, and some anglerfishes and on the illuminated tail tip of the gulper eels. The typical anglerfish lure consists of an elongate dorsal spine, the **illicium**, tipped by an expanded structure called the **esca** (Fig. 18.4). Escae tend to have species specific shapes, can regenerate if damaged, and are moved in a variety of motions that imitate the swimming of a small fish or shrimp (see Pietsch 1974).

Most mesopelagic fishes undertake evening migrations from the relatively unproductive mesopelagic region to the richer epipelagic zone to feed; they then return to the mesopelagic region at dawn (see Fig. 18.1). The migration involves movements to near the surface from as deep as 700 m, can take an hour or more, and may entail considerable energy expenditure. This movement is so characteristic of mesopelagic fishes, crustaceans, and mollusks that the community of organisms that migrates is referred to as the **deep scattering layer**, whose presence is discernible on sonar screens because of reflection of sonar signals off the

Figure 18.4

An adult female wolftrap angler, *Lasiognathus amphirhamphus* (Thaumatichthyidae), about 15 cm long. The rodlike structure pointing tailward is the skin-covered caudal end of the dorsal spine that forms the illicium. The spine slides in a groove on the head, allowing the anglerfish to move it forward when fishing but to retract it otherwise. Photo courtesy of T. W. Pietsch.

gas bladders of the fishes. Hypotheses about the adaptiveness of the migration include: (i) a net energy gain from feeding in warm water and metabolizing in cold water; and (ii) exploiting surface currents that bring new food into the water column above the migrator. It is apparent that the migration serves a foraging purpose, given the 100-fold difference in plankton biomass between the two regions and also given that stomachs of migrators are empty in the evening before migration and full in the morning after migration.

It is in the deeper region of the bathypelagos that we find the most extreme adaptations for opportunistic prey capture and energy conservation. Bathypelagic fishes remain in place, perhaps because external cues of changing daylight are lacking or the energetic costs of migrating are too high. They instead lure prey with bioluminescent lures. Observations from submersibles suggest that bathypelagic forms adapt a "float-and-wait" foraging mode, hovering relatively motionless in the water column and making quick lunges at prey. This motionless hovering and luring even occurs when purportedly bathypelagic anglerfish forage near the bottom, as evidenced by fortuitous observations of a Whipnose Anglerfish, *Gigantactis*, swimming slowly upside-down just off the bottom, its illicium held stiffly in front in a slight downward-pointing arc (Moore 2002) (Fig. 18.5).

Energy conservation

Deepsea fishes minimize their daily and long-term expenditure of calories in many ways. Biochemically, rates of enzymatic and metabolic activity and even levels of adenosine triphosphate (ATP) generating enzymes are lower in deepsea fishes than in shallow water relatives, which conserves energy used in locomotion, osmotic regulation, and protein synthesis (Somero et al. 1991). Energy savings are also accomplished via elimination or replacement of heavy components. Structurally, bathypelagic fishes are fragile compared with shallow water, mesopelagic, and even deepsea benthic fishes. Many of the heavy bony elements of shallow water relatives have been eliminated. Pelvic fins are often missing or reduced to rudiments, bones of the head are reduced to thin strands, and many species are scaleless. Spines are rare among deepsea fishes; even the few acanthopterygian groups that have managed to invade the deep sea, such as melamphaid bigscale fishes and chiasmodontid swallowers, have very feeble fin spines. Body musculature is also greatly reduced, by as much as 95% in the trunk and caudal regions compared with shallow water forms.

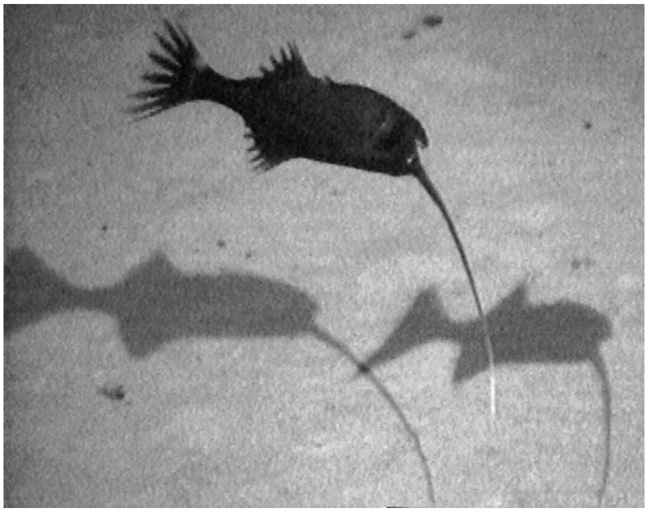


Figure 18.5

A 50 cm long Whipnose Anglerfish presumably foraging just above the bottom at 5000 m depth. Its illicial lure is extended down toward the bottom (lower two profiles are shadows cast by photographic lights). Interestingly, in gigantactinids, the teeth of the lower jaw are elongated and curved, much like the upper jaw teeth of other anglerfishes, implying that upside-down foraging may be common in Whipnose Anglerfishes. From Moore (2002), used with permission.

Lacking trunk musculature, predator evasion becomes a problem. Most deepsea fishes are colored in ways that should minimize their detection by potential predators. Mesopelagic fishes tend to be silvery or brown with ventral photophores that point downward. Silvery fishes disappear in open water (see Chapter 20, Invisible fishes). Ventral photophores may aid in breaking up the silhouette of the fish when viewed from below against the backdrop of weak downwelling light (Johnsen et al. 2004). Bathypelagic fishes are generally dark brown or black, as would be expected where the background is black. Additional energy savings are attained by replacing heavy structural components with less dense substances. Where glycerol lipids occur in shallow water fishes, deepsea forms have less dense waxy esters. These structural changes save energy because metabolic costs of both construction and maintenance are reduced. In addition, elimination and replacement of heavy elements reduces the mass of the fish, making it closer to neutral buoyancy and eliminating costs associated with fighting gravity.

Bathypelagic fishes as a group tend to have **free neuromasts** in their lateral lines, rather than having lateral line organs contained in canals, as in mesopelagic and benthic groups. Free neuromasts in shallow water fishes, such as goosefishes, cavefishes, and many gobies, are usually associated with a very sedentary life style, again suggesting a premium on energy-conserving tactics and an ability to detect minor water disturbances among bathypelagic species.

Convergence in the deep sea

The deep sea offers numerous striking examples of the Principle of Convergence. Benthopelagic fishes from at least 12 different families have evolved an eel-like body that tapers to a pointed tail, often involving fusion of elongated dorsal and anal fins with the tail fin (Gage & Tyler 1991). Another aspect of convergence exemplified in the deep sea is that selection pressures can override phylogenetic patterns, producing closely related fishes that are biologically very different because they live in different habitats (Marshall 1971). *Gonostoma denudatum* and *G. bathyphilum* are Atlantic bristlemouths in the stenopterygian family Gonostomatidae. *G. denudatum* is a mesopelagic fish, whereas *G. bathyphilum*, as its name implies, is a bathypelagic species. *G. denudatum* is silvery in color and has prominent photophores, well-developed olfactory and optic organs and body musculature, a well-ossified skeleton, a large gas bladder, large gill surface per unit weight, large kidneys, and well-developed brain regions associated with these various structures. *G. bathyphilum*, in contrast, is black, has small photophores and small eyes, small olfactory organs (except in males), weak lateral muscles, a poorly ossified skeleton, no gas bladder, small gills and kidneys, and smaller brain regions. Only the jaws of *G. bathyphilum* are larger than its mesopelagic congener. Similar comparisons can be drawn between other mesopelagic and bathypelagic gonostomatids, and between mesopelagic and bathypelagic fishes in general. Even bathypelagic forms derived from benthopelagic lineages, such as the macrourids and brotulids, have converged on bathypelagic traits (Marshall 1971).

The extreme demands of the deepsea habitat have also led to convergence in non-teleostean lineages. The mesopelagic cookie cutter sharks, *Isistius* spp., have a high squalene content in their livers that increases buoyancy. They also possess photophores and migrate vertically with the biota of the deep scattering layer (the widespread nature of bioluminescence, some fish producing their own light and others using symbiotic bacteria, is in itself a remarkable convergence). Deepsea sharks and holocephalans also possess visual pigments that absorb light maximally at the wavelengths that penetrate to mesopelagic depths, as is also the case for another mesopelagic non-teleost, the Coelacanth, *Latimeria chalumnae*. Deepsea crustaceans and mollusks have also evolved anatomical and physiological traits similar to those of fishes, including the emission of luminous ink (e.g., platytroctids, ceratioids, squids) (Marshall 1980; Hochachka & Somero 1984).

The open sea

The epipelagic region is technically the upper 200 m of the ocean off the continental shelves (see Fig. 18.1), but the terms **epipelagic** and **pelagic** are often used synonymously to describe fishes that swim in the upper 100–200 m of coastal and open sea areas (pelagic fishes can be further divided into 12 subgroups based on constancy of occurrence, relative depth, ontogenetic shifts, diel migrations, and use of structure; see Allen & Cross 2006). Common pelagic groups include many species of elasmobranchs (mako, Whitetip, Silky, and Whale sharks), clupeoids (herrings, sardines, sprats, shads, pilchards, menhadens, anchovies), atherinomorphs (flying fishes, halfbeaks, needlefishes, sauries, silversides), opahs, oarfishes, Bluefish, carangids (scads, jacks, pilotfishes), dolphinfishes, remoras, pomfrets, barracudas, scombroids (cutlassfishes, mackerels, Spanish mackerels, tunas, swordfishes, billfishes), butterfishes, and tetraodontiforms (triggerfishes, molas). Diversity overall is estimated at around 325 species (Fig. 18.6).

The pelagic realm is unquestionably the most important and productive region of the sea as far as human consumption is concerned. Pelagic fishes constitute nearly half of the 70–80 million tons of fish captured annually worldwide. Coastal pelagics, particularly clupeoids, make up about one-third of the total, and offshore pelagics such as tunas and billfishes make up an additional 15% (Blaxter & Hunter 1982; Groombridge 1992; FAO 2004).

Characteristic of the pelagic region are high solar insolation, variable production that can be very high in regions of **upwelling** or convergence of major currents, large volume, and a lack of physical structure. The abundance and diversity of fishes in the open sea is made possible by the periodic high productivity that occurs as nutrient-rich cold water upwells to the surface, promoting the bloom of algal plankton species and creating a **trophic cascade**, at least until the nutrients are used up. The greatest concentrations of fishes in the sea, and the largest fisheries, occur in such areas of upwelling. Upwelling areas may account for 70% of the world fisheries catch (Cushing 1975). The anchovy fisheries of South America and Africa, and the sardine fisheries of North America and Japan have been direct results of pelagic fishes accumulating in areas of upwelling. Several of these fisheries have collapsed through a combination of overexploitation and shifts in oceanographic conditions that reduced the magnitude of the upwelling (see Chapter 26, Commercial exploitation). The boom and bust cycles of temperate pelagics result from a patchy distribution of food in both time and space interacting with life history patterns of high-latitude pelagic species, which puts a premium on an ability to travel long distances and locate blooms.

Adaptations to the open sea

Many common threads run through the biology of pelagic fishes, suggesting convergent adaptation to pronounced and predictable selection pressures. In general, pelagic fishes are countershaded and silvery, round or slightly compressed, streamlined with forked or lunate tails, schooling, have efficient respiration and food conversion capabilities and a high percentage of red muscle and lipids, are migratory, and account for all fish examples of **endothermy**. Differences in most of these characters correspond to how pelagic a species is; extreme examples are found amongst

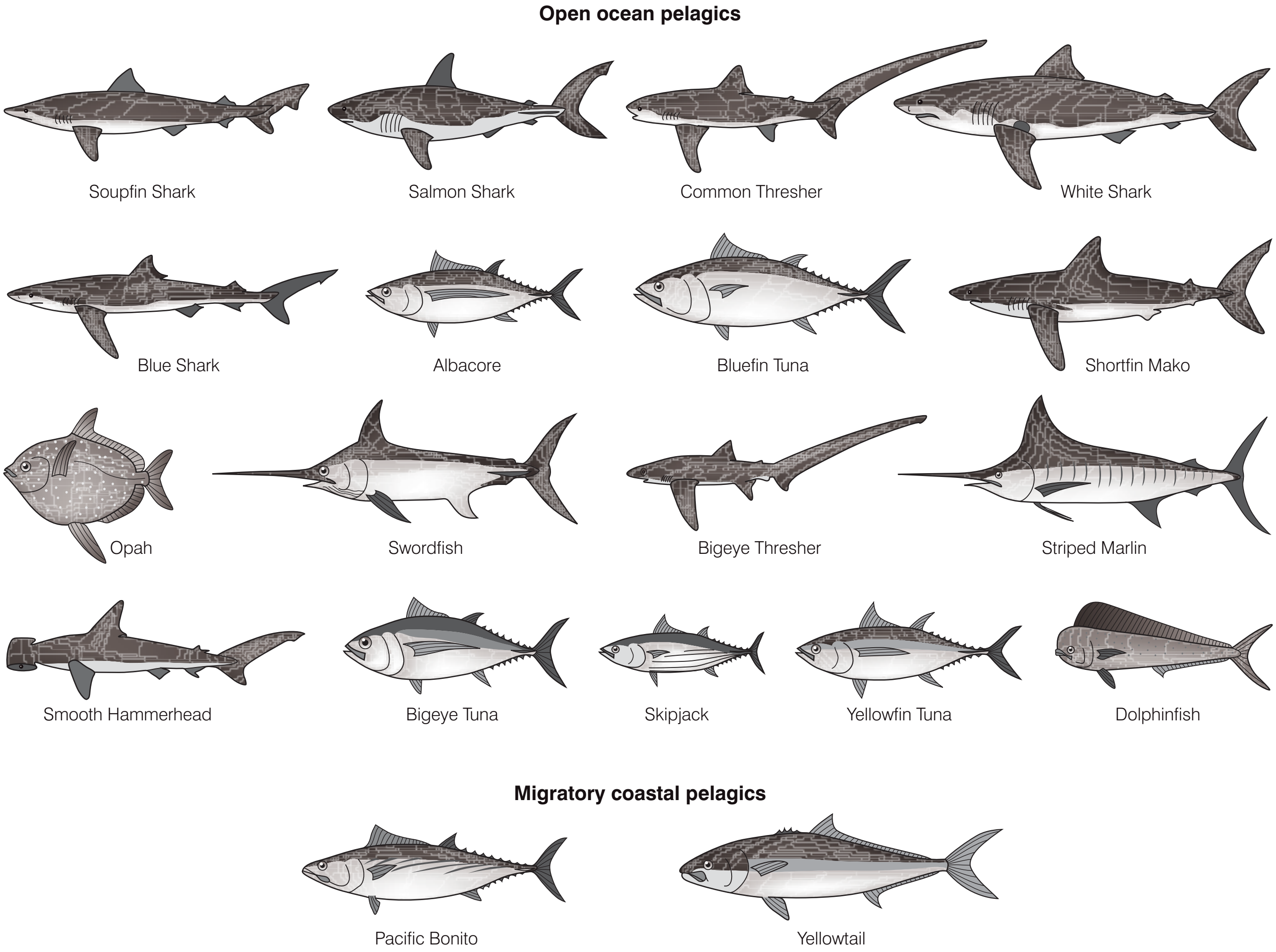


Figure 18.6

Open ocean and migratory coastal pelagic species of the California coast. Many of the open ocean species occur worldwide in temperate and especially tropical oceans. After Allen and Pondella (2006).

the open water, migratory tunas, which have the fastest digestion rates, the highest metabolic rates, and the most extreme specializations for sustained levels of rapid locomotion of any fishes (Magnuson 1978) and are among the most advanced of the teleost fishes.

Several superlatives apply to pelagic fishes and reflect adaptations to life in open water and an emphasis on continual swimming, often associated with long-distance migrations. Large sharks, salmons, tunas, and billfishes move thousands of kilometers annually (see Chapter 23, Annual and supra-annual patterns: migrations), but even smaller coastal pelagics can make annual migrations of 150 km (sprats) and even 2000 km (herring) (Cushing 1975). To sustain continual swimming, pelagics have the highest proportion of red muscle among ecological groups of fishes. Within the mackerels and tunas, the amount of red muscle increases in the more advanced groups, which are also increasingly pelagic and inhabit colder water during their seasonal migrations. In more primitive mackerels, the red muscle is limited to a peripheral, lateral band of the body, whereas in advanced tunas the red muscle is more extensive, occurs deeper in the body musculature, and is kept warm by the countercurrent heat exchangers that are also more developed in advanced scombrids (Sharp & Pirages 1978; see Chapter 7, Heterothermic fishes). Countercurrent exchangers have evolved convergently in tunas and mackerel sharks – both pelagic fishes that range into cold temperate and deep waters. This convergence suggests that endothermy and heat conservation arose independently in these groups and allowed otherwise tropical fishes to expand their ranges into colder regions (Block et al. 1993).

Body shapes and composition in pelagics reflect the demands of continual swimming. Unlike benthic fishes with depressed bodies and littoral zone fishes with deep, circular, compressed bodies, pelagic fishes tend to have **fusiform** shapes that minimize drag. This is accomplished with a rounder cross-section and by placing the maximum circumference of the body one-third of the way back from the head, an ideal **streamlined** shape also evolved convergently by pelagic sharks, whales, dolphins, and extinct ichthyosaurs (see Chapter 8, Locomotion: movement and shape). Streamlining is enhanced by having relatively small fins or having depressions or grooves on the body surface into which the fins can fit during swimming (e.g., tunas, billfishes). In high-speed fishes such as sauries, mackerels, and tunas, a series of small finlets occur both dorsally and ventrally anterior to the tail. These finlets may prevent vortices from developing in water moving from the median fins and body surfaces towards the tail, which would allow the tail to push against less turbulence. The extremely small second dorsal and anal fins of mackerel sharks, swordfishes, and billfishes could function analogously.

Tunas add a corselet of large scales around the anterior region of maximum girth that may reduce drag and thus create more favorable water flow conditions posteriorly, where actual propulsion occurs. In the region of the caudal peduncle and tail, sharks, jacks, tunas, Swordfish, and billfishes have a single or multiple **keels** that extend laterally. In the tunas, a single peduncular keel is supplemented by a pair of smaller caudal keels that angle towards each other posteriorly (Fig. 18.7). Peduncular keels reduce drag as the narrow peduncle is swept through the water, whereas caudal keels may act as a nozzle that accelerates water moving across the tail, adding to its propulsive force (Collette 1978). Peduncular keels have evolved convergently in cetaceans, but the keels are oriented vertically, as would be expected from their mode of swimming.

Many pelagic fishes swim continuously. In the Bluefish, jacks, tunas, Swordfish, and billfishes, this constant activity is linked to a respiratory mode known as **ram gill ventilation** (see Chapter 5, Water as a respiratory environment). Instead of pumping water via a muscular buccal pump, pelagic fishes swim with their mouths open while water flows across the gill surfaces. Ram gill ventilation requires that a fish swim continually at speeds of at least 65 cm/s, which is easily attained by any but the smallest tunas at their cruising speed of 1 body length/s. The more common buccal pump mechanism accounts for 15% of the total

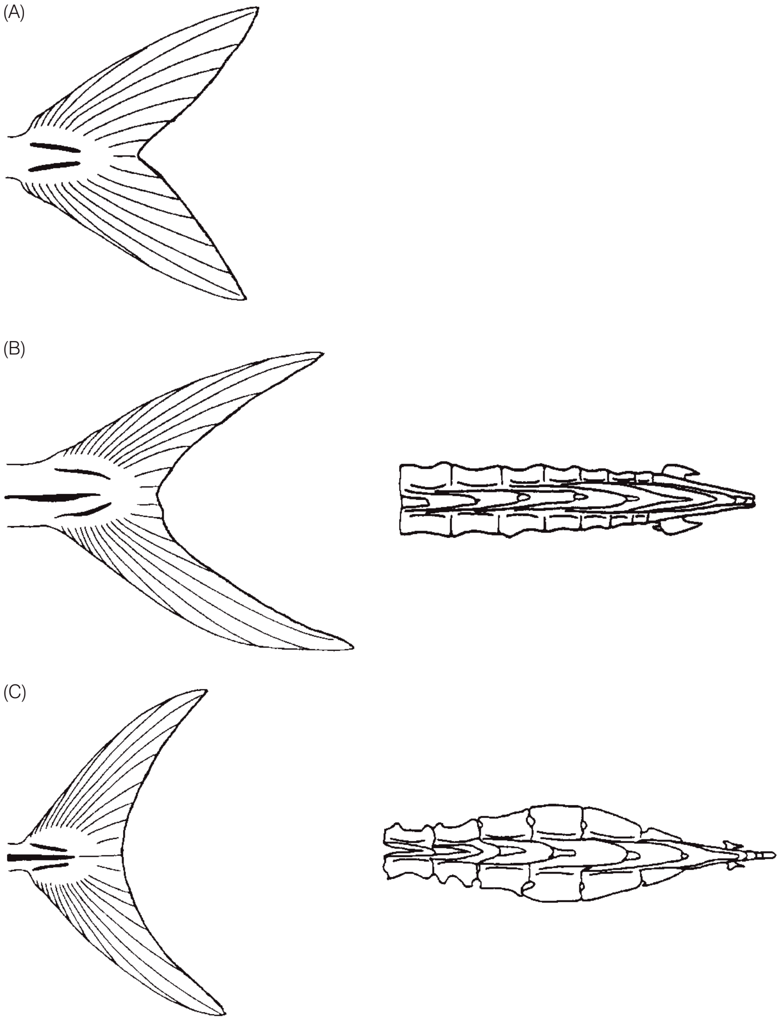


Figure 18.7

Keels and tails in scombrid fishes. The evolution of mackerels and tunas has involved increasing degrees of pelagic activity. The more primitive mackerels and Spanish mackerels live inshore and swim more slowly and less continuously. More advanced high seas tunas swim continuously and faster and are more migratory. These ecological differences are reflected in tail shape and accessories, with more efficient, high aspect ratio tails and more elaborate keels characterizing the more pelagic tunas. (A) Mackerels have forked tails with one pair of fleshy caudal keels. (B) Spanish mackerels have a semilunate tail, caudal keels, and a median peduncular keel, but the peduncular keel is external only, lacking internal bony supports (right: dorsal view of peduncle skeleton). (C) Tunas have lunate tails and multiple keels, with lateral extensions of the peduncular vertebrae supporting the keels (shown on the right). Lunate tails and peduncular keels have also evolved in mackerel sharks, jacks, and billfishes. From Collette and Chao (1975) and Collette (1978), used with permission.

energy expended by a fish, suggesting that ram ventilation conserves energy. A trade-off arises because tunas and billfishes have minimal branchiostegal development and have lost the ability to pump water across their gills. They must therefore move continually to breathe. However, these fishes are negatively buoyant and must move to keep from sinking anyway (Roberts 1978).

The high levels of activity of pelagics are fueled by an efficient circulatory system. Pelagics have an enhanced capacity for supplying oxygen to their muscles. For example, menhadens, bluefish, and tunas have two to three times the hemoglobin concentration of typical inshore, sedentary forms; hemoglobin concentration in tunas is more like that of a homeothermic mammal than like a fish. Tunas have large hearts that account for 2% of body mass and have concomitantly large blood volumes. The uptake of oxygen and release of carbon dioxide at the gills in herrings and mackerels is facilitated by exceedingly thin lamellar walls (5–7 μm thick) and numerous lamellae (> 30/mm); comparable values for less active, inshore species are 10–25 μm and 15–25 lamellae/mm. The surface area of the gill lamellae relative to body weight is very high in mackerel sharks, menhadens, Bluefish, dolphinfishes, and tunas. The efficiency of the lamellae is enhanced by the fusion of adjacent lamellae and elaboration of the leading and trailing edges of the gill filaments. These modifications have occurred convergently in tunas, Swordfish, and billfishes but not in the less pelagic mackerels. Tunas remove more oxygen from the water as it passes over their gills than any other fish. This highly efficient oxygen uptake system is necessary to fuel their extremely high metabolic rates (Steen & Berg 1966; Collette 1978; Blaxter & Hunter 1982).

Foraging

An open water existence limits the foraging options available to pelagic fishes. As a result, the fishes feed on phytoplankton, zooplankton, or each other. Many clupeoids utilize phytoplankton directly by swimming through plankton concentrations with an open mouth, thereby filtering the particles out of the water in a **pharyngeal basket** that has densely packed gill rakers (100–300/cm) and includes an **epibranchial organ** that releases digestive enzymes while the food is still in the oral region. The digestive tract is long and has numerous pyloric caeca. Food passes very rapidly through this system, often taking less than an hour, but these fish can utilize a broad array of food types and are very efficient at converting food into protein.

The foraging and migratory patterns of such pelagics as tunas and billfishes become clearer when the nature of food availability in open tropical seas is considered. Estimates of zooplankton resources in the central Pacific indicate average densities on the order of 25 parts per *billion*. Large pelagic predators are feeding at even higher trophic levels, so their food is scarcer by one or two orders of magnitude. Since no animal is going to survive on food distributed evenly at such low densities, the success and rapid growth rates of many tunas attest to the extreme patchiness of food on the high seas. A nomadic life style, driven by high metabolism and rapid swimming, makes sense when vast expanses must be covered in search of such patchily distributed resources (Kitchell et al. 1978).

Life history patterns in pelagic fishes

Pelagics are by definition open ocean fishes throughout their lives. Two general patterns characterize the overall life histories of pelagic fishes, brought on by the relationship of parental versus larval food requirements, life span, spawning frequency, oceanic currents, and fish mobility. These patterns are referred to as cyclonic or anticyclonic.

Cyclonic patterns characterize higher latitude species such as Atlantic Herring, in which the adults and larvae live in different parts of the ocean. Adults have a seasonal feeding area and tend to spawn once per year. Before they spawn, they migrate upcurrent to a region where food for larvae and juveniles will be particularly abundant. Larvae and, later, juveniles drift with the currents to the adult feeding region. These fish invest considerable energy into each spawning episode, both in terms of the costs of the migration and also in egg production. Because of the spatial separation of adult and larval habitats, adults may not have reliable cues for predicting conditions at the spawning grounds, which leads to highly variable spawning success and large fluctuations in year class strength (see Chapter 24, Population dynamics and regulation).

Anticyclonic patterns are more characteristic of low-latitude species such as tropical tunas and scads. The comparative aseasonality of tropical waters leads to less temporal fluctuation but extreme spatial variation in productivity. Adults move in a roughly **annual loop** through a major ocean basin, during which time they spawn repeatedly (with the exception of Bluefin Tuna) rather than only in particular locales. Larvae and juveniles develop and feed along with adults, carried by the same current system in their relatively nomadic existence. The energy put into reproduction is spread out amongst several spawning episodes. Adults can use local environmental cues to determine the appropriateness of conditions for larvae, which is critical given the low productivity and patchiness of tropical open oceans. Hence anticyclonic species often show weaker fluctuations in year class strength. Within families, tropical species mature more quickly and live shorter lives.

Interestingly, tunas evolved in the tropics but some species such as the Giant Bluefin spend a large part of the year feeding in productive temperate locales (see Block & Stevens 2001). Bluefin show the phylogenetic constraint of their tropical history by returning to the tropical waters of the Gulf of Mexico or Mediterranean Sea to spawn, forcing them into what is more of a cyclonic than an anticyclonic pattern (Rivas 1978). The same historical factors constrain anguillid eels such as the American, European, and Japanese species, which also return from temperate feeding locales to tropical breeding locales, but several years pass between the two life history stages (see Chapter 23, Representative life histories of migratory fishes).

The high but periodic productivity of small planktonic animals in the open sea and the presence of major ocean currents have been contributing factors in the evolution of dispersive, planktonic larvae in most marine fishes, regardless of whether the adults are planktonic, pelagic, demersal, deep sea, or inshore (see Chapter 9).

Flotsam

A special open ocean fauna occurs around what little structure is found in the open sea. Floating bits of seaweed (usually sargassum), jellyfishes, siphonophores, and driftwood almost always have fishes associated with them. Many **flotsam-associated** fishes such as filefishes and jacks are the juveniles of inshore or pelagic species; others such as sargassumfishes and driftfishes are found nowhere else, attesting to the reliability of occurrence of such objects. Flotsam also serves as an attractor for large predators, such as sharks, dolphinfishes, tunas, and billfishes (Gooding & Magnuson 1967); a single log will commonly have more than 400 tuna of 5 kg each associated with it, often involving several species (Sharp 1978). It has been suggested that concentrations of flotsam are indicators of regions of high productivity in the open sea because the flotsam accumulates at the top of vertical circulation patterns (Langmuir cells) that also concentrate nutrients and zooplankton (Maser & Sedell 1994). The mechanisms by which pelagics locate floating objects and their importance to fishes that do not feed around them remain a matter of conjecture (see Fig. 20.6).

Evolution and convergence

The greatest development of a pelagic fish fauna is in the ocean. However, most major lakes have an open water fauna that consists partly of members typically associated with open waters as well as species whose ancestors were obviously inhabitants of nearshore regions. These **limnetic** fishes include osteoglossomorphs (Goldeye, Mooneye), clupeids (shads), characins, cyprinids (Golden Shiner, Rudd), salmonids (whitefishes, trouts, chars), smelts, silversides, moronid temperate basses, and cichlids. Many of these fishes live at the air–water interface and show specializations that are apparently influenced by this habitat, including upturned mouths, ventrally positioned lateral lines, and convergent fin placement and body proportions. These surface-dwelling traits occur in both marine and freshwater families, including characins, minnows, silversides, marine and freshwater flyingfishes (exocoetids and gasteropelicids), halfbeaks, and killifishes (Marshall 1971). Regardless of ancestry, the same anatomical and behavioral themes that are seen in the ocean recur in freshwater limnetic species, including silvery color, compressed bodies, forked tails, schooling, high lipid content, and planktivorous feeding adaptations. Analogously, *Pleuragramma antarcticum*, a pelagic nototheniid in Antarctic waters, shows many traits characteristic of epipelagic fishes worldwide. Although derived from stocky, dark-colored, benthic ancestors, *Pleuragramma* has deciduous scales, a silvery body, forked tail, high lipid contents for buoyancy, and is compressed in cross-section. The pelagic larvae of many benthic Antarctic fishes are also silvery, compressed, and have forked tails (Eastman 1993; see below, Antarctic fishes). These examples of convergence suggest that fairly uniform and continuous selection pressures characterize the open water habitat.

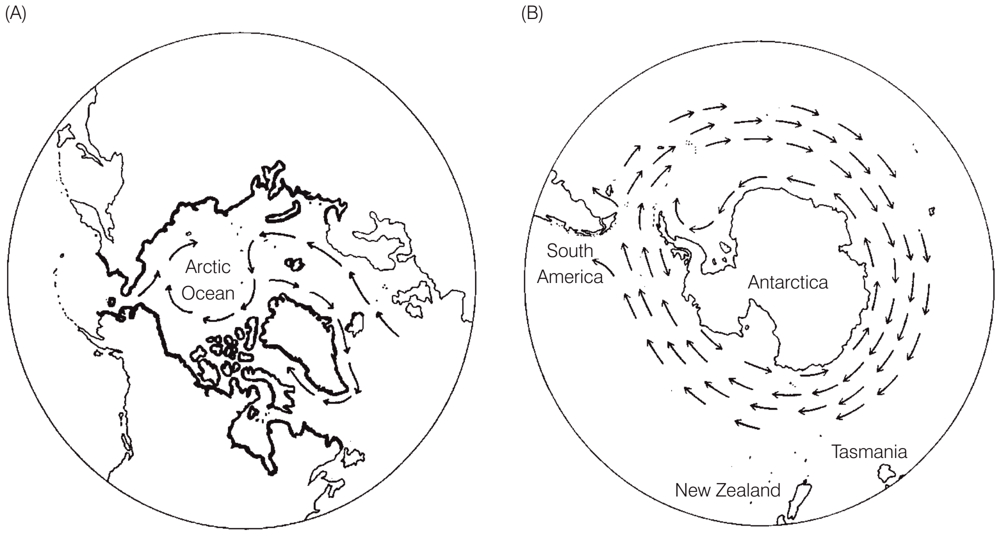
With the exception of the clupeoids, most successful taxa of adult marine pelagic fishes are acanthopterygians. Missing among otherwise successful marine groups are elopiforms and paracanthopterygians, although both groups have done well in deepsea mesopelagic and bathypelagic regions. These two groups may be phylogenetically constrained from inhabiting shallow open water regions, not the least because of their tendency to be nocturnal in habit. Other strongly nocturnal taxa are also missing from pelagic and limnetic habitats, including the otherwise successful catfishes, seabasses, croakers, grunts, and snappers, to name a few. Which is not to say that pelagic waters are devoid of life at night. The diel vertical migrations of many mesopelagic fishes bring them near the surface after sunset, where they can forage comfortably in the dark.

Polar regions

The far north (**Arctic**) and south (**Antarctic**) polar regions are roughly the areas above 60° latitude. They have much in common, primarily related to cold water temperatures and short growing seasons, but they differ geologically and environmentally and support very different biotas, including fishes. The Arctic is a frozen oceanic region surrounded almost entirely by land, whereas the Antarctic is a frozen continent surrounded by ocean (Fig. 18.8). Freshwater fishes are lacking from the Antarctic because most water bodies have permanent ice cover and many freeze to the bottom during the winter. High Arctic lakes and rivers have a limited fish fauna; 55 species occur in the Canadian Arctic, but most of these are primarily temperate species at the northern edge of their range (Scott & Crossman 1973). Freshwater fishes at high latitudes show interesting behavioral adjustments to the strong effects that seasonality has on light levels, day length, and growing season (Box 18.1). Polar oceans are in a liquid state below the first few meters

Figure 18.8

North and south polar regions. General oceanic circulation patterns are shown by arrows. (A) The Arctic Ocean centers on the North Pole; the southern limits of the region are indicated by the dark continental borders. (B) The Southern Ocean surrounds Antarctica. Some of the islands on the periphery of the south polar region are indicated.



Box 18.1

BOX 18.1

The effects of high latitude on activity cycles and predator–prey interactions

As discussed in Chapter 23 (Diel patterns), most fishes have particular periods of activity, feeding either during daylight or darkness, with a small number primarily active during crepuscular periods of dawn and dusk. These cycles of activity have a strong endogenous basis and are maintained for some time under laboratory conditions of constant light or darkness. However, in nature, the activity cycles are cued by the rising and setting of the sun.

The situation at high latitudes presents a very different set of environmental influences and selective pressures. Above the Arctic Circle, light levels never reach "nighttime" values during mid-summer, and growing seasons are short and intense. Winter brings a time of continual relative darkness and low food availability. Summer and winter therefore present extreme and opposite light conditions. Do fishes maintain strict diurnality or nocturnality under such variable and extreme conditions, or do they adjust their activity patterns to the changing seasons?

Laboratory studies with European species whose natural ranges extend beyond the Arctic Circle have produced some striking and seemingly adaptive departures from the standard picture developed at lower latitudes. The Burbot, *Lota lota*, belongs to a family of strongly nocturnal fishes, the cods (Gadidae). At intermediate latitudes below the Arctic Circle, burbot are nocturnal throughout the year. However, at higher latitudes, a peculiar pattern occurs. During the summer the fish are continually active, whereas during the winter they shift to diurnal behavior. During spring and fall they are primarily nocturnal. Similar activity cycles have been observed in other nocturnal or crepuscular species, including sculpins and Brown Trout, and can be induced experimentally in Brown Bullheads.

Interpreting these patterns is not immediately easy. The best explanation, however, is that the change to arrhythmic, continual behavior in summer is a means of taking advantage of high, continuous, and aperiodic levels of algal and aquatic insect production during the short growing season of summer. Limiting activity to the short nighttime period each day during summer would severely restrict an animal's intake. Nocturnality during spring and fall may represent a return to the normal, evolved response of the species as day length and twilight length closely approximate the more usual and widespread conditions at lower latitudes. The switch to diurnality during winter in an animal well adapted to function in the dark remains puzzling. Regardless, changes in the length of, and light intensity during, twilight provide the apparent cues that lead to the phase shifts observed in these fishes (Muller 1978a, 1978b).

The influence of **twilight length** at high latitudes is also shown in the predator–prey relations of marine fishes. Dawn and dusk at low latitudes are the times when fish switch between feeding and resting and are often times of maximal predator activity. If twilight is a dangerous time for prey fishes at low latitudes where twilight lasts for a relatively short time, we might expect the prolonged twilight that occurs at higher latitudes to be even more dangerous.

Conducting extensive underwater observations at high latitudes can be uncomfortable and few such studies have been attempted. In the one instance where the question of twilight interactions was addressed, observers found that extended twilight meant extended periods of predation. Hobson (1986) watched sculpins, greenlings, and flatfishes preying on Pacific Sand Lances, *Ammodytes hexapterus*, in Alaska. Sand lances school and feed on zooplankton during the day and bury in the sand at night. Schools of sand lances are relatively immune to these benthic predators during daylight, and the predators do not occur at night in the limited resting areas that the sand lances use. However, during twilight, the predators aggregate in the resting area under the schools as they break up. The predators are particularly effective at capturing Sand Lances that have just entered the sand or that re-emerge shortly after burying because of apparent dissatisfaction with their initial choice of resting site. The twilight transition from schooling to resting appears to be the most dangerous time for the Sand Lances.

Twilight conditions at the date and latitude of observation (May, 57°N) were very long, lasting about 2 h. This is about twice as long as at tropical latitudes where similar observations have been made with different predators and prey. The period of intense predation in Alaska is also about twice as long as that observed at tropical locales. The longer days of spring and summer at high latitudes mean that diurnal fishes experience a much longer foraging period, but this increase is bought at the high price of increased predation during the lengthened twilight periods.

and have more fishes, but the superabundance of ice at the surface, plus scouring by ice or ice anchored to shallow bottoms limit the distribution and behavior of polar fishes, which have developed remarkable adaptations to avoid freezing to death.

Antarctic fishes

Antarctica is surrounded by at least 900 km of the open, deep Southern Ocean that flows around and away from the Antarctic continent. Strong **circumpolar currents** and distinct temperature differences occur between the polar and subpolar regions, delimited by a region known as the **Antarctic Convergence** at 50–60°S. This region creates a distance, depth, and thermal barrier to interchange between the cold-adapted species of the Antarctic region and warm-adapted species to the north. Antarctic fishes have also had sufficient time to adapt and speciate; the Antarctic region has been at its present locale with its present climate for about 20–25 million years, having separated from Australia during the Early Cenozoic (Hubold 1991; Eastman 1993). Spatial and temporal seclusion and climatic extremes have resulted in a diverse fish fauna dominated by endemic notothenioid thornfishes, cod icefishes, channichthyid crocodile icefishes, plunderfishes, and dragonfishes, as well as several non-notothenioid groups (Farrell & Steffensen 2005; Fukuchi et al. 2006; see Chapter 16, Marine zoogeographic regions).

Notothenioids as a group are benthic fishes and fully half of all species still live on the bottom in less than 1000 m of water (Fig. 18.9). As is general among benthic fishes, they lack gas bladders, are dark in coloration, and are

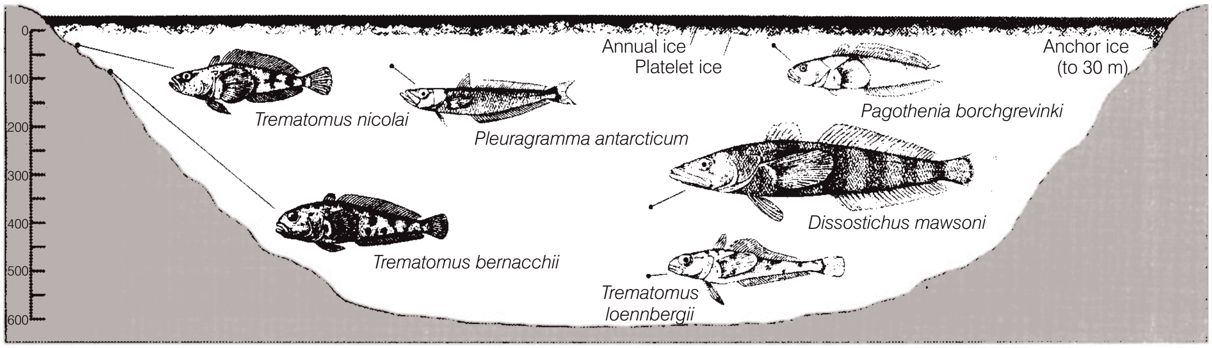


Figure 18.9

Body form and habitat types of common Antarctic nototheniid fishes. The dots show the preferred depths and habitats. From Eastman (1993), after Eastman and DeVries (1986), used with permission of Scientific American, Inc., all rights reserved.

round or depressed in cross-section with a square or rounded tail. Benthic forms often seek cover inside sponges, either as a refuge from predatory mammals or as a spawning substrate. Eggs placed inside hard sponges such as hexactinellid glass sponges are probably protected from most predators (Dayton et al. 1974; Konecki & Targett 1989). Larvae are pelagic and show adaptations specific to shallow, open water existence, including silvery coloration, relatively compressed bodies, and forked tails (see above, The open sea). Notothenioids have also radiated into most non-benthic niches and consequently show substantial variation in body form and behavioral tactics, starting with a common body plan.

A few species, including the abundant Cod Icefish, *Pleuragramma antarcticum*, are pelagic zooplanktivores. So-called **cryopelagic fishes** live in open water just below the ice. The food chain for these fishes starts with ice algae, which is eaten by amphipods and euphausiids, which are in turn eaten by the fishes. Cryopelagic fishes have a uniform light coloration that may help them blend in with the icy background against which they would be viewed. They also possess better chemical defenses against freezing and have greater buoyancy than benthic relatives.

Notothenioids are interesting reproductively because they produce a small number of relatively large, 2–5 mm eggs during a short, 1–2-month spawning season. The unhatched larvae have developmental periods of 2–6 months, followed by a long, slow-growing pelagic stage that lasts a few months to 1 year. Many benthic species exhibit parental and biparental guarding (Daniels 1979; Kellerman & North 1994).

Notothenioids are opportunistic feeders, taking a wide range of prey types, with many pelagic and mesopelagic juveniles and adults feeding on the ubiquitous krill, *Euphausia superba*, that is also the major prey of whales, penguins, and other seabirds. Although the annual temperature variation in Antarctica is seldom more than 4°C (–2° to +2°C), and in some locales as little as 0.1°C, fishes show marked variation in summer versus winter feeding rates. Rates are still relatively high during winter (e.g., 65% of summertime intake in *Harpagifer antarcticus*; Targett et al. 1987), unlike temperate locales where many fishes cease feeding in **winter**.

Mesopelagic fishes are particularly abundant throughout the water column of the Southern Ocean. Lanternfishes are the most diverse group of mesopelagic fishes at lower latitudes, but are epipelagic in the Antarctic. The lanternfish *Electrona antarctica* is the most common fish above 200 m. It feeds heavily during the day, in contrast with the typical mesopelagic pattern of nocturnal foraging that characterizes lanternfishes at lower latitudes. "Mesopelagic" species are also an important component of the community living near the ice edges or "oceanic marginal ice zone". Large numbers of myctophid lanternfishes are eaten in the open sea and at the edge of the pack ice by seabirds, whales, and seals. A commercial midwater trawl fishery even exists for mesopelagic species, with annual catches of the lanternfish *Electrona carlsbergi* exceeding 78,000 tons (>70 × 10^6 kg) from the South Georgia Island region. As with their more northerly, low-latitude relatives, deep-living mesopelagic fishes in the Antarctic show lower enzyme activity and slower metabolic rates than shallow water forms, which is interpreted as an adaptation to low food availability at depth (Kellerman & North 1994; see above, The deep sea).

Harpagiferid plunderfishes, which are advanced perciform fishes, are remarkably similar in morphology and behavior to the relatively primitive scorpaeniform sculpins of northern temperate waters. Similarities may represent adaptations to a predominantly benthic existence, including a relatively depressed, elongate, tapering body; large, spiny head with large eyes and a large, terminal mouth; long dorsal and anal fins; large pectoral fins; rounded caudal fin; and a dorsally located lateral line. Both groups show ecological and behavioral similarities as well, feeding by a sit-and-wait mode on relatively large, mobile benthic invertebrates. In essence, plunderfishes and sculpins have converged to fill similar niches in their respective communities (Wyanski & Targett 1981).

Adaptations and constraints of Antarctic fishes

Notothenioids are best known for two adaptations related to existence in the cold, often energy-limited waters of the area, where water temperatures average –1.87°C and total darkness prevails for 4 months each year. First, their blood contains remarkably effective **antifreeze compounds** that depress the freezing point of their body fluids and make it possible for them to live in water that is colder than the freezing point of most fish blood including, remarkably, their own. Second, some have evolved **neutral buoyancy**, which has permitted these species to move off the crowded bottom where most notothenioids live and into the water column.

No known species of fish can actually tolerate having its tissue freeze. The major threat to fishes in the Antarctic is ice, which floats at the surface in the form of bergs, sheets, and platelet ice, but also attaches to the bottom in water less than 30 m deep in a form called anchor ice. The greatest danger comes from ice crystals penetrating or propagating across the body and seeding the formation of ice inside the fish, which would cause cell rupture. Many Antarctic fishes live in water that is colder than their blood's freezing point. Fishes from lower latitudes typically freeze when placed in water colder than –0.8°C, whereas Antarctic fishes can live in water as cold as –2.19°C. They accomplish this because their blood contains the salts normally found in fish blood and also as many as eight different glycopeptide antifreeze compounds. The glycopeptides apparently function by keeping the ice from propagating across the fish's skin. A notothenioid can be cooled as low as −6°C without freezing, as long as free ice is not in the water.

Several other adaptations accompany the production of antifreeze compounds. Notothenioids are relatively unusual among teleosts in that their kidneys lack glomeruli, which are the structures that remove small molecules from body fluids and transfer them to the urine for excretion. Glomeruli would remove the antifreeze glycopeptides, which would be energetically expensive to continually replace (see Chapter 7, Coping with temperature extremes). A fairly strong correlation exists between antifreeze effectiveness and the frequency with which a species encounters free ice. For example, the shallow water bathydraconid dragonfishes frequently come in contact with ice and have the highest levels of antifreeze compounds. Within the cod icefish genus *Trematomus*, shallow water species that live in the coldest water and rest in ice holes or on anchor ice have freezing points of −1.98 to −2.07°C, whereas deeper living species that seldom encounter ice crystals freeze at −1.83 to −1.92°C. Even within species, shallow water populations have significantly more freezing resistance than deeper water populations (DeVries 1970). The primitive bovichtid thornfishes of New Zealand live in temperate waters and do not produce antifreeze. Bovichtids possess glomeruli, indicating that the aglomerular condition of Antarctic species evolved along with other adaptations to the colder Antarctic environment (Eastman 1993).

Neutral buoyancy has developed in at least two water column dwelling members of the family Nototheniidae, the Cod Icefish, *Pleuragramma antarcticum*, and its giant predator, the Antarctic Toothfish, *Dissostichus mawsoni*. Whereas most Antarctic fishes are 15–30 cm long, toothfish reach lengths of 1.6 m and weights of over 70 kg. Neutral buoyancy allows these fishes to occupy the comparatively underutilized water column zone, thus taking them away from threatening anchor ice crystals and into a region of seasonally abundant food sources such as fish larvae and krill. Both species have evolved from benthic ancestors and have retained what can only be viewed as a phylogenetic constraint on living in open water: they are similar to benthic notothenioids in that they lack a gas bladder. As fish muscle and bone are relatively dense, a gas bladderless fish would constantly have to fight gravity to stay in the water column. Neutral buoyancy in these two nototheniids is achieved via several mechanisms. Toothfish have cartilaginous skulls, caudal skeletons, and pectoral girdles, which reduces their mass because cartilage is less dense than bone. The skeleton itself is less mineralized than in benthic relatives, by a factor of six in the toothfish and 12 in *Pleuragramma*. Bone is also reduced in the vertebral column, which is essentially hollow except for the notochord. Additional buoyancy is achieved by lipid deposits dispersed around the body, including a blubber layer under the skin, and fat cells or sacs located between muscle fibers or muscle bundles (Eastman & DeVries 1986; Eastman 1993). Weightlessness via analogous routes of weight reduction and replacement is also seen convergently in bathypelagic fishes, another water column dwelling group where evolution has placed a strong premium on energy-saving tactics.

A unique trait of channichthyid icefishes may represent an evolutionary adjustment to polar conditions. These fishes are sometimes referred to as "white blooded" or "bloodless" because their blood contains no hemoglobin and their muscles contain no myoglobin, giving them a very pale appearance. The highly oxygenated, cold waters of Antarctica may have been responsible for the evolutionary loss of respiratory pigments, perhaps via a "regressive" evolutionary process similar to the one that led to pigmentless, eyeless cave fishes (see below, Caves). Channichthyids possess a number of other characteristics that have evolved in conjunction with a lack of hemoglobin, including relatively low metabolic requirements (reduced protein synthesis, reduced activity, slow growth), increased vascularization of skin and fins to increase gas exchange, and an increase in cardiac size, output, and blood volume (Hemmingsen 1991). Some nototheniids have increased blood volumes and reduced hemoglobin concentrations, perhaps reflecting an intermediate stage in the response to respiratory conditions in the Antarctic that have led to the hemoglobin-free condition of the channichthyid icefishes (Wells et al. 1980).

Arctic fishes

The Arctic has fewer endemic fishes due to the combined effects of less geographic isolation and younger age. The oceanic environment between **subarctic** or **boreal** and Arctic areas is fairly continuous. On the western, Pacific side, the Bering Sea flows into the Arctic Ocean and has done so since the Bering Strait opened up 3.5 million years ago. Similarly, on the eastern, Atlantic side, the Arctic Ocean is directly connected to the Greenland Sea. Hence, Arctic fishes are either species that evolved there since the current climate developed or are cold-tolerant Pacific or Atlantic species that experience gene flow from source areas rather than being endemic to the Arctic itself. The Arctic has undergone repeated warming and cooling until about 3 million years ago when the present cold conditions stabilized, leaving less time for organisms to adapt to current conditions (Briggs 1995). Consequently, fishes in the northern polar region have had less time to speciate.

Adaptations to cold are evident in Arctic fishes, where species have converged with Antarctic fishes in the production of antifreeze compounds (Farrell & Steffensen 2005). Glycoprotein antifreeze occurs in Arctic and Greenland Cod, whereas Warty Sculpin, Canadian Eel-pout, and Alaska Plaice possess peptide antifreezes (Clarke 1983). Arctic Cod are frequently observed resting in contact with ice and taking refuge inside holes in ice, so their potential for encountering seed crystals is very high. In some of these fishes, kidney glomeruli are convergently reduced to help retain antifreeze compounds in the body (Eastman 1993). Several boreal cods, sculpins, eel-pouts, and flatfishes whose ranges extend into Arctic water also have antifreeze compounds in their blood.

Water temperatures show greater annual and latitudinal variation in the Arctic than in the Antarctic, which means that fishes are likely to encounter extreme winter cold but also relatively high summer temperatures. Winter temperatures do commonly drop to –1.8°C as in the Antarctic, but water can reach 7 or 8°C during the summer. The greater seasonal range is reflected in the tolerance of different species to warm temperatures, as well as differences in seasonal production of antifreeze. Few Antarctic fishes can tolerate water temperatures above 7 or 8°C regardless of acclimation temperature, whereas Arctic species have upper lethal temperatures of 10–20°C depending on species and acclimation temperature (DeVries 1977). Several north polar species produce less antifreeze during the summer, particularly among boreal fishes that may encounter temperatures well above freezing. Winter Flounder, *Pleuronectes americanus*, have a blood volume of 3% antifreeze in winter and 0% in summer. Reduced antifreeze production during warmer months probably saves energy and may also increase the blood's capacity to carry oxygen or nutrients.

Deserts and other seasonally arid habitats

Deserts appear inhospitable for fishes. However, algae and many invertebrates capitalize on the periodic availability of water in arid regions. It is not surprising then to find a small number of fishes capable of surviving under conditions of periodic **dewatering** in desert regions around the world, presenting dramatic examples of adaptation and convergent evolution.

Deserts are difficult to define because they differ in altitude, temperature range, amount of rainfall, and seasonality of water availability, among other traits. Many treatments define a desert as an area that receives less than 30 cm of rainfall annually. A more general definition is that a desert is an area where "biological potentialities are severely limited by lack of water" (Goodall 1976), a definition that stresses the common thread of water scarcity as the significant selection factor and can therefore apply to areas with seasonal droughts, such as swamplands that dry up periodically. For fishes, the disappearance of water is only the most extreme stage in a continuum of conditions that occur during dewatering. As water evaporates, temperatures generally rise, dissolved substances such as salts become more concentrated, oxygen tension drops, carbon dioxide increases, and competition and predation intensify. Desert fishes must therefore be tolerant of widely varying and extreme salinity, alkalinity, temperature, and depleted oxygen (Box 18.2). They may also have to be able to outcompete other fishes and avoid predators despite physiological stress. Desert stream fishes also have to withstand periodic flash flooding. Desert-adapted fishes, not counting species that migrate to more permanent habitats when waters recede, often show three general adaptations: (i) an annual life history involving egg deposition in mud during the wet season, an egg resting period (**diapause**) during the dry season, death of the adults, and egg hatching when habitats are reinundated the next year; (ii) **accessory respiratory structures** for using atmospheric oxygen (lungs, gill and mouth chambers, cutaneous respiration); and (iii) in

Box 18.2

BOX 18.2

Acidity, alkalinity, and salinity

The acidity or alkalinity of a water body strongly determines the existence and types of fishes that occur there. Sea water is naturally buffered against abnormal shifts in hydrogen ion content (**pH**) and hence pH is seldom a concern for marine fishes; sea water usually has a pH of about 8.0–8.3. Fresh water, in contrast, is easily affected by substances that alter pH. Changes in acidity in turn affect the activity of metals and other potential toxins in the water. Freshwater fishes normally live in water with a pH range between 6 and 8, a pH of 7 being neutral. **Acidic** conditions (pH $\ll$ 7) often result from the decay of organic matter that is not filtered through soil or further broken down. The black or tea-stained coloration of many swamps, and the black water rivers of the southeastern USA and of major tributaries of the Amazon such as the Rio Negro and of many African rivers, are examples of naturally occurring low pH water (pH 3.8–4.9). Such "soft" waters are also low in dissolved substances and inorganic ions, but high in organic acids such as humic and fovic acids (Lowe-McConnell 1987). Some fishes have evolved under conditions of low pH and do best in slightly acidic waters (e.g., many tetras), whereas other groups are intolerant of acidic waters. Minnows, which are so widespread throughout North America, are often missing from river systems where the pH falls below 4.5 (Laerm & Freeman 1986), although cyprinids do well in Southeast Asian waters with low pH. **Acid rain**, a lowering of pH that results from industrial pollution, causes reproductive failure in many fishes and has eliminated fishes from the poorly buffered lakes of the Adirondack Mountains in New York and in many lakes throughout Scandinavia (Baker & Schofield 1985; Helfman 2007).

High pH is caused by an abundance of hydroxyl (OH) groups, producing **alkaline** conditions. High alkalinity occurs naturally in waters that run through or over limestone rocks, or where extensive evaporation occurs. Some fish have adapted to alkaline conditions that are lethal to most other animals. A small (< 8 cm) African cichlid, *Oreochromis grahami*, is the only fish that can live in Lake Magadi in Kenya under conditions of extreme alkalinity, salinity, and temperature. Water flows into the lake from hot springs at a pH of 10.5, a salinity of 40 ppt, and a temperature of 45°C. The water has a high load of sodium bicarbonate, sodium chloride, sodium sulphate, and sodium fluoride and has a conductivity of 160,000 μmho/cm (most African lakes have a pH of 7–9 and a conductivity of 100–1000 μmho/cm). The fish occupy pools and graze on algae at temperatures below 41°C. Their upper temperature limit creates a distinctive browse line where inflowing spring water has cooled sufficiently to allow fish activity. Algae in regions above 40°C are safe from fish grazing (Coe 1966; Fryer & Iles 1972).

Salinity determines the distribution of many if not most fish families. Biogeographic categories of freshwater fishes focus on whether taxa can tolerate salinities greater than a few parts per thousand (ppt). In one approach (see Briggs 1995; Berra 2001), freshwater fishes are classified as **primary** (those that cannot cross saltwater boundaries, such as minnows, characins, most catfishes, pike), **secondary** (those that can cross at least short saltwater regions, e.g., cyprinodontoids, cichlids), and **peripheral** (those derived from marine families or that spend part of their lives in the ocean, e.g., salmons, sculpins) (see Table 16.2).

The actual barriers to free movement between regions of high and low salt concentration are physiological in nature. At the simplest, freshwater fishes have a need to conserve salts and eliminate water, whereas saltwater fishes must conserve water and stem the influx of salts (see Chapter 7, Osmoregulation, ion and pH balance, and excretion). Extremes of and rapid changes in ionic concentration can cause **osmotic stress**. Although pure distilled water is stressful, it is also unusual in nature and hence an uncommon limitation. Hypersalinity occurs in many areas, either as a result of heated water flowing through easily soluble rocks, or due to daily or seasonal evaporation and concentration of salts as water courses dry up during low tides or droughts.

Some of the most widely distributed families in fresh water turn out to be those that show a high tolerance to both rapid fluctuations and extreme conditions of salinity. Many cyprinodontoid killifishes and pupfishes can tolerate ranges of salinity from 0% to 100% of sea water (100% is about 35 ppt) and appear to tolerate rapid shifts in salinity from high to low concentration, such as those brought on by rainstorms. Some, such as the Mediterranean *Aphanius* and several North American *Cyprinodon*, live in water two to three times saltier than sea water. These capabilities have preadapted them for life in isolated habitats such as desert springs and pools (Roberts 1975b). Similar abilities characterize cichlids and gobies, two of the world's largest families of fishes. *Tilapia amphimelas*, a cichlid, inhabits Lake Manyara in Africa, where the sodium content is twice that of sea water and is increased ionically by abundant potassium salts (Fryer & Iles 1972). Certain large inland water bodies are too saline to support even the most osmotically tolerant species, including the Dead Sea of the Middle East and the Great Salt Lake in Utah, where salinities exceed 200 ppt. Water withdrawal due to human activities can cause salinization of a lake and threaten the fishes there, as has occurred in the Aral Sea of the former Soviet Union (see Chapter 26).

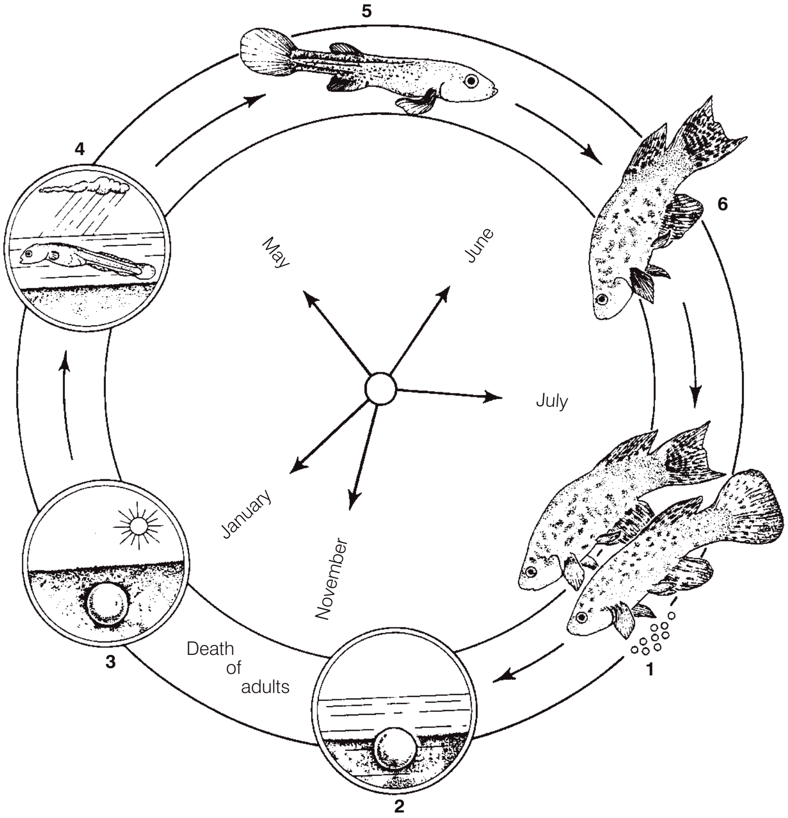
perennial species, **estivation**, where adults pass the dry season in some sort of resting state.

Deserts occur on all major continents and many of these deserts contain fishes. Africa has many habitats that dry up seasonally and that contain fishes with desert adaptations. Among the most successful groups in Africa are cyprinodontiform killifishes and rivulines, which are popular aquarium species. Many of these fishes (e.g., *Fundulosoma*, *Notobranchius*, *Aphyosemion* spp.) are **annual**, living for 8 months in mud holes, swamps, and puddles (Fig. 18.10). They mature after only 4–8 weeks, spawning daily and burying eggs as much as 15 cm deep in muddy bottoms, a remarkable feat for fishes that seldom exceed 5 cm long. The adults die and the eggs spend the dry season in a state of arrested development until the next rains come. Some eggs can remain in such a state of diapause for up to 5.5 years. An annual life history effectively maintains a permanent population in a temporary habitat (Wourms 1972; Simpson 1979).

African and Asian clariid or walking catfishes are capable of leaving drying water bodies and moving across up to 200 m of moist grass in search of water. They will also bury

Figure 18.10

Life cycle of annual cyprinodontoids, as shown by the Venezuelan *Austrofundulus myersi*: 1, spawning occurs over a protracted period; 2, shelled eggs are deposited in the mud; 3, as water dries up, adults die but eggs remain viable in an arrested developmental stage; 4, with the return of the rains, eggs hatch; 5, larvae and juveniles grow rapidly; 6, maturation occurs after only a month or two, followed by spawning. From Wourms (1972), used with permission.



themselves as deep as 3 m in sandy sediments as water levels drop. They can survive by employing aerial respiration via treelike **suprabranchial organs** over the second and fourth gill arches, although they cannot survive if the sand dries up (Bruton 1979).

The African lungfishes (Protopteridae) are true estivators. During a drought, they burrow into mud, secrete a cocoon, and enter a torpid condition in dry mud until the next rains, an event for which they can wait 4 years (see Chapter 13, Subclass Dipnoi, Order Ceratodontiformes: the lungfishes). Many other fishes in African swamps are adapted to the deoxygenation that accompanies seasonal dry periods, using a variety of air-breathing mechanisms (see Table 5.1). Mochokid catfishes, killifishes, and *Hepsetus odoe*, the Pike Characin, are surface dwellers, taking advantage of higher oxygen tensions near the air–water interface. Lungfishes and bichirs use lungs, clariid catfishes have gill chamber organs, anabantids have labyrinth organs, snakeheads have pharyngeal diverticula, and featherfin knifefishes and phractolaemids have alveolar gas bladders.

In South America, drought resistance has evolved in parallel to the African examples. Many fishes of the Amazon region have evolved means of using atmospheric oxygen when drought or vegetative decay lower oxygen levels (Kramer et al. 1978). Surface swimmers, such as arawanas and some characids (pacus, *Brycon*), have vascularized lips. Modifications of the alimentary tract to absorb oxygen are common, including the mouth region of Electric Eels and swamp eels, air-filled stomachs in loricariid catfishes, a vascularized hindgut in callichthyid armored catfishes, and a vascularized gas bladder in lungfish, Arapaima, and erythrinid trahiras. As with the walking catfishes, South American species are reported to abandon drying pools and cross small stretches of wet vegetation or mud in an apparent search for new and wetter habitats (e.g., erythrinids such as *Hoplias* and *Hoplerythrinus*, callichthyid catfishes, some rivulines) (Lowe-McConnell 1987).

Conventional desert areas also exist in South America. The Chaco region of northwestern Paraguay receives less than 30 cm of water annually, with a normal 3-month winter drought period that can last as long as a year (Smith 1981b). During the annual drought, aquatic habitats become isolated and dry up. During the rainy season, these habitats are often repopulated by fishes from overflowing portions of the Paraguay River. The ichthyofauna of the Chaco consists of both drought-adapted and nonadapted species. Adaptations to drought include estivation in mud by juvenile and adult lungfish (*Lepidosiren*), accessory respiratory structures for using atmospheric oxygen (lungfishes; catfishes, *Hoplosternum*, *Pterygoplicthys*; characiforms, *Hoplias*), and annual life histories and diapausing eggs among cyprinodontiforms, which are also successful throughout much of tropical South America (e.g., *Cynolebias*, *Rivulus*, *Austrofundulus*). Localized extirpation occurs annually in species that invade the Chaco region during the wet season but that lack the abilities to overcome drought conditions.

Australia is largely a desert continent. Its freshwater fish fauna is dominated by **marine derivatives**, such as river eels, plotosid catfishes, rainbowfishes, barramundi, temperate basses, grunters, pygmy perches, gobies, and sleepers. Several Australian fishes show distinct adaptations to periodic drought. The endemic, monotypic Salamanderfish *Lepidogalaxias salamandroides* occurs commonly in southwestern Australian habitats that dry up during the annual summer drought. As waters recede, the fish burrows into bottom sediments and surrounds itself with a thick mucus coat (Berra & Allen 1989; Pusey 1990). Two major problems faced by estivating fishes are water loss and a concomitant build-up of toxic nitrogenous wastes such as urea, which normally must be transported away with water-wasting urine. Salamanderfish conserve water by absorbing it from the surrounding soil until soil moisture content approaches zero. They avoid the production of nitrogenous wastes in part by metabolizing lipids rather than proteins; the endpoint of lipid metabolism is carbon dioxide, not nitrogen compounds (Pusey 1989).

Several species in the related family Galaxiidae in Australia and New Zealand occur in similar temporary habitats and may also estivate during dry periods. Some gobies and hardyhead silversides that live in desert springs in central Australia are exceptionally tolerant to high temperatures, high salinities, and low dissolved oxygen. The Desert Goby, *Chlamydogobius eremius*, typifies desert-adapted species in its ability to survive an extreme range of conditions, including ionic concentrations ranging from distilled water to water more saline than sea water, temperatures between 5 and 40°C, and oxygen concentrations below 1 ppm. To avoid lethal conditions in thermal springs or high summer temperatures, it seeks cooler vertical or lateral portions of springs, buries itself in cooler silt, and even emerges from the water to capitalize on evaporative cooling and aerial respiration (Glover 1982).

North American deserts

Additional examples of desert adaptations could be presented from almost any continent (except Antarctica), but some of the best studied desert fishes occur in the southwestern United States. The Basin and Range Province of North America contains four different deserts, the Great Basin, Mojave, Sonoran, and Chihuahuan deserts (Naiman & Soltz 1981). The province, which includes such seemingly inhospitable areas for fishes as Death Valley, Ash Meadows, Salt Creek, and Devil's Hole, constitutes < 10% of the total land area of North America. Although desert conditions have existed periodically in the region for approximately 70 million years, the southwestern deserts as they exist today are relatively young, no more than 12,000 years having passed since the last wetter, "pluvial" period when the area contained abundant, interconnected standing and running water. Despite their relative youth and small size, the southwestern deserts contain 182 native species, 149 of which are endemic to the basin and many of which are endemic to single locales (the area includes both US and Mexican endemics). Endemicity in the fishes of the desert southwest is the highest of any place in North America.

Two major types of desert habitat are occupied by fishes: (i) isolated pools and basins supplied by underground springs that have fairly regular flow; and (ii) intermittent marsh and arroyo habitats along flowing water courses that originate in wetter areas such as mountainous highlands and that flow into arid regions. The native fishes that occur there belong to five principal families and segregate according to fish size, habitat size, and environmental extremes. Small livebearers (Poeciliidae) and even smaller desert pupfishes of the family Cyprinodontidae live in the most extreme or isolated habitats such as intermittent streams and spring basins; these fishes include 20 desert-adapted species in the genus *Cyprinodon*. Small streams contain small minnows (Cyprinidae) that are < 6 cm long; larger streams and small rivers support medium-sized suckers (Catostomidae) and trout (Salmonidae). The largest fishes, such as large suckers and the Colorado Pikeminnow (*Ptychocheilus lucius*, up to 2 m), live in large rivers. Body size is intimately tied to habitat size (Smith 1981b). The smallest pupfish, the Endangered 2 cm **Devil's Hole Pupfish**, *Cyprinodon diabolis*, lives on an 18 m^2 shelf in a spring basin in the smallest habitat of any known vertebrate (Fig. 18.11). In contrast, the Colorado Pikeminnow is the largest minnow in North America and lives in the area's largest habitat, the Colorado River.

The fishes in marshes and small streams experience the harshest conditions and show the strongest adaptations to desert existence. Desert pupfishes show extraordinary tolerances to environmental extremes. They can live in water with as little as 0.13 mg O_2/L (0.13 ppm dissolved oxygen), which is a record for fishes that do not supplement gill respiration with some accessory breathing apparatus. Most fishes show stress at < 5 ppm, depending on water temperature. Although these are freshwater fishes, some desert pupfishes can tolerate salinities over 100 ppt and as high as 140 ppt, three to four times that of sea water. Pupfishes experience water temperatures that vary from freezing in winter to 44°C in summer, the highest recorded for a habitat containing live fishes; the Cottonball Marsh Pupfish tolerates higher temperatures than any other known teleost (Feldmeth 1981). Many of the spring-dwelling pupfishes have lost their lateral lines and pelvic fins, which may be energy-saving responses in isolated habitats that lack predators.

Other taxa show physiological and behavioral adjustments to drought conditions, such as the Longfin Dace,

Figure 18.11

Devil's Hole, Nevada, natural home of the Devil's Hole Pupfish, the first fish listed under the US Endangered Species Act. Visible are water-level monitoring equipment and a platform for people to walk on while doing fish counts. Photo by J. Barkstedt, used with permission.

Agosia chrysogaster, of the Sonoran Desert, adults of which move into moist algae during hot days and emerge during cooler nights to forage in only a few millimeters of water (Minckley & Barber 1971).

Although most emphasis is given to periods of low water in deserts, a major influence on stream- and river-dwelling fishes is the periodic occurrence of flash floods, when waters can change from low-flow, nearly stagnant conditions to raging torrents in a matter of seconds (Naiman 1981). Colorado River endemics (see Fig. 26.3), such as the Humpback Chub (*Gila cypha*), Bonytail Chub (*G. elegans*), and Razorback Sucker (*Xyrauchen texanus*), have anterior humps, flattened heads, keeled napes, cylindrical bodies, small scales, and elongate, narrow caudal peduncles that have been postulated to provide hydrodynamic stability during periods of high or turbulent flow, although the large humps could also be a convergent response to gape-limited predation by another endemic, the Colorado Pikeminnow (e.g., Portz & Tyus 2004).

High-flow adaptations are not restricted to large fishes. The Threatened 5 cm Gila Topminnow, *Poeciliopsis occidentalis*, has been extirpated through much of its range due to predation by introduced Mosquitofish, *Gambusia affinis*. However, Topminnows are able to coexist with Mosquitofish in streams that experience periodic flash floods because the Topminnows show instinctive behavioral adaptations to high discharge, including rapid movement to shoreline areas as waters rise, and proper orientation to strong currents. Mosquitofish, which evolved in southeastern regions that lack flash floods, behave inappropriately and are flushed out of rivers when floods occur (Meffe 1984).

Although the desert pupfishes and other fishes survive and reproduce in the extreme conditions of the desert southwest, these fishes do not exhibit several other traits common to many desert forms, such as estivation, air breathing, or diapausing eggs. Adaptations of the desert pupfishes are most likely extensions of capabilities possessed by ancestral lineages rather than being newly evolved. Cyprinodontids are small fishes that frequently inhabit estuaries where temperature, salinity, and oxygen availability vary widely. Adaptation to such estuarine conditions would constitute **preadaptation** for desert conditions. Given the superlatives accompanying the above descriptions of thermal, salinity, and oxygen tolerance in pupfishes, additional adaptation may have been unnecessary. Working against the evolution of desert-specific adaptations are the comparative youth of the region, as well as the periodic connection of desert water courses and pools with each other and with estuarine and riverine areas that serve as sources of new immigrants. Selection for desert adaptations would be relaxed during wetter periods, and dilution of such adaptations would also occur due to gene flow from source areas.

Given the limited extent, isolation, and small populations characteristic of desert habitats, it is not surprising that southwestern fishes are very sensitive to environmental degradation (Miller 1981; Soltz & Naiman 1981; Contreras-Balderas et al. 2002). A variety of activities have led to declines and extinctions, including pumping of springs and groundwater, pollution by humans and livestock, draining of marshes, damming of streams, introductions of exotic competitors and predators, and hybridization (see Chapter 26). Approximately 15 species and numerous localized populations of southwestern fishes are extinct. Desert species account for nearly two-thirds of the federally listed Endangered and Threatened fishes in North America. The International Union for the Conservation of Nature (IUCN 2004) lists 14 desert cyprinodontiform species as Critically Endangered. Some species have been described after they were exterminated (e.g., the aptly named La Trinidad Pupfish, *C. inmemoriam*, described on the basis of a single specimen collected before its single habitat dried up due to water extraction; Lozano-Vilano & Contreras-Balderas 1993). The fishes of this region have adapted well to the environmental challenges of extreme desert conditions, but nothing in their history allows them to handle the kinds of

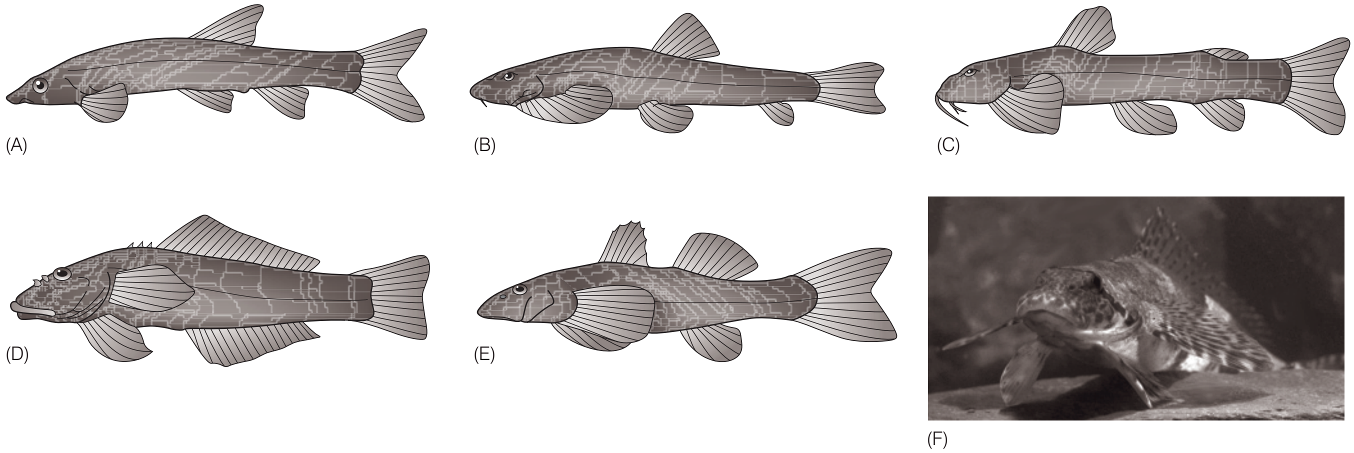


Figure 18.12

Convergence in body form among unrelated fishes that occupy swiftwater habitats in streams and rivers. (A) *Kneria*, an African kneriid (Gonorynchiformes). (B) *Gastromyzon*, an Asian balitorid hillstream loach (Cypriniformes). (C) *Amphilius*, an African amphiliid loach catfish (Siluriformes). (D) *Cheimarrichthys*, a New Zealand cheimarrichthyid Torrentfish (Perciformes, Trachinoidei). (E) *Rhyacichthys*, an Indo-Australian rhyacichthyid loach goby (Perciformes, Gobioidei). (F) Head-on photo of a Torrentfish, showing body profile and fin shape and placement characteristic of swiftwater fishes (*c*. 10 cm). (A–E) after Nelson (2006); (F) from McDowall (2000), used with permission.

insults that often result from careless or callous humans (Pister 1981; Minckley & Deacon 1991; Rinne & Minckley 1991; Contreras-Balderas et al. 2002).

Strong currents and turbulent water

High-energy zones in both marine and fresh waters – wave-swept rocky shores in the ocean and rapids in rivers and streams – appear unsuitable for fishes because of the difficulties of remaining in place, let alone feeding and breeding under such conditions. Invertebrates successfully occupy such locales but, except for the groups that hide behind or under rocks, tend to be rather sessile or essentially glued in place (e.g., chitons, limpets, barnacles, and sea anemones in the ocean; caddis fly larvae, black fly larvae, and water penny beetle larvae in streams). With the exception of parasitic male anglerfishes, fishes have not evolved immobile forms and yet some species are exposed to the force of the waves and currents in the same habitats as these stay-at-home invertebrates.

Fishes have converged on a general body shape, fin shape and distribution, and special devices for living in high-energy zones. Good examples in marine habitats are inhabitants of wave-swept, **intertidal surge regions**. Groups include various scorpaeniform cottid sculpins, perciform blennioids (blenniid combtooth blennies, tripterygiid triplefins, clinid kelp blennies, labrisomid blennies), sicydiine gobies, and especially the aptly named clingfishes (Gobiesocidae). All tend to have bodies that are depressed dorsoventrally and somewhat tapered (= terete) or teardrop-shaped when viewed from above, often with enlarged pectoral fins placed low on the body (e.g., Horn 1999; Boyle & Horn 2006). In the extremes, the pelvic fins are fused to form a suction disk (e.g., in clingfishes and gobies). *Sicyases sanguineus*, a large (30 cm) Chilean gobiesocid, lives in and above the intertidal zone in locales exposed directly to waves (Paine & Palmer 1978; Cancino & Castilla 1988).

High-energy freshwater habitats have produced the most striking convergences, exemplified by fishes that live in **torrent zones** and share a body form clearly appropriate to maintaining position in strong, unidirectional currents (Fig. 18.12). The suite of anatomical traits on which these fishes have converged include:

- A dorsoventrally depressed, small (<15 cm) body, sometimes triangular or square in cross-section with a flattened ventral surface.
- Large, horizontally oriented pectoral fins positioned low on the body; pelvic fins are also sometimes enlarged.
- A suction device, such as the mouth (e.g., suckermouth catfishes, algae eaters), or formed either by joined paired fins (hillstream loaches, gobies, clingfishes) or fins in combination with the ventral body surface (loach catfishes, loach gobies), sometimes with adhesive pads (sisorid catfishes and perhaps kneriids).
- Subterminal or inferior mouths in just about all species.
- A missing swim bladder (psilorhynchids, amblycipitid loach catfishes).
- Modifications to respiratory behavior (rapid inhalations followed by a quiescent period of several

minutes; Berra 2001) or respiratory structures, such as the incurrent opening at the top of the gill cover in gyrinocheilids, an analogous arrangement in astroblepid climbing catfishes, and a special fold of skin on which gill membranes rest in loach catfishes.

The common habitat indicated for many of these fishes is "mountain streams". Some are algae scrapers (gyrinocheilds, loricariid catfishes, parodontids, loach gobies), others are well known for ascending waterfalls (kneriids, astroblepid climbing catfishes, *Lentipes* gobies). Many have scientific or common names that reflect specialized morphologies or suggest habitat preferences. The list includes species from perhaps 16 families and at least five different orders of teleosts (Table 18.2); other taxa in North American streams that use similar habitats and show some of the modifications include catostomid hognose suckers (*Hypentelium*), scorpaeniform sculpins (*Cottus*), and several percid darters (*Etheostoma*, *Percina*).

The relationship between form and function in many of these is fairly obvious. The depressed-flattened shape of the body as well as the large, horizontally oriented paired fins would help push the fish down against the substrate. An adhesive or suction device similarly prevents being dislodged. Subterminal mouths allow for algae scraping or benthic feeding, whereas opening a terminal mouth creates drag. Many have reduced or lost the gas bladder, a broadly convergent trend among benthic fishes in general but an obvious necessity in swift flowing water.

Undoubtedly, some anatomical characteristics reflect phylogeny as much as adaptation to habitat, although phylogeny can preadapt organisms to particular habitats as well as constrain them from occupying others (see below, Preadaptation, evolution, and convergence). Preadaptation may help explain the abundance of catfish families in Table

Table 18.2

A sampling of freshwater fishes that inhabit torrent and rapid zones of streams and rivers. Most if not all have converged on body shapes and proportions, fin arrangements and shapes, and other traits that reflect the need to hold position on the bottom in swift flowing water.

Order	Family	Scientific name[a]	Common name
Gonorynchiformes	Kneriidae	*Kneria*	Knerias
Cypriniformes	Cyprinidae	*Rhinichthys cataractae*	Longnose Dace
Cypriniformes	Psilorhynchidae	*Psilorhynchus*	Mountain carps
Cypriniformes	Gyrinocheilidae	*Gyrinocheilus*	Algae eaters
Cypriniformes	Balitoridae	*Balitora*, *Gastromyzon*	Hillstream loaches
Characiformes	Parodontidae	*Parodon*	Parodontids
Siluriformes	Amphiliidae	*Amphilius*	Loach catfishes
Siluriformes	Nematogenyidae	*Nematogenys inermis*	Mountain Catfish
Siluriformes	Astroblepidae	*Astroblepus*	Climbing catfishes
Siluriformes	Loricariidae	*Otocinclus*, *Farlowella*	Suckermouth armored catfishes
Siluriformes	Amblycipitidae	*Amblyceps*	Torrent catfishes
Siluriformes	Sisoridae	*Sisor rheophilus*	Sisorid catfishes
Perciformes	Cheimarrhichthyidae	*Cheimarrichthys fosteri*	New Zealand Torrentfish
Perciformes	Gobiesocidae	*Gobiesox fluviatilis*	Mountain Clingfish
Perciformes	Rhyacichthyidae	*Rhyacichthys*	Loach goby
Perciformes	Gobiidae	*Lentipes concolor*	O'opu Alamo'o

[a] The specific name is given for representative or monotypic species, and the generic name is given when several species exist.

18.2; catfishes as a group are freshwater benthic dwellers and somewhat depressed in body shape. Existing adaptations probably facilitated the invasion of high-energy, freshwater habitats by marine gobiesocid clingfishes, given their flattened, teardrop-shaped bodies, benthic habits, absent swim bladder, and pelvic fins fused into a suction disk. Most of the seven clingfishes that inhabit fresh water (of a total of 140 species in the family) live in high-velocity stream zones at moderate to high elevations of Central and northern South America, regions where few of the other fishes listed in Table 18.2 occur. These clingfishes likely encountered an available, relatively unoccupied **adaptive zone** for which they already possessed appropriate traits (e.g., Guzman et al. 2001). Similar circumstances may help explain the successful invasion of insular fresh waters by the other perciforms in Table 18.2, such as the cheimarrhichthyidae Torrentfish (New Zealand), rhyacichthyid loach gobies (New Guinea, New Caledonia), and the gobiid O'opu Alamo'o (Hawaii).

Caves

Among the more extreme aquatic environments imaginable are underground water systems where no light penetrates and where food availability depends on infrequent replenishment from surface regions. However, **cave living** has advantages, including a scarcity of competitors and predators and a constant, relatively moderate climate. Fishes have evolved independently in caves around the world and, not surprisingly, similar adaptations to cave life have evolved repeatedly despite phylogenetic differences. The darkness, low productivity, and even high atmospheric pressure of cave environments have also led to some surprisingly strong convergences between cave and deepsea fishes.

Caves usually develop in limestone formations (**karst**) because of the solubility of carbonaceous rock, although caves exist in other rock types such as lava tubes on volcanic slopes. Caves include places where water dives underground and resurfaces after a short distance, or where springs upwell near the surface and are illuminated by dim but daily fluctuating daylight (technically a **cavern**). The classic cave environment is a continually dark, subterranean system where fluctuations in temperature, oxygen, and energy availability are minimal and where little interchange occurs with other areas. The biota of caves are especially interesting because a continuum of habitats exists between the surface, caverns, and deep caves. We can consequently often identify closely related and even ancestral organisms from which cave populations and species evolved. This allows comparison of cave and surface forms and analysis of the processes and selection pressures that have produced cave adaptations.

Approximately 136 species and 19 families in 10 different orders of teleostean fishes have colonized caves. These unusual fishes – termed variously **hypogean**, **troglobitic**, **phreatic**, and **stygobitic** – occur in scattered locales at tropical and warm temperate latitudes on all continents except Antarctica and Europe (Proudlove 1997a, 2006; Weber et al. 1998). With the exception of some bythitid cusk-eels and gobies, the families are restricted to fresh water. Most cave fishes are ostariophysans (characins, loaches, minnows, and eight catfish families), which is not surprising given the overwhelming success of this superorder in freshwater habitats. The remaining four families are either paracanthopterygian (ambloypsid cavefishes) or acanthopterygian (poeciliid livebearers, synbranchid swamp eels, and cottid sculpins). Only one family, the amblyopsid cavefishes, consists primarily (four of six species) of cave-dwelling forms. Many are known from only one or a few locations, although sampling difficulties make accurate population estimations difficult. But isolation seems to be commonplace: at least 48 species are known from only their type locality.

Adaptations to cave living

Typical cave-adapted fishes are characterized by a lack of pigmentation, reduced squamation, a reduction or loss of light receptors (involving eyes and the pineal gland) (Fig. 18.13), greatly expanded lateral line and external chemo-

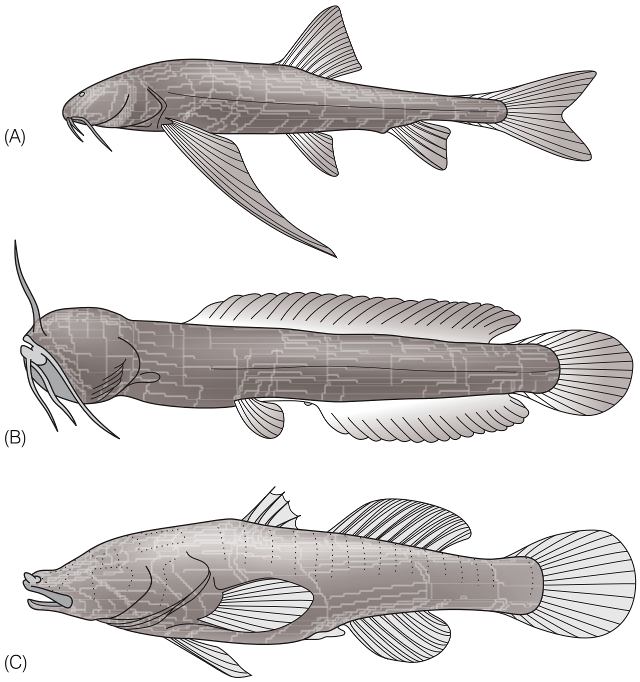


Figure 18.13
Cave fishes from three different orders, showing convergent loss of eyes, among other oddities. (A) A balitorid river loach, *Triplophysa xiangxiensis* (Cypriniformes), from China. (B) A clariid catfish, *Horaglanis krishnai* (Siluriformes), from India. (C) An eleotrid sleeper, *Typhleotris madagascariensis* (Perciformes), from Madagascar. After Weber et al. (1998).

sensory receptors, and relative decreases versus increases in brain areas associated with vision versus hearing and chemoreception, respectively. Behaviors typically mediated by vision are lost, such as schooling, the dorsal light reaction, and circadian rhythms (Wilkens 1988; see Chapters 6, 23). Taste buds in surface-dwelling *Astyanax fasciatus*, a characin, are generally restricted to the mouth region, whereas in cave-adapted populations of the same species they cover the lower jaw and ventral areas of the head. Chemosensory capabilities are better in cave forms; cave-adapted *A. fasciatus* are about four times more effective in finding meat on the bottom of a darkened aquarium than are the surface forms.

Adaptations to unpredictable or irregularly occurring food supplies also exist. When fed *ad libitum* (as much as they can consume), cave *Astyanax* build up larger fat reserves than surface forms, again by a factor of four (37% of body mass vs. 9%). Parallel comparisons can be made within the family of cavefishes (Amblyopsidae). The cave genera (*Amblyopsis*, *Typhlichthys*, *Speoplatyrhinus*) swim more efficiently, have lower metabolic rates, and find prey quicker and at greater distances in the dark than surface forms (*Chologaster*). The cave forms are also better at avoiding obstacles and at memorizing the locations of objects than are the surface fish. Cave catfishes (blindcats) in the North American family Ictaluridae show parallel changes with respect to eye loss, absence of pigmentation, pineal reduction, enlarged lateral line pores and canals, and brain modifications. Many analogous adaptations have also been observed in other cave-adapted taxa, including beetles, amphipods, crickets, crayfishes, shrimps, and salamanders (Poulson 1963; Poulson & White 1969; Culver 1982; Langecker & Longley 1993; Parzefall 1993).

Adjustments to cave existence also occur in the reproductive biology and life history traits of cave-dwelling fishes. Not surprisingly, visual displays are generally lacking during courtship of cave species, even in taxa such as livebearers and characins where they occur commonly in surface forms (Parzefall 1993). With respect to life history traits, cave-adapted amblyopsids produce fewer but larger eggs with greater yolk supplies, have larvae that spend more time before hatching, and have a later age at maturation and longer life spans (Bechler 1983). Reproductive rates of cave populations are surprisingly low. Only about 10% of the mature fish in a population of cavefishes may breed in any one year, each female producing 40–60 large eggs. These eggs are incubated in the mother's gill cavity for 4–5 months, long after the young are free-swimming. This may be the longest period of parental care for an externally fertilized fish species. Many of these characteristics are what one would expect in a habitat where adult mortality and interspecific competition are low, environmental conditions stable, and food scarce (Culver 1982; see Chapter 24).

The degree of anatomical and behavioral change in a cave population is often correlated with the length of time available since the cave was colonized. Eye loss, characteristic of cave-adapted forms, shows some responsiveness to light availability. When young *Astyanax fasciatus* from caves of different presumed ages are raised in the presence of light, individuals from old cave populations do not develop eyes, surface populations develop eyes, and populations thought to have invaded caves more recently vary in eye size (Parzefall 1993).

Food sources in caves are rather limited. Since no photosynthesis can occur in the sunless cave environment, food can only arrive if brought in by other animals or carried in by percolation through the rock or by water currents, such as during occasional floods. Common food types differ among families, but bat and cricket guano, bacteria, algae, small invertebrates (isopods, amphipods, copepods), and conspecifics are the common food types of most groups (Parzefall 1993). In Mexican caves containing the livebearer *Poecilia mexicana*, bat guano is supplemented by bacteria associated with sulfur springs in the cave, an interesting analog to deepsea vent communities (see above, The deep sea). Cave fishes respond to chemical or mechanical cues given off by the food; a clay ball dropped into the water containing cave fishes will induce active swimming and searching by fish within 1 m of the ball.

Cave fishes usually live at low densities, particularly those in isolated deep caves; most populations involve hundreds or at most thousands of individuals. Population density is strongly correlated with food availability, which again correlates with degree of isolation. Typical population densities of such fishes as the amblyopsid cavefishes are low, ranging from 0.005 to 0.15 fish/m^2. The Blind Cavefish, *Astyanax fasciatus*, can reach densities of 15/m^2 and *Poecilia mexicana* can reach densities of 200/m^2 where sulfur springs occur, and near-surface caves that contain bats as an energy source host even higher densities of cave-dwelling fishes.

Not surprisingly, small populations living in isolated habitats with few competitors or predators and evolving life histories that include slow growth and reproduction, make cave fishes exceedingly vulnerable to environmental disturbance, a convergent trend that cave fishes share with desert spring forms for many of the same reasons. Pollutants, water withdrawal, and competition, predation, and disease brought in by introduced species are major threats. As an ecological grouping, caves must be the habitat type with the proportionately highest rate of imperilment among fishes (and other organisms). The IUCN (2004) listed 52 cave fish species as at high risk, and experts consider at least another eight species to be in need of protection (Proudlove 1997b). The Congo Blind Barb, *Caecobarbus geertsii*, is threatened by the aquarium trade and is consequently listed in Appendix II of the Convention on International Trade in Endangered Species (CITES). In the USA, the Alabama Cavefish, *Speoplatyrhinus poulsoni*, is federally protected as Endangered and the Ozark Cavefish, *Amblyopsis rosae*,

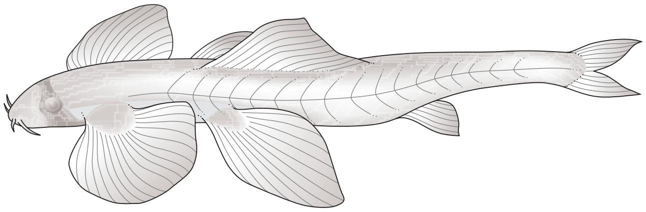


Figure 18.14

Cryptotora thamicola, a cave-dwelling torrentfish from Thailand. Known only from two locales and designated Vulnerable by IUCN because of small populations and limited distribution, this remarkable 30 mm fish shows classic specializations for both cave and swift water. Illustration by S. Madsden. See also the BBC Planet Earth video on Caves for live footage.

is Threatened. Two other cavefishes that occur in the USA – the Northern Cavefish, *Amblyopsis spelaea*, of Kentucky and Indiana and the Southern Cavefish, *Typhlichthys subterraneus*, found in five southeastern states, Indiana, and Missouri – are both designated as Vulnerable by the IUCN (2004) (see Romero 1998; Romero & Bennis 1998).

At the pinnacle of this discussion of evolution in special habitats is a specialized freshwater fish that truly exemplifies the Principle of Convergence. *Cryptotora thamicola* is a balitorid from Thailand, a member of the hillstream loach family along with several torrent-dwelling fishes. Its morphology conforms with other torrent dwellers: greatly enlarged pectoral and pelvic fins with adhesive pads, and a short, blunt, sloping forehead. It occurs in fast-flowing, cascading water where it has been observed to climb waterfalls (Kottelat 1988; Trajano et al. 2002; Proudlove 2006). Except the waterfalls are in caves, and *Cryptotora* is a classic cave dweller: naked, eyeless, and colorless (Fig. 18.14). Strong selection pressures produce predictable adaptations, and adaptation to one selective regime does not preclude simultaneous adaptation to other, strong selection factors.

Preadaptation, evolution, and convergence in cave fishes

Adaptation to the cave environment often involves two contrasting trends in the development of structures. Organs that may have been useful to surface ancestors but are of limited use in the cave, such as eyes and pigment, are gradually lost, a process known as **regressive evolution**. They are replaced by **hypertrophied** ("overdeveloped") structures, such as widely distributed and enlarged lateral line and chemosensory receptors and their neural correlates. The mechanisms and agents of selection leading to regressive evolution – namely the relative importance of neutral or directional selection, pleiotropy, energy economy, population size, time since isolation, and gene flow – remain a matter of active debate (Culver 1982).

Some groups possess preadaptations that may have made the transition to cave life quicker. Surface-dwelling Mexican characins show reduced eye development when raised in the dark, and blinded surface fish are as effective at avoiding obstacles as are cave-adapted fish. At least 10 cave families commonly contain nocturnal species; nocturnality and its attendant emphasis on non-visual sensory modes would be an important preadapation for cave living. Some cave-dwelling characins develop taste buds outside the mouth. This pattern also exists in surface-dwelling ictalurid catfishes; in fact, taste buds are more numerous on the barbels and general body surface than in the mouth of ictalurids, which could make transition to a cave environment easier. An elongate body and other eel-like features occur in nearly one-third of cave forms, such as the synbranchid swamp eels, cusk-eels, clariid catfishes, loaches, trichomycterid catfishes, and arguably the amblyopsid cavefishes themselves. Seven acanthopterygian species (i.e., non-anguilliforms) are eel-like. Anguilliform swimming may be advantageous in the narrow confines of many caves (see Chapter 8, Locomotory types). Evolution of eel-like bodies has occurred in several dozen non-anguilliform fishes, another case of convergent evolution worth studying in its own right (see Chapter 24, Habitat use and choice).

Several authors have noted the similarities in traits between cave fishes and bathypelagic deepsea forms, referring to the similarities as the **deepsea syndrome**. Similar adaptations in the two habitat types include losses of pigmentation, squamation, and light receptors, expanded lateral line and chemosensory receptors, and attendant modifications in the brain. In the blind catfishes, which live deeper than most other cave fishes (400–500 m), additional convergences occur in terms of reduced body size, gas bladder regression, large lipid deposits, and reduction of body musculature and skeletal ossification. These changes can be viewed as adaptations to overcome problems associated with energy conservation in an environment with limited food availability (Langecker & Longley 1993). These parallels underscore once again the descriptive power of the Principle of Convergence: if selection pressures and processes are strong and analogous, convergence can occur not just among species within a habitat but also between habitats.

Summary

SUMMARY

1. The Principle of Convergence states that strong selection pressures tend to produce strong similarities in unrelated animals. Several aquatic habitats offer examples. Mesopelagic ocean depths between 200 and 1000 m contain 750 species of fishes that are typically dark in color, with photophores, large mouths, slender teeth, reduced skeletons and squamation, long rete mirabiles, low enzyme activity, and daily vertical migrations. Bathypelagic fishes (1000–4000 m, 200 species) show stronger and more bizarre convergences, including sex reversal, extreme skeletal and musculature reduction, eye loss, longer retes, marked sexual dimorphism, and behavioral energy conservation. These characteristics are apparent adaptations to low energy availability.
2. Oceanic, pelagic fishes swim in the upper 100–200 m of water. This is the primary region for commercial fish production and is the habitat of herringlike fishes, sauries, carangoids, dolphinfishes, mackerels, tunas, and billfishes. Pelagic fishes are typically streamlined, silvery, and migratory, with a high proportion of red muscle for sustained swimming. They respire efficiently and save energy by using ram-gill ventilation. Life history differences between temperate and tropical species are influenced by seasonal and spatial food availability, and lead to dramatic differences in year class fluctuations. Freshwater pelagics have converged on many traits with oceanic species.
3. The polar Arctic and Antarctic regions lie above 60° latitude. The Antarctic has more endemic, specialized fishes, half of which are in the icefish suborder Notothenioidei. Antarctic fishes avoid freezing because their blood contains antifreeze compounds. Channichthyids are unusually pale because they lack hemoglobin and myoglobin. Some notothenioids have evolved neutral buoyancy via reduced skeletal mineralization and increased lipid deposition. Arctic fishes have converged on similar traits.
4. Desert freshwater fishes live on almost all continents in regions where water scarcity creates extreme conditions. Desert fishes often possess accessory respiratory structures for using atmospheric oxygen, and have a life cycle that includes a resting stage during droughts, either involving a diapausing egg or an estivating adult. In addition to low oxygen, desert fishes often encounter extremes of salinity and alkalinity. The deserts of the southwestern USA and western Mexico have a surprising diversity of endemic fishes, many of which are threatened.
5. Fishes that inhabit high-energy zones such as the wave-swept intertidal zone or steep stream beds have converged upon a body shape that is depressed, paired fins that are expanded, a suction device, subterminal mouths, and small body size. All these traits appear to facilitate the holding of position on the bottom despite strong water flow.
6. Cave fishes live in lightless, freshwater environments where food is scarce. Cave-adapted forms typically have reduced eyes, pigmentation, and squamation; low metabolic activity and reproductive rates; low population densities; and increased chemosensory and lateral line development. Their biology makes them especially vulnerable to habitat disturbances. Cave-dwelling fishes have converged on many of the traits evolved by deepsea fishes, probably in response to food and light scarcity.

Supplementary reading

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Pelagic Fish Research Group, http://pelagicfish.ucdavis.edu.

The Congo Project (torrent fishes), http://research.amnh.org/ichthyology/congo.