Figure I *(opposite)*

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 pantropical Great Barracuda, *S. barracuda*, frequently causes ciguatera fish poisoning among humans (Chapter 25). Photo by D. Hall, www.seaphotos.com.

Figure 1.1

Fish versus fishes. By convention, "fish" refers to one or more individuals of a single species. "Fishes" is used when discussing more than one species, regardless of the number of individuals involved. Megamouth, paddlefish, and char drawings courtesy of P. Vecsei; oarfish drawing courtesy of T. Roberts.

Figure 2.1

Cladogram of hypothesized relationships of the Louvar (*Luvarus*, Luvaridae) and other Acanthuroidei. Arabic numerals show synapomorphies: numbers 1 through 60 represent characters from adults, 61 through 90 characters from juveniles. Some sample synapomorphies include: 2, branchiostegal rays reduced to four or five; 6, premaxillae and maxillae (upper jawbones) bound together; 25, vertebrae reduced to nine precaudal plus 13 caudal; 32, single postcleithrum behind the pectoral girdle; 54, spine or plate on caudal peduncle; 59, teeth spatulate. From Tyler et al. (1989).

Figure 2.2

Some meristic and morphometric characters shown on a hypothetical scombrid fish.

Figure II *(opposite)*

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). Photo by D. Hall, www.seaphotos.com.

Figure 3.1

Osteology of the Little Tuna (*Euthynnus alletteratus*). From Mansueti and Mansueti (1962).

Figure 3.2

Lateral view of the skull of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collette and Chao (1975).

Figure 3.3

Lateral view of the neurocranium of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collete and Chao (1975).

Figure 3.4

Dorsal view of the neurocranium of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collete and Chao (1975).

Figure 3.5

Ventral view of the neurocranium of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collete and Chao (1975).

Figure 3.6

Left infraorbital bones in lateral view of the Spanish Mackerel (*Scomberomorus maculatus*). From Collete and Russo (1985b).

Figure 3.7

Rear view of the skull of a bonito (*Sarda chiliensis*). The crosses indicate points of attachment of epineural bones. From Collete and Chao (1975).

Figure 3.8

Lateral bones of face and lower jaw suspension of a generalized characin (*Brycon meeki*). From Weitzman (1962).

Figure 3.9

Major types of jaw suspension in fishes. From Walker and Liem (1994).

Figure 3.10

Left hyoid complex in lateral view of a Spanish mackerel (*Scomberomorus commerson*). From Collete and Russo (1985b).

Figure 3.11

Branchial arch of a Spanish mackerel (*Scomberomorus semifasciatus*). Dorsal view of the gill arches with the dorsal region folded back to show their ventral aspect. The

epidermis is removed from the right-hand side to reveal the underlying bones. From Collete and Russo (1985b).

Figure 3.12

Junction of precaudal and caudal vertebrae in a left lateral view of the King Mackerel (*Scomberomorus cavalla*). The middle vertebra, with an elongate haemal spine, is the first caudal vertebra. Vertebrae numbered from the anterior. From Collete and Russo (1985b).

Figure 3.13

Representative precaudal and caudal vertebrae of a generalized characin (*Brycon meeki*). (A) Anterior view of the 20th precaudal vertebra. (B) Anterior view of the 24th precaudal vertebra. (C) Anterior view of the second caudal vertebra. (D) Lateral view of the 20th precaudal through second caudal vertebrae. From Weitzman (1962).

Figure 3.14

Posterior vertebrae and caudal complex of a generalized characin (*Brycon meeki*). From Weitzman (1962).

Figure 3.15

Caudal complex in left lateral view of a Spanish mackerel (*Scomberomorus semifasciatus*). From Collete and Russo (1985b).

Figure 3.16

Left pectoral girdle of a generalized characin (*Brycon meeki*). From Weitzman (1962).

Figure 3.17

Structure of fish skin.

Figure 3.18

Fish scales. (A) A cycloid scale (length 3.14 mm) of the Shiner, *Notropis cornutus*. (B) A ctenoid scale (length 3.5 mm) of the Yellow Perch, *Perca flavescens*. The scales are oriented with the anterior field to the left; the lengths were measured along the anterior–posterior diameter. AF, anterior field; AN, annulus; CI, circulus (ridge); DF, dorsal field; FO, focus; PF, posterior field; PR, primary radius; SR, secondary radius; VF, ventral field. From Van Oosten (1957).

Figure 4.1

Cheek muscles of a sculpin, *Jordania zonope*. (A) Superficial musculature. (B) After removal of A1 and A2. A1, A2, and A3, adductor mandibulae; AAP, adductor arcus palatini; DO, dilator operculi; LAP, levator arcus palatini; LIP, ligamentum primordium; LO, levator operculi. From Yabe (1985).

Figure 4.2

Extrinsic eye muscles of a fish. The cranial nerves that supply the muscles are indicated by Roman numerals. From Walker and Liem (1994).

Figure 4.3

Stimulation of the modified muscle cells of the billfish brain heater releases calcium from the sarcoplasmic reticulum (SR), which is then transported back across the SR membrane. The cycling of calcium at the membrane generates heat. It is speculated that the excess calcium may also stimulate mitochondrial metabolism, generating heat.

Figure 4.4

Block diagram showing the simplest type of fish circulatory system. Solid black vessels contain blood of lower oxygen content; white vessels contain blood with higher oxygen content. Arrows indicate direction of blood flow. From Mott (1957).

Figure 4.5

Gills and blood vessels of the head of a cod (*Gadus*). From Lagler et al. (1977).

Figure 4.6

Main blood vessels of a bony fish. After Lagler et al. (1977).

Figure 4.7

Anterior arterial system in ventral view in the Scombridae, showing the phylogenetic increase in development of the subcutaneous circulatory system (darkened vessels). Numbers indicate vertebrae; stippled areas show where pharyngeal muscles originate. (A) Wahoo (*Acanthocybium*); (B) Frigate tuna (*Auxis*); (C) Little tuna (*Euthynnus*); (D) Skipjack (*Katsuwonus*); (E) Longtail Tuna (*Thunnus tonggol*); (F) Albacore (*Thunnus alalunga*). From Collette (1979).

Figure 4.8

Variation in intestinal length and other features among carnivorous and herbivorous fishes. (A) An herbivorous catfish (Loricariidae). (B) Spiral valve in cross-section of intestine of a shark. (C) A carnivore, the Northern Pike (*Esox lucius*). (D) A carnivore, a perch (*Perca*). From Lagler et al. (1977).

Figure 4.9

The gas bladder. (A) Position of gas bladder in a deepsea snaggletooth (*Astronesthes*). (B) Details of the gas bladder in *Astronesthes*. (C) Generalized blood supply of the gas bladder in physoclistous bony fishes. From Lagler et al. (1977).

Figure 4.10

Representative types of urogenital systems in fishes. Upper series (A–D), males; lower series (E–H), females; black organs, mesonephric kidneys; stippled organs, testes; organs with circles, ovaries; stippled lines, vestigial structures; a, Müllerian duct; cl, cloaca; f, open funnel of oviduct; gp, genital papilla; l, Leydig's gland; md, mesonephric duct; n, nidamental gland; ov, oviduct; u, uterus; up, urinary pore; vd, vas deferens. From Hoar (1957).

Figure 4.11

Dorsal views of brains of representative fishes: (A) sturgeon; (B) Bowfin; (C) trout; (D) minnow; (E) catfish; (F) elephantfish (Mormyridae). Major brain parts from anterior to posterior: bolf, olfactory lobe; tel, telencephalon; dienc, diencephalon; tect, optic lobe; aur, auricular cerebelli; cocb, cerebellum; emgr, eminentia granularis; rhomb, myelencephalon; valvcb, valvula cerebelli. From Nieuwenhuys and Pouwels (1983).

Figure 5.1

(A, B) The gill arches of a fish support the gill filaments (also called the primary lamellae) and form a curtain through which water passes as it moves from the buccal cavity to the opercular cavity. (C) As water flows across the filaments of a teleost, blood flows through the secondary lamellae in the opposite direction. (D) In elasmobranchs, even though septa create some structural differences in gill filaments, water flow across the secondary lamellae is still countercurrent to blood flow. (E) The countercurrent flow of water and blood at the exchange surface of the secondary lamellae ensures that the partial pressure of oxygen in the water always exceeds that of the blood, thereby maximizing the efficiency of oxygen diffusion into the blood.

Figure 5.2

The timing of the expansion and contraction of the buccal (oral) and opercular cavities ensures that the pressure in the buccal chamber exceeds that of the opercular chamber throughout nearly all of the respiratory cycle. This creates a nearly steady flow of water from the buccal chamber to the opercular chamber, passing over the gill lamellae, which have blood flowing through them in the opposite direction. The fish is viewed from below. Adapted from Hildebrand (1988).

Figure 5.3

(A) Hagfishes have one or more external gill openings on each side. Movement of the scroll-like velum draws water in through the nostril and pushes it through the pharynx and branchial pouches. Excurrent branchial ducts then direct the water to the gill openings. (B) Lampreys have multiple external gill openings on each side. Expansion and contraction of the branchial pouches provides ventilation through each external opening. This permits continued breathing while the mouth is attached to substrate or a host.

Figure 5.4

(A) Lateral views of the gill arches of the Walking Catfish (*Clarias batrachus*) show the respiratory fans, respiratory membranes of the suprabranchial chamber, and treelike extensions (arborescent organs) that permit the fish to extract oxygen from air when it is out of water. (B) A cut-away view of the branchial region of the Giant Gourami (*Osphronemus goramy*) shows a labyrinth of platelike extensions to accomplish the same goal. A, from Munshi (1976); B, from Peters (1978).

Figure 5.5

Oxygen dissociation curves. Vertical axes indicate the percent of total oxygen-binding sites that are occupied by oxygen. The horizontal axes indicate the concentration of oxygen dissolved in the solution surrounding the hemoglobin, typically blood plasma. A decrease in pH results in a shift of the curve to the right (the Bohr shift, A), and may also prevent full saturation of hemoglobin with oxygen (the Root effect, B). (C) Toadfish can survive better than mackerel in low oxygen conditions because their hemoglobin has a higher affinity for oxygen than mackerel hemoglobin. After Hall and McCutcheon (1938). (D) Largemouth Bass are better suited for warmer water with somewhat less oxygen than are Smallmouth Bass because the hemoglobin of the Largemouth Bass has a higher affinity for oxygen. After Furimsky et al. (2003).

Figure 5.6

The uptake of carbon dioxide at the tissues is enhanced by the presence of carbonic anhydrase in the red blood cells. This enzyme catalyzes the conversion of CO_2 to carbonic acid (H_2CO_3), which dissociates to form bicarbonate (HCO_3^-) and a hydrogen ion (H^+). The increase in intracellular levels of H^+ causes a drop in pH, causing hemoglobin (Hb) to lose its oxygen (the Bohr effect). Hemoglobin can bind some CO_2, as well as some H^+ to help buffer against too great a drop in pH. Bicarbonate diffuses out of the red blood cell into the plasma, permitting further uptake of CO_2. To balance the loss of negative charges, chloride (Cl^-) diffuses into the cell (the chloride shift). These reactions occur in reverse at the gills.

Figure 5.7

The amount of oxygen used by stream fishes while holding position at different water velocities varies with fish morphology and lifestyle. Water column species, such as Rainbow Trout (*Oncorhynchus mykiss*) must increase swimming effort as water velocity increases. The resulting exponential increase in oxygen consumption rates with increasing velocity has been shown in numerous studies of swimming fishes. Mottled Sculpin (*Cottus bairdi*) are benthic fish that lie on and cling to the substrate. Hence, their oxygen consumption rates do not change with increasing water velocity. Longnose Dace (*Rhinichthys cataractae*) combine tactics. At low and moderate velocities they remain on the substrate, and oxygen consumption rates do not change much. At higher velocities, however, they must swim, and oxygen consumption increases dramatically. After Facey and Grossman (1990).

Figure 5.8

Schematic representation of the gas bladders of a physostome (A) and a physoclist (B). The pneumatic duct permits gas release via the esophagus in a physostome, whereas a physoclist must rely on a specialized area of the bladder wall for gas resorption. Both have gas glands with associated retia for gas addition. (C) Production of lactate and hydrogen ions by gas gland tissue triggers the hemoglobin's release of oxygen (the Bohr and Root effects) and a decrease in gas solubility (the salting-out effect). Countercurrent exchange of ions and dissolved gases in the rete creates very high gas pressures in the gas gland, thereby facilitating the diffusion of gases into the gas

bladder. (A, B) after Denton (1961); data presented in (C) are for eels (*Anguilla*), from Kobayashi et al. (1989, 1990).

Figure 5.9

Partitioning of the energy consumed by a fish. Only energy not required to meet basic physiological needs (digestion, standard metabolism, repairs) or needed for activity is available for growth and gametes. Adapted from Videler (1993).

Figure 6.1

Mechanoreception involves sensory hair cells, which are found in the lateral line system of fishes and the inner ear of fishes and other vertebrates. The apical surface of a sensory hair cell usually has numerous stereocilia and a single, much longer kinocilium. Deflection of the stereocilia toward or away from the kinocilium causes an increase or decrease in the firing rate of the sensory neuron innervating the hair cell at its basal surface.

Figure 6.2

(A) Cross-section of the lateral line on the trunk of a fish showing the distribution and innervation of neuromast receptors and the location of pores that connect the canal to the external environment. (B) Each neuromast is composed of several sensory hair cells, support cells, and innervating sensory neurons. The apical kinocilia and stereocilia project into a gelatinous cupula which overlays the entire neuromast.

Figure 6.3

The inner ear of fishes. After Hildebrand (1988).

Figure 6.4

A lateral view of the left side of the anterior portion of the vertebral region of an otophysan fish (*Opsariichthys*, Cyprinidae). The Weberian ossicles (tripus, intercalarium, scaphium, claustrum) transmit sound vibrations from the gas bladder to the inner ear. The skull of the fish is to the left. Adapted from Fink and Fink (1981).

Figure 6.5

Schematic diagram of the structure of ampullary (A) and tuberous (B) electroreceptive organs. Both organs are surrounded by layers of flattened cells that join tightly to one another. This helps prevent current from bypassing the organs. Tight junctions between the receptor cells and supporting cells help focus incoming electric current through the base of the receptor cells, where they synapse with sensory neurons. Supporting cells in ampullary organs produce a highly conductive gel that fills the canal linking the sensory cells to the surrounding water. Adapted from Heiligenberg (1993), drawing courtesy of H. A. Vischer.

Figure 6.6

Dorsal view of an *Eigenmannia* and its electric field. From Scheich and Bullock (1974).

Figure 6.7

The jamming avoidance response (JAR) of two *Eigenmannia* kept in separate aquarium tanks. When electrically isolated, both fish converge on frequencies of about 370 Hz. When the tanks are connected electrically the fish shift and maintain an approximately 10 Hz difference in the frequencies of their EODs. From Scheich and Bullock (1974), originally in Bullock et al. (1972).

Figure 6.8

Cross-sectional view of the eye of a teleost. From Hildebrand (1988).

Figure 6.9

(A) External view of the nares of a fish. (B) The obvious flap of skin directs water across the sensory epithelium. Adapted from Lagler et al. (1977).

Figure 7.1

(A) The anal fin of a normal male *Gambusia* is elongated to form the gonopodium (arrowed), an intromittent organ used to inseminate females. (B) In normal females, the anal fin is fan-shaped. (C) A masculinized female exposed to pulp mill effluent, in which the anal fin has developed into a gonopodium.

Figure 7.2

(A) The circulatory system of a "typical" fish sends blood from the gills down the core of the fish, making it impossible to maintain an elevated core temperature in cold water. Arrows indicate the direction of blood flow. (B) In the warm-bodied Bluefin Tuna (*Thunnus thynnus*), most of the blood from the gills is shunted toward cutaneous vessels near the body surface and is carried through a heat exchanging rete en route to the active swimming muscles, which stay warm through this heat conservation mechanism. After Carey (1973).

Figure 7.3

Maintaining osmotic balance in fresh versus sea water. (A) Freshwater bony fishes must produce a large volume of dilute urine to offset the passive uptake of water across their gills. They also must actively transport ions into the blood at the gills to compensate for the loss of these ions to the dilute freshwater environment. (B) Marine bony fishes passively lose water to their environment and gain salts by diffusion across their gills. They must, therefore, take in water through their food and by drinking sea water. Monovalent ions are actively transported out of the blood at the gills. Magnesium and sulfate ions, which are abundant in sea water, are excreted in the urine. Marine fishes conserve water by producing urine that is isosmotic to their blood.

Figure 7.4

(A) In addition to the abundant mitochondria that provide the energy needed for high levels of active transport, mitochondria-rich (MR) cells have a highly infolded basolateral membrane that greatly increases surface area by creating a tubule system within the cell. This also brings the extracellular fluid within the tubules in close proximity to the apical surface of the cell, allowing the establishment of concentration gradients that assist with ion exchange. (B) The apical surface of some of the MR cells in the gills of freshwater fishes take up chloride ions from the surrounding water in exchange for the secretion of bicarbonate ions created by combining carbon dioxide with water. Proton pumps that transport hydrogen ions out of the cell and into the blood help to drive this process indirectly. (C) Other MR cells in freshwater fish gills take up sodium ions from the water by the excretion of hydrogen ions across the apical surface, removing sodium from the cell and transporting it into the blood at the basolateral surface. (D) Marine bony fishes actively transport chloride into the MR cells of the gills from the blood, creating a high intracellular concentration that results in the diffusion of the chloride across the apical surface and into the surrounding sea water. The outward flow of negatively charged chloride ions helps draw positively charged sodium ions out through the leaky membrane connecting the MR cell to an adjacent accessory cell. In B, C, and D the active transport of calcium ions out of the cell into the blood helps to draw in more calcium from the surrounding water. After Marshall and Grosell (2006) and Tresquerres et al. (2006).

Figure 8.1

The anatomy of swimming in teleosts. (A) Lateral view of a Spotted Sea Trout, *Cynoscion nebulosus*, with the skin dissected away to show the location of two myomeres on the left side. (B) The same myomeres as they appear relative to the backbone in a sea trout. The hatched region is the part of the myomere located closest to the skin, the dashed line shows the interior portion of the myomere where it attaches to the vertebral column. The anterior and posterior surface of each myomere is covered by a myoseptum made of collagen fiber in a gel matrix, shown as a slightly thickened line. (C) Cross-section of a generalized teleost near the tail, showing the distribution of the various septa and their relationship to the backbone. Myosepta join to form median and horizontal septa. (D) How contractions produce swimming in a generalized fish (an eel is shown here). Progressive, tailward passage of a wave of contractions from the head to the tail **push** back on the water, generating **forward thrust** as one component of the **reactive force**. Sideways slippage (**lift**) is overcome by the inertia of the large surface area presented by the fish's head and body. After Wainwright (1983) and Pough et al. (1989).

Figure 8.2

Anterior, posterior, and lateral views of a Smooth Trunkfish *Lactophrys triqueter*, showing its unusual body shape and protrusions, all which aid in hydrodynamics. After Bartol et al. (2003).

Figure 8.3

The two competing models that explain how horizontal locomotion is accomplished in sharks. (A) The modified classic model interprets the shape of the heterocercal tail as generating a downward and backwards thrust (F_{water}), lifting the tail up (F_{tail}); these produce a resultant force ($F_{reaction}$) that moves the body upwards and forwards. The flattened ventral profile of anterior body regions also provides lift (F_{body}). $F_{reaction}$ plus F_{body} counter the shark's tendency to sink because of its negative buoyancy (F_{weight}). The result is horizontal swimming. (B) In the alternative Thomson model, the upper and lower lobes of the tail provide counteracting forces that drive the fish directly ahead. The most recent research supports the modified classic model. However, the alternative model appears to explain locomotion dynamics in sturgeons, which also have heterocercal tails but which – unlike sharks – vary the flexibility and shape of dorsal and ventral tail lobes (Liao & Lauder 2000). After Wilga and Lauder (2002).

Figure 8.4

Opening, protrusion, and closing of the jaw in most percoids. (A) Jaw opening involves three major couplings of muscles, ligaments, and bones: 1, epaxial muscles that lift the cranium; 2, levator operculi muscles that move the opercular bones up and out and help depress the mandible; and 3, hypaxial muscles that depress the mandible via actions of the hyoid apparatus. (B) Electrical activity of different muscles groups as measured during four phases of jaw opening and closing. Blackened bars represent major muscle activity, cross-hatched bars indicate occasional activity. Abductors move bones outward, adductors move bones inward. (C) The sequence of events during the opening and closing of the jaw of a cichlid, *Serranochromis*: 1, preparatory; 2–4, expansion; 5–6, compression. (A, B) slightly adapted from Lauder (1985); (C) from Lauder (1985), after Liem (1978), used with permission.

Figure 8.5

Extreme jaw protrusion in the Sling-jaw Wrasse, *Epibulus insidiator*. The Sling-jaw has novel bone shapes, extreme bone and ligament rotations, and has even invented a new ligament involved in jaw protrusion. (A) A 15 cm-long wrasse approaches its crustacean prey with its mouth in the retracted condition. Note that the posterior extension of the lower jaw, involving the articular and angular bones, extends as far back as the insertion of the pectoral fin. (B) During prey capture, the wrasse protrudes both its upper and lower jaws forward, extending them a distance equal to 65% of its head length. Jaw expansion creates suction forces that draw the prey into the mouth. Positions (A) and (B) are separated by about 0.03 s. From Westneat and Wainwright (1989), used with permission.

Figure 8.6

Crushing ability of the pharyngeal jaws in three related wrasses as a function of body size. Larger wrasses can crush larger snails because of their stronger pharyngeal jaws, and differences among species also influence preferred food types. Clown Wrasses have relatively weak jaws and feed on relatively soft-bodied prey, particularly when the fish are younger. Slippery Dicks and Yellowhead Wrasses have strong jaws and feed on shelled prey throughout their lives. After Wainwright 1988a; fish drawing from Gilligan (1989).

Figure 8.7

Convergence in dentition among predatory fishes. The triangular, razor-sharp teeth of a piranha, *Pygocentrus nattereri*, are remarkably similar in shape and action to those of many sharks. Note the small lateral cusps at the base of the teeth, a feature also shared with many sharks. Piranhas also replace their teeth as do sharks, but piranhas alternately replace all teeth in the left or right half of a jaw, rather than replacing individual teeth or rows of teeth. The teeth in the left side of the jaw (= right side of photo) have recently erupted. From Sazima and Machado (1990), used with permission.

Figure 8.8

Fishes that feed on hard-bodied prey crush their prey with molariform teeth located far back in their mouths, but often have different tooth types in different parts of the jaw. In the Wolf-eel, *Anarrhichthys ocellatus*, caninelike anterior jaw teeth grasp prey and molariform teeth farther back in the marginal jaws crush the prey. Photo by G. Helfman.

Figure 8.9

Correspondence among mouth position, feeding habits, and water column orientation in teleosts. Fishes with "superior" mouths frequently live near and feed at the surface, whereas fishes with "inferior" mouths often scrape algae or feed on substrate-associated or buried prey. Fishes with terminal mouths often feed in the water column on other fishes or zooplankton, but are also likely to feed at the water's surface, from structures, and on the bottom. Fish drawings from Nelson (2006), used with permission.

Figure 9.1

Events during, and terminology describing, the early life history of teleost fishes. The three basic stages – egg, larva, juvenile – can be further subdivided depending on definable events that occur during development and growth. The top half of the diagram summarizes one commonly used set of terminology, particularly for pelagic marine larvae. Alternative systems for describing these events are given in the lower half of the diagram (see Kendall et al. (1984) for reference details); the approach of Balon (1975b, second from bottom) may be more descriptive of many freshwater taxa. From Kendall et al. (1984), used with permission.

Figure 9.2

Stages during the early life history of the Horse Mackerel, *Trachurus symmetricus*. From Ahlstrom and Ball (1954).

Figure 9.3

Behavioral, physiological, and anatomical events during the postembryonic early life history of a representative teleost, the Northern Anchovy, *Engraulis mordax*. The horizontal axis at the bottom represents days after hatching for larvae growing in 16°C water; events noted are those occurring after the larva begins exogenous feeding, when it is no longer solely dependent on yolk for energy. Photopic refers to daytime vision, scotopic refers to nighttime vision. Reynolds number is a measure of the difficulties that small larvae have with water viscosity (see below, Larval behavior and physiology). Time to 50% starvation refers to how long larvae can live without feeding, based on half of the larvae in an experiment dying after a given number of days without food. RBCs, red blood cells. From Hunter and Coyne (1982), used with permission.

Figure 9.4

Fish sperm and their utility in constructing phylogenies. (A) Schematic diagram of the sperm of the percichthyid *Macquaria ambigua*; the entire structure is about 5 mm long. (B) Longitudinal section of the sperm of the Coral Trout, *Plectropomus leopardus* (Serranidae); a, axoneme; cc, cytoplasmic canal; dc, distal centriole; m, mitochondrion; n, nucleus; pc, proximal centriole. (C) Schematic diagrams of spermatozoa of non-neopterygian fishes and a cladogram based on sperm characteristics; the cladogram is basically similar to the one presented in Chapter 2, showing the parallel evolution of sperm and other taxonomically useful characteristics. From Jamieson (1991; C slightly modified), used with permission of Cambridge University Press.

Figure 9.5

Stages in the development of teleostean eggs, as shown by the Multiband Butterflyfish, *Chaetodon multicinctus*. (A) Primary oocyte growth and yolk development (vitellogenesis). (B) Yolk vesicle or cortical alveoli stage (left cell), early vitellogenesis (right cell). (C) Maturing egg, where the nucleus has migrated to the cell periphery and the yolk granules have coalesced. (D) Postovulatory ovary, after the eggs are shed. CA, cortical alveoli; F, follicle that holds oocyte; N, nucleus; OD, oil droplets; PF, postovulatory follicle, from which egg has been released; PO, primary oocyte; YG, yolk granule; YGF, yolk granule fusion; ZR, zona radiata of the vitelline membrane. From Tricas and Hiramoto (1989), used with permission.

Figure 9.6

Embryonic development of the Lake Trout, *Salvelinus namaycush*. (A) At 17 days after fertilization (at 7.8°C), as the somites and brain ventricle just begin to form. (B) At 22 days, when the auditory vesicles and eye lens placodes have developed. (C) At 23 days the tail is lifting off and pericardial cavity is evident. (D) At 67 days, showing the fully formed embryo at about the time of hatching (at 4.4°C); note pigmentation, upturned notochord, gut tube, dorsal and ventral fin folds, pectoral fins, pigmented eye, and well-developed yolk circulation and large yolk sac. From Balon (1980), used with permission of Kluwer Academic Publishers.

Figure 9.7

A recently hatched, marine teleost larva, as represented by a 6 mm clingfish, *Gobiesox rhessodon*. Note development of the mouth, eyes, median fin supports, and melanophores, and upward flexion of the notochord at the base of the tail. From Allen (1979).

Figure 9.8

Development of scales in the Black Crappie, *Pomoxis nigromaculatus*, showing the general pattern of scales developing initially near the tail and spreading anteriorly. From Ward and Leonard (1954), used with permission.

Figure 9.9

Anatomical and behavioral development of Atlantic salmon during embryonic life and the first 2 months after hatching. Note that even embryos are capable of avoiding aversive stimuli via fin and body movements. "Emergence" refers to yolk sac larvae moving up out of the gravel of the nest. From Huntingford (1993), after Abu-Gideiri (1966) and Dill (1977b), used with permission.

Figure 9.10

Larval diversity in marine fishes. Fish larvae often bear little external resemblance to the adults into which they grow. Spines probably make larvae harder to swallow, whereas trailing appendages could mimic siphonophore tentacles and therefore be avoided by predators, or may aid in flotation by slowing the sinking rate of the larva. (A) A 26 mm lantern fish larva, note eyes on stalks and trailing gut. (B) A 17 mm lanternfish larva (*Loweina*), note elongate pectoral ray and dorsal and anal finfolds. (C) An 8 mm seabass larva, note serrated dorsal and pelvic spines. (D) An 11 mm seabass larva, note elongate dorsal spine. (E) A 64 mm "exterilium" larva of an unknown ophidiiform, note trailing gut. (F) An 8 mm squirrelfish larva, note spines on head and snout. (A) from Moser and Ahlstrom (1974); (B) from Moser and Ahlstrom (1970); (C) from Kendall (1979); (D) from Kendall et al. (1984); (E) from Moser (1981), used with permission of Washington Sea Grant Program; (F) from McKenney (1959).

Figure 9.11

The general sequence of movement of marine larvae from offshore to inshore nursery grounds, as exemplified by events along the Oregon coast. Larvae are spawned offshore and carried onshore by shallow, wind-driven currents (e.g., Ekman transport). They then move alongshore by drifting with nearshore currents until encountering stimuli from estuaries, which they enter probably via selective tidal stream transport. From Boehlert and Mundy (1988), used with permission.

Figure 10.1

Sequence of events during smolting in the Coho Salmon, *Oncorhynchus kisutch*, and correspondence with changing levels of important hormones. Hormones implicated in the parr–smolt transformation tend to peak prior to, and may cause, the acquisition of the various anatomical, physiological, and behavioral traits that characterize the smolt stage. One group, the catecholamines, remains low throughout the smolting process but climbs if the fish does not migrate to sea and instead reverts to the parr stage. Drawing by W. W. Dickhoff, in Hoar and Randall (1988), used with permission.

Figure 10.2

Progressive eye migration in a developing Summer Flounder, *Paralicthys dentatus*. When the flounder larva is about 10 mm long, the right eye begins to migrate over to the left side of the fish via a process that includes bone resorption and rotation of the fish's neurocranium. The entire process takes 3–4 weeks, during which time the larva grows 5–10 mm. The position of the right eye on the right side of the body is depicted in stages 1 through 3 (faint circle). Note other developmental changes, including development of eye structures, anterior migration of the dorsal fin, growth and elaboration of the pectoral and pelvic fins, and mouth growth. After Keefe and Able (1993), used with permission.

Figure 10.3

Metamorphosis from a pelagic to a benthic life in flatfishes involves numerous traits and behaviors. A sequence of changes occurs along with eye migration, some at different times and at different rates. eyed, traits on the eyed side of fish; blind, traits on the blind side; DFO to UJ, distance from dorsal fin origin to anterior edge of upper jaw; Branching, branching of dorsal fin rays. Slightly modified from Neuman and Able (2002), used with permission.

Figure 10.4

Patterns of sexual determination and maturation among fishes. Sex determination (SD) can be under genetic or environmental control, with sex-determining genes located on defined sex chromosomes (XY, ZW) or distributed among autosomal chromosomes. Among most sex-changing fishes, individuals mature as female first (protogyny) or male first (protandry). See text for details. From Devlin and Nagahama (2002), used with permission.

Figure 10.5

Methods for determining fish age. Growth lines are added periodically to hard body parts, but the best body part to count differs among taxa. Scales, otoliths, fin rays, and vertebrae are the most commonly investigated structures. Body parts used for determining growth of pelagic oceanic fishes are shown in the figure. From Casselman (1983).

Figure 10.6

The correspondence between growth zones on an otolith and habitat use in an American eel, *Anguilla rostrata*. This sagittal otolith indicates that the eel was 16 years old when captured. It spent 3 years at sea or in the estuary of the St. Lawrence River (fast-growth nucleus zone), migrated upriver over a 2-year period (slow-growth transition zone), and finally took up residence in the upper St. Lawrence–Lake Ontario area (fast-growth edge zone). Habitat use was confirmed by measuring strontium : calcium ratios in the different zones of the otolith, using an electron microprobe associated with an electron microscope. Different ratios arise when an animal inhabits oceanic versus fresh water. From Casselman (1983); American eel drawing from Bigelow and Schroeder (1953).

Figure 10.7

Growth curves and their statistical description. The plotted lines indicate growth over time for the Round Scad, *Decapterus punctatus*. The thin line and the upper equation are calculated from the von Bertalanffy equation; the thicker line and lower equation are based on a related calculation, the Gompertz equation. The von Bertalanffy equation predicts asymptotic growth; the Gompertz equation predicts a sigmoidal curve where growth increases and then decreases. The two lines are statistically similar, showing how growth slows with age and eventually approaches an asymptote. From Hales (1987), used with permission of the author; Round Scad drawing from Gilligan (1989).

Figure 10.8

Salmonids differ in the minimum size at which they develop the necessary salinity tolerance to undergo the parr–smolt transformation. Observed differences among species could be explained by heterochronic shifts in the development of this trait. Such shifts might have changed the timing of the onset of the various physiological processes involved in salinity tolerance. It is not known what the ancestral condition was, and so either acceleration or deceleration of timing could be responsible. Hence either paedomorphosis (increasing size at smoltification) or recapitulation (decreasing size at smoltification), or both, could have affected the evolution of this trait. From McCormick and Saunders (1987), used with permission; salmon drawing from the US National Oceanic and Atmospheric Administration's Historic Fisheries Collection.

Figure 10.9

Paedocypris progenetica of Indonesia is the world's smallest vertebrate species, maturing at less than 8 mm length. It retains numerous larval traits, including minimal pigmentation, reduced squamation, and a largely cartilaginous skeleton with many bones absent. An 8.8 mm adult female is shown. From Kotellat et al. (2006), used with permission.

Figure III *(opposite)*

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

Figure 11.1

Periods of occurrence of major jawless fish taxa based on the fossil record. Thickened portions of lines indicate periods of increased generic diversity within a group. Time periods are not drawn to scale (e.g., the Cretaceous lasted almost 50 million years longer than the Silurian, but both are given equal space). Early Cambrian fossils that were arguably fishlike are not included (see text). Fossils are lacking for myxiniforms and petromyzontiforms during the Mesozoic. Data largely from Carroll (1988), Pough et al. (1989), Nelson (2006), and references therein.

Figure 11.2

Conodonts. (A) Conodont apparatus. The various elements (A–G) occur on the right (dextral) and left (sinistral) sides of the head region of the conodont animal and function as the feeding apparatus. (B) The 350-million-year-old, 40 mm long conodont animal. (A) from Clark (1987), used with permission; (B) as reconstructed by Aldridge and Briggs (1989).

Figure 11.3

The earliest known fishes were jawless pteraspidomorphs with armored head shields. Pteraspidomorphs included such small, primitive forms as (A) *Arandaspis* (subclass Arandaspida) from Australia, as well as more advanced forms such as (B) *Pteraspis* (subclass Heterostraci) from Devonian Europe. (A) after Rich and van Tets (1985); (B) after Moy-Thomas and Miles (1971).

Figure 11.4

Other jawless fishes are placed in the superclasses Anaspida and Thelodonti. (A) Anaspids, such as *Pharyngolepis*, were convergent in body form with the thelodonts, but probably led a benthic existence. (B) Thelodonts were more streamlined, such as *Phlebolepis* with its hypocercal tail. (C) The furcacaudiform forktail thelodonts may be among the first fishes to occupy the water column. (A, B) after Moy-Thomas and Miles (1971); (C) after Wilson and Caldwell (1993).

Figure 11.5

Cephalaspidomorphs were diverse jawless forms that appeared during the Silurian and lasted into the Devonian. The largest order was the cephalaspidiforms, including (A) *Hemicyclaspis*. (B) Thin sections of headshields clearly show brain differentiation and cranial nerves (roman numerals), organized similarly to modern lampreys. (A) after Moy-Thomas and Miles (1971); (B) from Stensio (1963), used with permission.

Figure 11.6

One view of relationships among early agnathous fishes, modern jawless forms, and jawed vertebrates. Notable here is the stem or sister position of cephalochordates relative to all craniates, of conodonts relative to all jawless vertebrates except lampreys, and of osteostracomorphs (Osteostraci, Galeaspida, Pituriaspida) relative to jawed fishes. Major geological time periods are given at the top of the figure, with abbreviated subdivisions immediately below. The time scale is millions of years before present. Most groups depicted are discussed in the text. From Donoghue et al. (2000), used with permission.

Figure 11.7

Periods of occurrence of major jawed (gnathostome) fish taxa based on the fossil record. Column width represents familial diversity within a group (only half of chondrichthyan and acanthomorph diversity is shown). The time scale is millions of years before present. A glance at the figure reveals why the Devonian is commonly referred to as the Age of Fishes: during the Middle Devonian, most major groups discussed in this chapter, including jawless forms shown in Fig. 11.1, were represented. Slightly modified from Stiassny et al. (2004).

Figure 11.8

Placoderms. (A) The coccosteomorph *Coccosteus*, (B) the ptyctodontid *Rhamphodopsis*, (C) the antiarch *Bothriolepis*, (D) the rhenanid *Gemuendina*, and (E) *Dunkleosteus*, a giant arthrodire placoderm from the Devonian. In *Dunkleosteus*, the meter high head was followed by a proportionately large body, but actual lengths are unknown because fossilized remains of the posterior skeleton are lacking. (A–D) after Jarvik (1980) and Stensio 1963; (E) photo by Chip Clark, used with permission.

Figure 11.9

Acanthodians. (A) *Climatius*, a primitive acanthodian with multiple gill covers and multiple, unembedded spines. (B) The more advanced *Acanthodes*, with fewer, thinner, more deeply embedded spines, a single gill cover, and a more symmetrical caudal fin. After Moy-Thomas and Miles (1971).

Figure 11.10

One view of relationships among euteleostome bony fishes ("Osteichthyes"), showing actinopterygians as the sister group to the various extant and extinct sarcopterygian taxa. After Forey (1998).

Figure 11.11

Phylogenetic relationships and fossil occurrence among the 24 coelacanth genera. Thick vertical bars show time ranges of occurrence for long-lived genera. The time scale is million years before present. Coelacanths are among the best-studied fossil groups, stimulated in part by the discovery of a living species after an 80-million-year hiatus in the fossil record. After Forey (1998).

Figure 11.12

Extinct and extant lungfishes. (A) *Scaumenacia*, an Upper Devonian lungfish from eastern Canada; (B) Toothplates from a fossil lungfish, *Ceratodus*, from the Upper Triassic (*c*. 5 cm wide) and from the extant Australian lungfish, *Neoceratodus* (upper structure). The Australian lungfish is considered to be more similar to ancestral forms than are

the living African and South American species. The *Neoceratodus* toothplate is mounted on a piece of modeling clay. (A) from Jarvik (1980), used with permission; (B) photo by G. Helfman.

Figure 11.13

Eusthenopteron foordi, a well-known osteolepidiform and member of a lineage considered close to the direct ancestor to tetrapods. (A) The full restoration, and (B) the neurocranium, endoskeleton, and fin supports. Note the large mouth, large symmetrical tail, and posteriorly placed median fins, all characteristics of active predators. From Jarvik (1980), used with permission.

Figure 11.14

Presumed key traits that characterized the sarcopterygian ancestors of tetrapods, as evidenced by *Eusthenopteron*. Among the traits are (A) an intracranial joint in the skull roof associated with the profundus nerve foramen; (B) the arrangement of the dermal skull bones; (C) axial elements of the pectoral fin skeleton (e.g., humerus, ulna, ulnare); and (D) support skeleton of the second dorsal fin. After Ahlberg and Johanson (1998).

Figure 11.15

Comparative pelvic appendages of: (A) *Eusthenopteron*, a Devonian osteolepidiform fish; (B) *Ichthyostega*, a Devonian stem tetrapod; and (C) *Neoceratodus*, a modern lungfish. Note the apparent homologous bone series of the osteolepidiform and tetrapod limb, as compared with the less similar central axis and radials of the "archipterygial" lungfish fin. (A, B) from Jarvik (1980), used with permission; (C) from Semon (1898).

Figure 11.16

Dorsal (A) and lateral (B) views of the reconstructed elpistostegalian fish, *Tiktaalik roseae*. Features evident are the lack of opercular bones, the tetrapod-like arrangement of elements in the pectoral fins/limbs, and the stout ribs forming a rib cage that may have protected the lungs. From Daeschler et al. (2006), used with permission.

Figure 11.17

A cladogram of relationships among sarcopterygians and tetrapods, evidenced by changes in the pectoral fin and limb. *Tiktaalik* retains the central axis of enlarged endochrondral bones of more primitive sarcopterygians, but has fewer lepidotrichia (fin rays) and more radial elements than ancestral fishes. *Tiktaalik* is more advanced in its proliferation of transverse joints across the distal region of the fin, allowing for propping up and moving the body. *Glyptolepis* was a porolepiform dipnomorph related to lungfishes; its archipterygial fin is representative of the basal condition. From Shubin et al. (2006), used with permission.

Figure 11.18

Cladogram (strict consensus tree) of relationships among sarcopterygians and tetrapods, showing *Tiktaalik*'s intermediate position as a sister group (with *Elpistostege*) to the early tetrapods *Acanthostega* and *Ichthyostega*. The cladogram was calculated from an analysis of 114 characters and nine taxa. After Daeschler et al. (2006).

Figure 11.19

Actinopterygian fishes at different grades of development. (A) *Moythomasia* and (B) *Mimia*, two primitive palaeoniscoid fishes from the Upper Devonian, with thick rhomboidal scales extending onto the fins, broadly triangular dorsal and anal fins, fulcral (ridge) scales along the back, a long mouth, and an asymmetrical heterocercal tail. (C) *Parasemionotus*, a pre-teleostean neopterygian from the Triassic, showing more flexible fins, shorter mouth, and abbreviate heterocercal tail. (D) *Eolates*, an advanced euteleost from the Lower Eocene, with characteristic teleostean diversified dorsal and anal fins, shortened vertebral column, premaxillary dominated upper jaw, and homocercal tail. (A) after Jessen (1966); (B) after Gardiner (1984); (C) after Lehman (1966); (D) after Sorbini (1975).

Figure 11.20

Morphological (and ecological) convergence in fish evolution. Palaeoniscoids were ancestral to early neopterygians, which were ancestral to modern teleosts. Certain body designs or plans have apparently been repeatedly favored in actinopterygians, leading to convergent designs among unrelated lineages. These striking convergences in body shape and presumably function are depicted for representative palaeoniscoids, early neopterygians, and teleosts. 1, Elongate piscivores with long, tooth-studded jaws and dorsal and anal fins placed posteriorly for rapid starts; 2, compressed-bodied, predatory, shallow water fishes with deeply forked tails and trailing fins; 3, broad-finned bottom feeders with subterminal mouths; 4, eel-like benthic forms; and 5, compressed, circular forms with large fins for maneuverability in shallow water habitats with abundant structure (see also Chapter 8). Gliding fishes such as the Triassic chondrostean *Thoracopterus* (Fig. 11.21) can also be equated with modern teleostean flyingfishes. Adapted from Pough et al. (1989), not drawn to scale.

Figure 11.21

Thoracopterus magnificus, a 6 cm-long perleidiform chondrostean from the Triassic adapted to gliding. Most notable are the expanded pectoral and pelvic fins and asymmetrical caudal fin with its larger lower lobe. These and other traits are strongly convergent with features that allow modern exocoetid flyingfishes to engage in biplane gliding. From Tintori and Sassi (1992), used with permission.

Figure 11.22

Leedsichthys problematicus, perhaps the world's largest fish ever. This 15 m+ zooplanktivorous pachycormid is known from fragments and several partial skeletons discovered in clay deposits from the Middle–Upper Jurassic. After Paul Vecsei, based on an illustration by Bob Nicholls, www.paleocreations.com.

Figure 11.23

Phylogenetic relationships among actinopterygian fishes. The numbered characteristics defining the branching points (synapomorphies) are selected from a much larger list; groups after a branch point share the traits (although traits may be secondarily lost), groups before the branch do not share the trait. Italicized numbers are unique derived traits (autapomorphies) particular to a group and not shared by other taxa. Pholidophoriforms are one of several possible groups ancestral to modern teleosts. Daggers indicate extinct groups. Additional details can be found in Lauder and Liem (1983), Pough et al. (1989, 2005), Nelson (1994, 2006), and papers cited in those publications.

1, single dorsal fin; ganoin in scales, which have an anterior peglike process; pectoral fin with enlarged basal elements ("propterygium"); *2*, fully ossified, sutureless adult braincase; 3, dentinous tooth cap; basal elements of pelvic fin fused; modifications to jaw and gill arch muscles; *4*, dorsal fin spines uniquely flaglike; pectoral fin base platelike; 5, modifications to dermal elements of skull, pectoral girdle, and fins; spiracle penetrates postorbital process of skull; fins preceded by specialized scales ("fulcra"); *6*, upper jaw bones fused; 7, number of endoskeletal elements supporting rays of median fins reduced to a 1 : 1 correspondence; caudal fin more symmetrical, with reduction in upper lobe;

dentition of upper pharyngeal consolidated into a tooth-bearing plate; clavicle reduced or lost; *8*, vertebral centra convex anteriorly and concave posteriorly ("opisthocoelus" condition); elongate upper jaw largely constructed from infraorbital bones; 9, maxilla mobile; interopercle and median neural spines present; *10*, jaw articulation involves quadrate and symplectic bones; gular plate present; 11, mobile premaxilla; posterior neural arches (uroneurals) elongate; ventral pharyngeal toothplates unpaired; 12, particular combination of skull bones present (basihyal, four pharyngobranchials, three hypobranchials); *13*, toothplate on tongue bites against roof of mouth; intestine lies to the left of stomach; 14, two uroneural bones extend over the second tail centrum; epipleural intermuscular bones abundant in abdominal and caudal region; 15, ribbon-shaped (leptocephalus) larva; 16, neural arch of first tail vertebra reduced or missing; upper pharyngeal jaws fused to gill arch elements; jaw joint with unique articulation and ossification; *17*, specialized ear to gas bladder connection; 18, dorsal adipose fin and nuptial tubercles on head and body; first uroneural bones of tail have paired anterior membranous outgrowth. Additional characteristics of modern teleosts are given in Chapters 14 and 15.

Figure 11.24

Diversification of the dorsal fin in modern teleosts. (A) Primitively, the dorsal fin is a single, spineless, subtriangular structure that serves as an antiroll device and pivot point during swimming, such as in the herrings (Clupeidae). However, this simple fin has been greatly modified in more advanced groups and can serve in locomotion, predator protection, and a variety of other functions. (B) In cods (Gadidae), three dorsal fins exist. (C) More commonly, a spiny anterior and soft-rayed posterior separation occurs, as in the squirrelfishes (Holocentridae). (D) In frogfishes (Antenariidae), modified dorsal spines serve as lures and as camouflage. (E) The sucking disk of the sharksucker (Echeneidae) is derived embryologically from the spiny dorsal fin. After Nelson (2006).

Figure 11.25

The phylogeny of paired fin locations in teleosts. The locations and functions of the pectoral and pelvic girdles have changed during evolution of the Teleostei. Pectoral fins move from a ventral to a lateral position and the pectoral fin base changes its orientation from horizontal to vertical. Pelvic fins move from abdominal to thoracic and even jugular locations. Extant representatives of phases in this observed trend are represented by (A) an elopomorph (bonefish, Albulidae), (B) a primitive paracanthopterygian (Troutperch, Percopsidae), and (C) a generalized acanthopterygian (cichlid, Cichlidae). This trend is by no means absolute: many specialized, relatively primitive teleosts have laterally placed pectorals (e.g., catfishes) and advanced teleosts may have pelvics in abdominal positions (e.g., atherinomorphs), but overall the trends describe a progressive change during teleostean phylogeny. After Nelson (2006).

Figure 11.26

Diversity in the body form of Paleozoic sharks from the two extinct infraclasses. (A) *Cladoselache*, a cladoselachid (Cladoselachimorpha); (B) *Xenacanthus*, a freshwater xenacanthid (Xenacanthiimorpha). (A) from Schaeffer (1967); (B) from Schaeffer and Williams (1977), used with permission.

Figure 11.27

Sharks allied with the infraclass Euselachii. (A) *Ctenacanthus*, an Upper Devonian ctenacanthid (Ctenacanthiformes); (b) *Hybodus*, a hybodontid, representative of the order Hybodontiformes, the most diverse elasmobranch group in the Triassic and Jurassic; and (C) *Squalus*, a modern squaliform shark in the division Neoselachii. From Schaeffer and Williams (1977), used with permission.

Figure 11.28

Tooth replacement in chondrichthyans. (A) Cross-section through the jaw of a modern shark, showing a functional tooth backed by rows of developing replacement teeth. Variations on this mechanism are found in many fossil groups. (B) Symphysial (middle) portion of the lower jaw of the late Paleozoic edestoid *Helicoprion*, thought to be a holocephalan, showing its spiral replacement tooth whorl. After Carroll (1988) and Pough et al. (1989).

Figure 11.29

Extinct holocephalans. (A) *Ischyodus*, a Jurassic callorhinchid in the same family as modern plownose chimaeras; (B) *Helodus*, an Upper Devonian helodontiform; and (C) *Chondrenchelys*, a Lower Carboniferous chondrenchelyiform. Note the convergence in body form between *Chondrenchelys* and the actinopterygian *Tarrasius* and the clinid in Fig. 11.20. From Patterson (1965), used with permission.

Figure 12.1

Phylogenetic relationships among living chondrichthyans. Relationships among the batoid rays remain a matter of debate, including discussion of whether the rhinobatiform guitarfishes are in fact monophyletic. From Stiassny et al. (2004), used with permission.

Figure 12.2

Taxonomic distribution and representative orders of the *c*. 950 species of modern sharks, skates, and rays. (A) Sharklike fishes in nine orders constitute 40% of modern euselachian species, with the carcharhiniform (ground or requiem) sharks outnumbering all other orders combined. The echinorhiniform bramble sharks, with two species, are not shown. (B) Raylike batoids make up 60% of the Euselachii, dominated by skates and stingrays; the four recognized orders are shown. Guitarfishes (Rhinobatidae, Rhinidae) are diverse members of the Rajiformes. Adapted from Compagno (1990b), used with permission.

Figure 12.3

Reconstructing the jaws and estimating the size of the extinct Megatooth Shark, *Carcharodon megalodon*. (A) Jaw reconstruction as inaccurately prepared in 1909. The jaws are about one-third too large because equal-sized, anterior teeth were used throughout the jaws, and the cartilage is about four times broader than in living sharks. (B) Recent reconstruction by the Smithsonian Institution, suggesting a body length of about 13 m. (C) Calculating the lengths of White and Megatooth sharks. Total body length is directly related to maximum tooth size (enamel height) in White Sharks (*Carcharodon carcharias*); hence body length can be estimated for sharks from which only teeth are available. This gives a maximal size of 6 m for the White Shark. Assuming a similar relationship existed for the extinct Megatooth Shark, placement of two of the larger known teeth along the same regression line (closed circles) suggests a body length of about 13 m; the largest tooth found indicates lengths up to 16 m. The approximate equation for calculating total length from tooth height is:

Total length (m) = 0.096 (enamel height, mm) − (0.22).

Data from Randall (1973), Compagno et al. (1993), and Gottfried et al. (1996). (A) from American Association for the Advancement of Science, © 1971, used with permission; (B) photo by Chip Clark, National Museum of Natural History, Smithsonian Institution, used with permission.

Figure 12.4

The Giant Freshwater Whipray *Himantura chaophraya*. This endangered species occurs in rivers of Southeast Asia, New Guinea, and tropical Australia. Photo by Z. Hogan, used with permission.

Figure 12.5

Sawfishes are among the most imperiled marine and estuarine fishes in the world. Although little directed fishing occurs for sawfishes, they are frequently entangled in nets of all types. Such bycatch remains the major threat to the US federally listed Smalltooth Sawfish *Pristis pectinata* and its congener, the Largetooth Sawfish *P. perotteti*. Both were once common from the Gulf of Mexico up the east coast from Florida to Cape Hatteras (Simpfendorfer 2000). Sawfishes in the USA now occur only in peninsular Florida, primarily in the Everglades region. Shown here are results from a fishing tournament, *c*. 1920, in Key West, Florida. Some of the fish were said to have weighed 765 kg. Photo courtesy of Matthew McDavitt, http://members.aol.com/_ht_a/nokogiri/index.html (photographer unknown).

Figure 12.6

The role of scales in drag reduction in sharks. (A) Scanning electron micrograph of a single denticle from a scyliorhinid cat shark, showing the pedestal and winged keel arrangement thought to absorb turbulence, which reduces drag. (B) Cross-sectional representation of placoid scales, showing reduction of turbulence along the body. Strength of water flow corresponds to thickness of the black arrows. (A) from Konstantinou et al. (2000); (B) from Moss (1984), used with permission.

Figure 12.7

The track of Nicole, a 4 m White Shark that had been seen over a 6-year period in South Africa. Nicole was then followed via satellite telemetry from South Africa to Australia between November 2003 and February 2004, and was then seen again off South Africa in August 2004. Her minimal roundtrip distance was 22,000 km. After Bonfil et al. (2005).

Figure 12.8

Head and jaw movements associated with feeding in the White Shark, *Carcharodon carcharias*. (A) Normal resting position; (B) snout is lifted and lower jaw depressed, achieving maximal gape; (C) lower jaw is lifted forward and upward and the palatoquadrate (teeth-bearing upper jaw) is rotated forward and downward, thereby closing the jaws (= the bite); (D) snout is dropped back down and palatoquadrate is retracted to resting position. The bite (component C) occurs quickly, requiring on average 0.8 s. From Tricas and McCosker (1984), used with permission.

Figure 12.9

Cookie cutter sharks. (A) *Isistius brasiliensis*, the Cookie Cutter Shark, is a small (about 40 cm) tropical species that lives at mid-ocean depths and parasitizes tunas, other fishes, Megamouth Sharks, and marine mammals, gouging circular plugs of flesh out of their sides with its specialized dentition. (B) The congeneric Largetooth Cookie Cutter Shark, *I. plutodus*, has the largest teeth for its body size of any known shark. Its teeth are twice as large relative to body size as a Great White Shark's teeth. (C) Drawing of the Cookie Cutter Shark, *I. brasiliensis*. (A) photo by C. S. Johnson, from Springer and Gold (1989), used with permission of the Smithsonian Institution Press; (B) from Compagno (1981), used with kind permission from Kluwer Academic Publishers; (C) after P. Vecsei.

Figure 12.10

Representative tooth types of modern sharks: (A) Nurse Shark; (B) Tiger Shark; (C) Shortfin Mako, upper jaw; (D) Shortfin Mako, lower jaw; (E) Sandbar Shark, upper jaw; (F) Sandbar Shark, lower jaw; (G) Kitefin Shark, upper jaw; and (H) Kitefin Shark, lower jaw. All except the Nurse Shark feed largely on fish and squid; Nurse Sharks eat a variety of reef invertebrates such as lobsters. Black bars are 1 cm. From Motta (2004), used with permission.

Figure 12.11

Pavement or molariform, crushing teeth characterize sharks and rays that feed on hard-bodied prey. (A) Lower jaw of the Horn Shark, *Heterodontus francisci* (Heterodontidae); the anterior teeth grasp and the posterior teeth crush prey. (B) Lower jaw dentition of a Cownose Ray, *Rhinoptera bonasus*, a predator on clams. (A) from Motta (2004), used with permission; (B) from Case (1973), used with permission.

Figure 12.12

The Megamouth Shark, *Megachasma pelagios*. This 4–5 m long zooplanktivore was first captured in 1976, northeast of Hawaii (Taylor et al. 1983). It became entangled at a depth of 160 m in a parachutelike sea anchor of a naval research vessel over much deeper water. As of July 2008, only 40 individuals were known, mostly from tropical and subtropical regions (www.flmnh.ufl.edu/fish/Sharks/Megamouth/mega.htm). Drawing by P. Vecsei.

Figure 12.13

Brain size in sharks. (A) Sharks have relatively large brains for their body size, overlapping in this respect with birds and mammals as much as with bony fishes. (B) Among pelagic, predatory fishes, many sharks have relatively large brains for their body mass. (A) from Springer and Gold (1989), based on Northcutt (1977) and Moss (1984), used with permission; (B) after Lisney and Collin (2006).

Figure 12.14

Placental viviparity in advanced sharks. A newborn Atlantic Sharpnose Shark (Carcharhinidae) showing the umbilical cord with outgrowths ("appendicula") for nutrient uptake. The cord terminates in a placenta that attaches to the uterine wall of the mother. Photo by W. Hamlett, from Hamlett (1991), used with permission.

Figure 12.15

Sexual dimorphism in the skin thickness of sharks. On the left is a cross-section through a male Blue Shark, on the right a female. Female sharks often have thicker skin than males, probably because during mating males typically bite and hold females. Photo by H. W. Pratt, from Pratt and Carrier (2001), used with permission.

Figure 12.16

Modern holocephalans. (A) *Chimaera cubana*, a 50 cm long Caribbean chimaerid; note the pelvic claspers and also the frontal clasper or tenaculum on the forehead of the male. (B) Head of a callorhinchid chimaera, *Callorhinchus milii* (the Elephant Fish), showing the unique hoe-shaped proboscis. (C) A juvenile *Rhinochimaera pacifica*, the

Pacific Spookfish, which grows to 1.5 m and could do anything with that fleshy snout. (A, B) from Bigelow and Schroeder (1953a), used with permission; (C) photographer unknown.

Figure 13.1

An adult lancelet, *Branchiostoma longirostrum*; actual length, 43 mm. (B) A stingray searches through a sand and seagrass bed off the west coast of Florida, spreading terror among Florida lancelets, *Branchiostoma floridae*. (A) adapted from Boschung (1983), used with permission; (B) drawing by D. W. Miller in Stokes and Holland (1998), used with permission (see www.syncreta.com).

Figure 13.2

Hagfishes. (A) Adult Atlantic Hagfish, *Myxine glutinosa*, 38 cm long. Portholelike structures along the side are mucous glands. (B) Ventral view of the head region of an Atlantic Hagfish. The upper orifice is the nasal opening, and the lower orifice is the mouth. (C) The lingual (tongue) teeth of a hagfish. (D) Hagfish egg, approximately 40 mm long. (E) A hagfish pressing a knot against the side of its prey to gain leverage when tearing off flesh. (A–D) from Bigelow and Schroeder (1948a), used with permission; (E) after Jensen (1966).

Figure 13.3

A single hagfish can produce prodigious quantities of slime when disturbed. Photo by J. Meyer.

Figure 13.4

Lampreys. (A) Adult parasitic Sea Lamprey, *Petromyzon marinus*, about 45 cm long. (B) Oral disk of the Sea Lamprey showing the disk teeth used in holding on to prey. (C) Central mouth of *P. marinus*, showing the lingual (tongue) teeth used to rasp a hole in the prey. (D) Ammocoete larva of River Lamprey, *Lampetra fluviatilis*. (A–C) from Bigelow and Schroeder (1948a); (D) after Hardisty (1979).

Figure 13.5

Reconstruction of the Carboniferous lamprey, *Mayomyzon pieckoensis*, from Illinois. The fossil, seen in lateral view, bears a striking resemblance to modern petromyzontid lampreys. Several recognizable relevant anatomical features are outlined in black: Ac, annular cartilage; Dt, digestive tract; E, eye; Gp, gill pouch; L, liver; Lw, lateral wall of braincase; Oc, otic capsule; Olc, olfactory capsule; Pc, piston cartilage. From Bardack and Zangerl (1971), used with permission.

Figure 13.6

Comparative life histories of a species pair of European lampreys. (A) The parasitic ancestor, the River Lamprey *Lampetra fluviatilis*. (B) The nonparasitic derived species, the Brook Lamprey *L. planeri*. The evolution of nonparasitic from parasitic forms involves a lengthening of the larval phase and a shortening of the maturational period. The onset of metamorphosis is denoted by M; unshaded areas represent nonfeeding periods. Adapted from Hardisty (1979).

Figure 13.7

The living African Coelacanth, *Latimeria chalumnae*, an extant member of a group thought to be extinct for 65 million years. Discovered by science in 1938, the two known species occur in small populations restricted to volcanic slopes off East Africa and northern Indonesia. Both are recognized internationally as endangered. (A) External anatomy; some traits that distinguish coelacanths from other living fishes are noted. (B) Skeletal anatomy; note skull joint, arrangement of bones of the fins, and the unconstricted notochord. (A) drawing by S. Landry, from Musick et al. (1991); (B) from Forey (1998), used with permission.

Figure 13.8

Marjorie Courtenay-Latimer's drawing and description of the first coelacanth, as sent to J. L. B. Smith. Key features pointed out by Courtenay-Latimer included bony plates on the head and the extra median lobe in the caudal fin. From Smith (1956), used with permission.

Figure 13.9

Coelacanths are as cuddly as pandas. (A) The Coelacanth Conservation Council's (CCC) image of a coelacanth, proposed to serve as the World Wildlife Fund's symbol for marine conservation, the panda representing terrestrial conservation. (B) An ichthyology student was moved by the plight of the coelacanth and had the CCC image tattooed on her hip. Photo by G. Helfman, courtesy of G. Hendsbee.

Figure 13.10

Modern lungfishes. (A) An African lungfish, *Protopterus annectens*, one of four species in the genus. (B) A live *Protopterus*; note the filamentous pectoral and pelvic fins. (C) The South American Lungfish, *Lepidosiren paradoxa*, showing the vascularized pelvic fins that develop on males during the breeding season. (D) The Australian lungfish, *Neoceratodus forsteri*. (A, D) from Jarvik 1980; (B) courtesy of L. and C. Chapman; (C) from Norman (1931), used with permission.

Figure 13.11

An African lungfish estivating in its mud and mucus cocoon, viewed from the ventral surface of the fish. Redrawn from Greenwood (1987).

Figure 13.12

A young African lungfish. The arrow indicates the external gills that misleadingly caused lungfishes to be classified as amphibians. From Herald (1961), used with permission of Chanticleer Press, Inc., New York.

Figure 13.13

The seventh living "lungfish", *Ompax spatuloides*. This is the illustration that appeared in the original species description by Castelnau (1879). It shows (1) lateral view, (2) dorsal view of the head, and (3) presumably a cross-section of the bill, but unlabeled in the original illustration. From Castelnau (1879).

Figure 13.14

Brachiopterygians. (A) A 29 cm long bichir, *Polypterus palmas polli*, from the Ivory Coast. Note the lobelike pectoral fin base and the horizontal flaglike fin rays that extend from the distal portion of each dorsal fin spine. (B) The "peculiar and overelaborated" pectoral fin of a bichir, showing the wishbonelike basal structure (propterygium and metapterygium) that supports the radials and fin rays. (A) from Hanssens et al. (1995), used with permission; (B) from Rosen et al. (1981), courtesy of the Department of Library Services, American Museum of Natural History.

Figure 13.15

Sturgeons. (A) An Atlantic Sturgeon, *Acipenser oxyrhynchus*. Note the rows of bony scutes on the body, distinct heterocercal tail, and elongate snout with barbels preceding the ventral mouth. (B) A live Beluga sturgeon, *Huso huso*, perhaps the largest freshwater fish in the world. The bright spot is the eye, which sits just posterior to the spiracle. (A) from Vladykov and Greeley (1963), used with permission; (B) photo by G. Helfman.

Figure 13.16

Paddlefishes. (A) The North American Paddlefish, *Polyodon spathula*. (B) The Chinese Paddlefish, *Psephurus gladius*, a poorly known, critically endangered chondrostean restricted to the Yangtze River system of China. (C) The rostral paddle of the North American Paddlefish in dorsal view; arrows indicate position of the eyes. (D) Area at lower left of (C) enlarged, showing the stellate bones (sb) that support the paddle, and the ampullary organs, which are the dark circular holes in the paddle that reportedly serve as electroreceptors. (A, B) drawings after P. Vecsei in CITES (2001); (C, D) from Grande and Bemis (1991), used with permission.

Figure 13.17

Gars. (A) A Florida Gar, *Lepisosteus platyrhincus*, showing the distinctive elongate, tooth-studded snout and posteriorly placed dorsal and anal fins characteristic of this family of North and Central American predators. (B) Head of the large Alligator Gar, *Atractosteus spatula*. Note the numerous bones in the head and cheek and the myriad needlelike teeth. (A) from Suttkus (1963), used with permission; (B) from Grande and Bemis (1998), used with permission.

Figure 13.18

A large Alligator Gar caught in Texas. Photo courtesy of Jean-Francois Healias, www.anglingthailand.com.

Figure 13.19

(A) The Bowfin, *Amia calva*, a member of a monotypic order endemic to North America. (B) Entire skeleton; note the elongate dorsal fin used in slow forward and backward locomotion and the upturned caudal vertebrae forming the abbreviate heterocercal fin. (C) Skull showing the multiplicity of bones that are later lost or fused in teleosts. (D) Anterior view looking into the mouth; the abundant, large teeth are evident, as is the single gular plate on the underside of the head. From Grande and Bemis (1998), used with permission.

Figure 14.1

Phylogenetic relationships among living teleosts. The numbered characteristics defining the branching points (synapomorphies) are selected from a much larger list; groups after a branch point share the traits (although traits may be secondarily lost), groups before a branch do not share the trait. Italicized numbers are unique derived traits (autapomorphies) particular to a group and not shared by other taxa. Characteristics 1–7 largely repeat characters 11–18 in the cladogram of Fig. 11.23. Monophyly and definition of some groups are a matter of debate and no synapomorphies are given (i.e., the Protacanthopterygii (osmeriform smelts, salmoniform salmons) remain a problematic group that lacks well-defined, unifying characteristics). Additional details can be found in Lauder and Liem (1983), Nelson (1994), Pough et al. (2005), and papers cited in those publications.

1, mobile premaxilla, posterior neural arches (uroneurals) elongate, ventral pharyngeal toothplates unpaired; particular combination of skull bones present (basihyal, four pharyngobranchials, three hypobranchials); *2*, toothplate on tongue bites against roof of mouth; intestine lies to the left of stomach; 3, two uroneural bones extend over the second tail centrum; epipleural intermuscular bones abundant in abdominal and caudal region; 4, ribbon-shaped (leptocephalus) larva; 5, neural arch of first tail vertebra reduced or missing; upper pharyngeal jaws fused to gill arch elements, jaw joint with unique articulation and ossification; 6, specialized ear-to-gas-bladder connection; 7, dorsal adipose fin and nuptial tubercles on head and body; first uroneural bones of tail have paired anterior membranous outgrowth; 8, anterior vertebrae and ribs modified to connect gas bladder to inner ear (Weberian apparatus); epidermal cells produce alarm substance; 9, first vertebra articulates with three bones of the skull (basioccipital and the two exoccipitals), retractor dorsalis muscle connects vertebral column with upper pharyngeal jaws, hinged jaw teeth capable of depression posteriorly; 10, unique photophore histology and tooth attachment; *11*, unique gill arch structure involving second and third pharyngobranchials; 12, fifth upper pharyngeal toothplate and associated internal levator muscle missing; *13*, upper pharyngeal jaw dominated by third pharyngobranchial; 14, configuration of rostral cartilage and its ligamentous connection to premaxilla; lateral ethmoids joined to vomer; 15, uniquely protrusible upper jaw; *16*, ligament connecting palatine and premaxilla in a unique position; 17, expanded premaxillary processes; *18*, dorsal (neural) spine attached to second preural vertebra; 19, branchial retractor muscle (retractor dorsalis) inserts only on third pharyngobranchial; well-developed ascending process of premaxilla allows increased jaw mobility; ligament supporting pectoral girdle (Baudelot's ligament) originates on basioccipital of skull rather than on first vertebra; *20*, no direct connection between pelvic girdle and cleithrum of pectoral girdle; *21*, jaw protrusion occurs without ball-and-socket joint between palatine and maxilla; fourth pharyngobranchial lost; *22*, pelvic girdle attached to pectoral girdle; anterior pelvic process displaced ventrally; pelvic fins have one spine and five soft rays. Additional characteristics are given in this and the following chapters. Fish drawings from Nelson (2006), used with permission.

Figure 14.2

Osteoglossomorphs. (A) A mormyrid elephantfish, *Gnathonemus petersi*, from Africa. (B) A notopterid featherfin or knifefish, *Chitala chitala*, from Asia. (C, D) The South American Arapaima or Pirarucu, *Arapaima gigas*, a large predator. (A, B) after Paxton and Eschmeyer (1994); (C, D) photos by G. Helfman.

Figure 14.3

The Asian Arawana or Golden Dragonfish, *Scleropages formosus*. Overcollecting for the aquarium trade pushed this species to the brink of extinction, desirable color morphs fetching up to $5000. Photo by Marcel Burkhard, Wikimedia Commons, http://en.wikipedia.org/wiki/Image:Arowanacele4.jpg#file.

Figure 14.4

Elopomorphs. (A) A Tarpon, *Megalops atlanticus*. (B) A 7 cm long leptocephalus larva of a ladyfish, *Elops saurus*. (C) An Atlantic Bonefish, *Albula vulpes*. (A, B) from Hildebrand (1963), used with permission; (C) photo by G. Helfman.

Figure 14.5

A Gulper or Pelican Eel, *Eurypharynx pelecanoides*. Ironically, this highly specialized, 40 cm long bathypelagic fish feeds on surprisingly small prey which they capture by opening their huge, dark mouths that probably generate little suction pressure. The related swallower eels feed on prey larger than themselves. Gulper Eels are unique among teleosts because they have five gill arches and six visceral clefts (Nelson 2006). From Briggs (1974), used with permission of McGraw-Hill.

Figure 14.6

Knightia alta, an Eocene herring from the Green River formation of Wyoming (actual length 12 cm). Excellent fossils of *Knightia*, such as this one in which the characteristic abdominal scutes of clupeids are clearly visible, are abundant and are sold as curios. Photo by G. Helfman.

Figure 14.7

"Minnows." The giant and imperiled Asian Carp, *Catlocarpio siamensis*, native to the Mekong River basin. Photo courtesy of Jean-Francois Healias, www.anglingthailand.com.

Figure 14.8

The extinct Harelip Sucker, *Moxostoma lacerum*. Once abundant in 13 eastern US states, this may have been the first American fish driven to extinction, around 1900 (see Jenkins & Burkhead 1993). Actual coloration is not known because no live fish were ever drawn or photographed; only one adult was preserved. After Trautman (1981).

Figure 14.9

A juvenile Robust Redhorse, *Moxostoma robustum*. Growing to large size (80 cm, 8 kg), this rare catostomid endemic to Atlantic slope rivers of the southeastern USA went unrecorded for over 120 years. Rediscovered in 1991, a cooperative effort among government, corporate, and nongovernmental organizations succeeded in captive propagation, release into the wild, and establishment and reproduction by propagated fish (see Helfman 2007; www.robustredhorse.com/h/reportpubs.html). Photo by G. Helfman.

Figure 14.10

Piranhas, *Serrasalmus* spp., are representative of the speciose tropical order of characiform fishes. Photo by G. Helfman.

Figure 14.11

Selected catfishes, showing some of the array of body types and shared characteristics among the 35 families. Drawings by John Quinn, in Burgess (1989), used with permission of TFH Publications.

Figure 14.12

Large catfishes. (A) The Mekong Giant Catfish, one of the world's largest catfishes. This specimen was caught from a stocked population in Bung Sam Lan Lake, Thailand. (B) Two *c*. 20 kg Flathead Catfishes, North America's second largest catfish. (A) photo courtesy of Jean-Francois Healias, www.anglingthailand.com; (B) photo by G. Helfman.

Figure 14.13

Two individual *Orthosternarchus tamandua*, an apteronotid knifefish from the Amazon basin. The small black dot on the head is the greatly reduced eye. These predators occur at depths of 6–10 m where they feed on insect larvae (Fernandes et al. 2004). Photo courtesy of C. Cox Fernandes.

Figure 14.14

Gymnotiform electric knifefishes. An accurate rendering of electric eels, *Electrophorus electricus*, in an otherwise dramatized setting. Anonymous source.

Figure 14.15

Protacanthopterygians. (A) An osmerid, the Capelin, *Mallotus villosus* (sexually mature female). (B) The Longfin Svetovidov's Char, *Salvethymus svetovidovi*, of Lake El'gygytgyn, Siberia. This long-lived, small char (30 years, 30 cm) is threatened by pollution and fishing. (C) A large Chinook Salmon, *Onchorhynchus tshawytscha*, from British Columbia. (A) from Bigelow (1963), used with permission; (B) drawing by Paul Vecsei, used with permission; (C) photo courtesy of R. Carlson.

Figure 14.16

Phylogeny of the salmonids. A cladogram of most living salmonids based on life history traits shows the evolution of the various species. The same cladogram is constructed if anatomical and biochemical traits are used. The first four lineages represent separate genera (*Thymallus*, *Brachymystax*, *Hucho*, *Salvelinus*), Atlantic Salmon and Brown Trout are in the genus *Salmo*, and the remaining eight species (those above trait 4) are all in the genus *Oncorhynchus*. The more primitive coregonine whitefishes would come off to the far left of the cladogram and are not shown. The following life history and reproductive characteristics are the shared derived characters that were used to construct the cladogram. The listed characters correspond to the numbered branch points in the cladogram. Groups to the right and above the number possess the trait, those to the left do not. From Smith and Stearly (1989), used with permission.

   1, egg diameter greater than 4.5 mm; females dig redds (nests); large males have hooked jaws (kype) during breeding season; 2, fall spawners; 3, commonly undergo long oceanic migrations; 4, most spawners undergo irreversible hormonal changes; 5, spring spawners; 6, anadromous forms die after spawning; 7, non-migratory individuals tend not to reproduce; 8, most smolt in first year, some go to sea as even younger fry; 9, juveniles are strong schoolers, parr are slender; 10, the freshwater phase is reduced; young migrate soon after emerging from gravel.

Figure 14.17

A Golden Trout, *Oncorhynchus aguabonita*, the state fish of California. Greatly depleted by introduced species and habitat destruction, Golden Trout are now the focus of restoration programs that include eradication of the European Brown Trout that were actively stocked in past decades. Photo by T. Kelsey, courtesy of E. P. Pister.

Figure 14.18

Neck flexibility in the Australian salamanderfish, *Lepidogalaxias salamandroides*. This unusual benthic fish is able to bend its neck sideways and downwards due to a unique arrangement of spaces between the skull and the cervical vertebrae. A lack of ribs throughout the vertebral column probably aids in neck bending and also allows the fish to make sinuous movements. (A) A 35 mm long salamanderfish in the bent-neck position. (B) A cleared and stained, 49 mm long salamanderfish showing intervertebral gaps and lack of ribs. (C) A comparison specimen of the related *Galaxiella munda* (Galaxiidae, 46 mm), showing the tightly coupled vertebrae and more elongate ribs. Note also the well-developed pelvic girdle of *Lepidogalaxias*, which is used as a prop during resting. From Berra and Allen (1989), used with permission.

Figure 14.19

The esocid Muskellunge, *Esox masquinongy*, one of the largest freshwater predators in North America. From Scott and Crossman (1973).

Figure 14.20

Phylogenetic relationships among formally recognized, advanced teleostean superorders above the level of the Protacanthopterygii. Along the diagonal line of the cladogram are commonly used designations that do not have formal rank but that are generally distinguishable by shared derived traits as discussed in the following accounts. After Nelson (2006).

Figure 14.21

Aulopiforms, from deep and shallow water. (A) Giganturid telescopefishes are mesopelagic, water column dwellers. (B) Ipnopid spiderfishes are deepsea benthic dwellers. (C) Synodontid lizardfishes are benthic, shallow water, sand bottom, lurking predators on coral reefs and in some subtropical areas. (A) from Walters (1964); (B) after Heezen and Hollister (1971); (C) photo by G. Helfman.

Figure 14.22

A myctophid lanternfish, *Diaphus mollis*, about 4 cm long. The round structures along the ventral half of the body are light-emitting photophores. From Nafpaktitis et al. (1977), used with permission.

Figure 14.23

Lampriformes. (A) An opah or moonfish, *Lampris regius*. This large pelagic predator has red fins, a silvery-white body, with a bluish back. (B) The oarfish, *Regalecus glesne*, the world's longest teleost, reaching lengths of 7 m to as much as 11 m. Whole specimens are rare. (B) courtesy of T. Roberts.

Fig. 14.24

Spawning behavior of the Pirate Perch, *Aphrododerus sayanus*, a fish with a jugular-positioned anus. Pirate Perch spawn in dense root mats, the female and then the male pushing into narrow canals to deposit eggs and sperm. Inset: a female in the process of laying eggs. From Fletcher et al. (2004), used with permission.

Figure 14.25

Paracanthopterygians. (A) A gadiform, the Atlantic Cod, *Gadus morhua*. (B) A Pacific Pearlfish, *Encheliophis dubius*, entombed in a black lip pearl oyster. (C) An ophidiiform, the Bearded Brotula, *Brotula barbata*. (A, C) from Jordan (1905); (B) courtesy of the Museum of Comparative Zoology and Harvard University.

Figure 14.26

Lophiiformes. (A) A 6 cm long Bloody Frogfish, *Antennarius sanguineus*, from the Galápagos Islands. Note the elaborate esca or lure at the end of the modified first dorsal spine or illicium. (B) Dorsal view of a Batfish, *Dibranchus spinosa*. Opercular openings are the tear-drop shaped holes at about midbody. (A) drawing by C. L. Starks, in Heller and Snodgrass (1903); (B) after Briggs (1974).

Figure 14.27

Brachionichthyid handfishes. A male and female Red Handfish (*Brachionichthys politus*) guarding their relatively large, yellow-brown eggs. Handfishes get their name from their pectoral fins, which are armlike appendages with an elbow and fingers. Handfishes are restricted to southeastern Australian waters, chiefly Tasmania. Photo by D. Hall, www.seaphotos.com.

Figure 14.28

Ceratioid anglerfishes. Shown are females from the 11 ceratioid families: (A) Caulophrynidae; (B) Melanocetidae; (C) Himantolophidae; (D, E) Diceratiidae; (F) Oneirodidae; (G, H) Thaumatichthyidae; (I) Centrophrynidae; (J) Ceratiidae; (K) Gigantactinidae; (L) Neoceratiidae; (M) Linophrynidae. See Pietsch and Orr (2007) for color photos. After Pietsch (2005), used with permission.

Figure 15.1

Two very different interpretations of relationships among acanthopterygian, spiny-rayed fishes: (A) from Nelson (2006) and (B) from Johnson and Patterson (1993b). From Nelson (2006), used with permission.

Figure 15.2

Phylogeny of acanthopterygian or higher spiny-rayed fishes. Most recognized clades are given ordinal or higher status and do not have accepted common names. The common names given are of better known representatives. This is basically the same phylogeny as shown in Fig. 15.1, except the synbranchiform swamp eels are now considered more advanced than, and not a sister group to, the gasterosteiform sticklebacks. See Fig. 14.1 for characters that define branching points in the phylogeny of the Acanthopterygii. After Nelson (2006).

Figure 15.3

A striped mullet, *Mugil cephalus*. From Jordan (1905).

Figure 15.4

Atherinimorphs. (A) A belonid needlefish, *Tylosurus crocodilus*. (B) A fundulid Striped Killifish, *Fundulus majalis*, showing the male above, and female below. (C) The Four-eyed Fish, *Anableps*. (A) from Collette (1995), used with permission; (B) drawing by H. L. Todd, in Collette and Klein-MacPhee (2002); (C) from Jordan (1905).

Figure 15.5

The Orange Roughy, *Hoplostethus atlanticus*, a trachichthyid beryciform. Photo by G. Helfman.

Figure 15.6

Gasterosteiforms. (A) A Three-spined Stickleback, *Gasterosteus aculeatus*. (B) A sea horse, *Hippocampus erectus*. (C) A 13 cm centriscid shrimpfish, *Aeoliscus strigatus*. Centriscids are extraordinary gasterosteiforms that often hover head-down among sea urchin spines, where they are particularly well camouflaged. The first dorsal spine forms the posterior end of the body while the second dorsal, caudal, and anal fins are directed downward. From Jordan (1905).

Figure 15.7

Protective resemblance in sea horses and their relatives. (A) The pygmy sea horse, *Hippocampus bargibanti*, resembles its sea fan habitat to a remarkable degree. (B) The protected leafy seadragon, *Phycodurus eques*, is a South Australian endemic that mimics the marine vegetation in which it lives. Go to www.dragonsearch.asn.au. Photos by David Hall, www.seaphotos.com.

Figure 15.8

Scorpaeniforms. (A) A Canary Rockfish, *Sebastes pinniger*, one of the numerous sebastine rockfishes of the North Pacific. (B) The Lumpfish, *Cyclopterus lumpus*, of the North Atlantic. (A) photo by G. Helfman; (B) drawing by H. L. Todd, in Collette and Klein-MacPhee (2002).

Figure 15.9

Representative percoid fishes. (A) A centropomid Snook, *Centropomus undecimalis*. (B) A serranid Black Sea Bass, *Centropristis striata*. (C) A centrarchid Smallmouth Black Bass, *Micropterus dolomieu*. (D) A percid darter, the Log Perch, *Percina caprodes*. (E) An echeneid Sharksucker, *Echeneis naucrates*, with a top view of the first dorsal fin that forms a suction disk. (F) A carangid Rough Scad, *Trachurus lathami*. (G) A chaetodontid Foureye Butterflyfish, *Chaetodon striatus*. (A, C, D, G) from Jordan 1905; (B, E, F) drawing by H. L. Todd, in Collette and Klein-MacPhee (2002).

Figure 15.10

The tangerine darter, *Percina aurantiaca*, the second largest of the nearly 200 species of darters endemic to North America (*c*. 18 cm). Photo by J. DeVivo. For a kaleidoscope of darter photos, see www.cnr.vt.edu/efish/families/percidae.html.

Figure 15.11

Banggai Cardinalfish, endemic to the Banggai Islands of Indonesia, were depleted due to collecting for the aquarium trade. However, captive animals in a holding facility escaped and multiplied and have even increased the originally limited natural range. See Helfman (2007) for details. Photo by G. Helfman.

Figure 15.12

Dolphinfish, dorado, or mahimahi, *Coryphaena hippurus*, exhibit extreme sexual dimorphism. The male shown here has a greatly enlarged supraoccipital bone in its forehead, which gives it the characteristic square-headed appearance. Females have a much narrower and streamlined profile. Skeletal preparation by Grant Stoecklin, www.helterskeletons.com.

Figure 15.13

A Mutton Snapper, *Lutjanus analis*, resting behind a gorgonian coral in St. Croix. Snappers are twilight and nocturnal predators on reef fishes throughout the tropics. Photo by G. Helfman.

Figure 15.14

A sphyraenid, the Great Barracuda, *Sphyraena barracuda*. Photo by G. Helfman.

Figure 15.15

This aquarium at the Georgia Aquarium is not unrepresentative of a scene over a rocky area of Lake Malawi where there has been an explosive speciation among cichlids. To view some of the spectacular body shape and color variation among African cichlids, go to www.cichlidworld.com/photo.html. Photo by G. Helfman.

Figure 15.16

Diversity in body shape among African cichlids. These fishes belong to several different genera of cichlids, yet are roughly similar in body form to several other teleostean families. Cichlid genera and suggested convergences are: (A) Tilapia versus a centrarchid sunfish; (B) *Xenotilapia* versus a malacanthid tilefish; (C) *Serranochromis* versus a serranid seabass; (D) *Xenotilapia* versus a gobiid goby; (E) *Boulengerochromis* versus a lutjanid red snapper; (F) *Telmatochromis* versus a batrachoidid toadfish; (G) *Rhamphochromis* versus a centropomid snook; (H) *Telmatochromis* versus an opistognathid jawfish; (I) *Julidochromis* versus a labrid wrasse; and (J) *Spathodus* versus a scarid parrotfish. From Fryer and Iles (1972), used with permission.

Figure 15.17

Variation in morphology of an ancient species flock. (A) A completely reconstructed individual of the Jurassic neopterygian *Semionotus*. (B) Variation in body form of species related to *Semionotus* that probably co-occurred in a single lake. From McCune (1990), used with permission.

Figure 15.18

Representative labroids. (A) A pomacentrid damselfish, the Sergeant Major, *Abudefduf saxatilis*. (B) A labrid, the California Sheephead, *Semicossyphus pulcher*. (C) Head of a Rainbow Parrotfish, *Scarus guacamaia*, showing the fused, parrotlike beak. (D) The Napoleon or Humphead Wrasse (*Cheilinus undulatus*), the largest member of the speciose wrasse family. (A, B) from Jordan (1905); (C) photo by G. Helfman; (D) photo by D. Hall, www.seaphotos.com.

Figure 15.19

The Garibaldi, *Hypsypops rubicundus*, a temperate pomacentrid damselfish common in kelp beds of southern California, It really is that orange. Photo by G. Helfman.

Figure 15.20

Zoarchoids. (A) A zoarcoid Atlantic wolffish, *Anarhichas lupus*. (B) A skull of the related Pacific Wolf-eel, *Anarrhichthys ocellatus*, showing the massive, diversified dentition of these predators (see also Fig.8.8). From Jordan (1905).

Figure 15.21

The Patagonian Toothfish, *Dissostichus eleginoides*, a large, long-lived nototheniid of southern oceans subjected to considerable illegal, unreported, and unregulated (IUU) fishing. Take a pass on Patagonian Toothfish. Drawn by Bruce Mahalski, from Lack and Sant (2001), used with permission of www.traffic.org.

Figure 15.22

A bleniid blenny, *Blennius yatabei*, from Japan. From Briggs (1974), used with permission of McGraw-Hill, Inc.

Figure 15.23

A gobiesocid clingfish, *Gobiesox lucayanus*, from the West Indies. From Briggs (1974), used with permission of McGraw-Hill, Inc.

Figure 15.24

A Japanese goby, *Pterogobius daimio*. From Jordan (1905).

Figure 15.25

A scombrid, the Albacore, *Thunnus alalunga*. From Briggs (1974), used with permission of McGraw-Hill, Inc.

Fig. 15.26

Snakeheads. (A) The Northern Snakehead, *Channa argus*. This Southeast Asian native was established in a pond in Maryland in 2002. (B) The Giant Snakehead, *Channa micropeltes*, a large (up to 1 m and 20 kg) freshwater predator of Southeast Asian still waters. (A) from Courtenay and Williams (2002); (B) photo by Jean-Francois Healias, Fishing Adventures Thailand, www.anglingthailand.com.

Figure 15.27

A pleuronectiform, the bothid Fourspot Flounder, *Paralichthys oblongus*. Drawn by H. L. Todd in Collette and Klein-MacPhee (2002).

Figure 15.28

Tetraodontiforms. (A) A balistid, the Gray Triggerfish, *Balistes capriscus*. (B) The spine-locking mechanism of triggerfishes, showing how the second dorsal spine fits into and helps lock the first spine in the erect position. Pushing posteriorly on the second spine causes the second basal pterygiophore to push against the first basal pterygiophore, releasing the first spine. (C) The Ocean Sunfish, *Mola mola*, a member of the family considered the evolutionarily most advanced of all teleosts. (A, C) drawn by H. L. Todd in Collette and Klein-MacPhee (2002); (B) redrawn from a photo by G. Helfman.

Figure IV *(opposite)*

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, lack of an illicial lure, jet propulsion and bouncing method of movement, and practice of hiding in holes, not to mention the spectacular head and body coloration. See Pietsch et al. (2009). Photo by D. Hall, www.seaphotos.com.

Figure 16.1

Percentages of Recent fish species living in various habitats. From Cohen (1970).

Figure 16.2

Distribution of marine populations of 11 species of needlefishes of the genus *Strongylura* in relation to the 23.9° isothere. Adapted from Cressey and Collette (1970).

Figure 16.3

The earth's important tectonic features. Dashed lines denote margins of major lithospheric plates; arrows indicate direction of plate movements. Adapted from Springer (1982).

Figure 16.4

The ranges of seven Indo-West Pacific species of Spanish mackerels (*Scomberomorus*), three continental and four Australian, with reference to Wallace's Line delimiting the continental margin. Adapted from Collette and Russo (1985b).

Figure 16.5

Distribution of coral reef fishes (shaded areas) in the tropical western Atlantic. Black dots indicate 14 stations where coral reef fishes were caught in association with sponges. Adapted from Collette and Rützler (1977).

Figure 16.6

Ranges of the regalis group of Spanish mackerels (*Scomberomorus*). Adapted from Collette and Russo (1985a).

Figure 16.7

Cladogram of the *Scomberomorus regalis* group of Spanish mackerels. Adapted from Collette and Russo (1985a).

Figure 16.8

Main ichthyological provinces in North and Middle America. Numbers refer to regions in the text. From Lévêque et al. (2008).

Figure 16.9

South American ichthyological provinces. Numbers refer to regions in the text. From Lévêque et al. (2008).

Figure 16.10

Main ichthyological provinces in western Europe. Numbers refer to regions in the text. From Lévêque et al. (2008).

Figure 16.11

Main ichthyological provinces in Africa. Numbers refer to regions in the text. From Lévêque et al. (2008).

Figure 16.12

Wallace's and Weber's lines separating the Oriental and Australian regions. The shaded areas show how the major landmasses would be connected if the sea retreated to the 200 m line. Adapted from Berra (2007).

Figure 16.13

Osteoglossidae and their distribution (inset below). (A) *Heterotis*. (B) *Osteoglossum*. (C) *Arapaima*. (D) *Scleropages*. From Norman and Greenwood (1975).

Figure 16.14

Summary of archaic freshwater fish distributions.

Figure 16.15

Distribution of the pickerels, Esocidae. Adapted from Lagler et al. (1977).

Figure 16.16

Distribution of the darters and perches, Percidae. Adapted from Norman and Greenwood (1975).

Figure 16.17

Distribution of the sunfishes, Centrarchidae, and cichlids, Cichlidae. Adapted from Lagler et al. (1977).

Figure 16.18

Summary of recent primary fish distributions (other than Ostariophysi).

Figure 16.19

Distribution of the minnows and carps, Cyprinidae. Adapted from Lagler et al. (1977).

Figure 16.20

Distribution of the suckers, Catostomidae. Adapted from Lagler et al. (1977).

Figure 16.21

Summary of otophysan distribution.

Figure 16.22

Distributional limits of certain primary and secondary freshwater fishes in Central America. A single characin (*Astyanax mexicanus*) and a single cichlid (*Cichlasoma cyanoguttatum*) reach north to the Rio Grande. CR, Costa Rica; P, Panama. Adapted from Miller (1966, fig. 1).

Figure 17.1

(A) A parsimony network (see below, Molecular evolution) for the Ocean Surgeonfish (*Acanthurus bahianus*), based on 608 bp of mtDNA cytochrome *b*. Parsimony networks are one method for describing relationships among mtDNA haplotypes. Each branch (regardless of length) indicates a single mutation. Branches interrupted by hash marks indicate additional mutations. Geographic segregation of haplotypes among regions of the tropical Atlantic (Brazil, Mid-Atlantic Ridge, North Atlantic) is indicated with dotted and solid enclosures. Haplotypes observed in more than one individual are dark (number of individuals shown inside the circle). The Mid-Atlantic Ridge and Brazil share haplotypes, indicating shallow population structure (F statistic $\Phi_{ST} = 0.064$), whereas the North Atlantic population is separated by 11 mutations ($d = 0.024$ sequence divergence; $\Phi_{ST} = 0.724$), indicating deep population structure and possibly an evolutionary separation. (B) Another method for describing relationships among haplotypes is a phylogenetic tree. This is a neighbor joining tree for the Redlip Blenny (*Ophioblennius atlanticus*) from five locations in the Atlantic Ocean, with bootstrap support (see below, Molecular evolution) indicated as a percentage value on each of the major branches. The scale at the bottom indicates the sequence divergence for each branch. The sister species *O. steindachneri* (Pacific) is used as an outgroup (see Chapter 2). Note that the oldest Atlantic branches are in the West Atlantic (Brazil and Caribbean) followed by progressively younger branches in the central Atlantic (Mid-Atlantic) and eastern Atlantic (Sao Tome, Cape Verde, Azores). This suggests a pathway of colonization from West to East Atlantic (see Chapter 16), with the Mid-Atlantic island of Ascension serving as a stepping stone. (A) from Rocha et al. (2002), used with permission; (B) from Muss et al. (2001), used with permission.

Figure 17.2

A parsimony network of mtDNA control region sequences, illustrating relationships among sardines (genus *Sardinops*) in five temperate upwelling zones of the Indian and Pacific oceans (hashmarks indicate multiple mutations along a branch). The 20 haplotypes are labeled A to T. Haplotype C occurs at both South Africa and Australia, and haplotype M occurs at both Chile and Mexico, indicating shallow population structure between these regions, and recent colonization around the rim of the Indian-Pacific Basin. The five regional forms were previously regarded as separate species, a taxonomy that is not supported by the mtDNA analysis. From Bowen and Grant (1997), used with permission.

Figure 17.3

Phylogeographic data for the Lake Whitefish (*Coregonus clupeaformis*) based on mtDNA sequence data from 41 populations across the species range. (A) The phylogeny of Whitefish lineages corresponding to four glacial refugia. The scale bar indicates sequence divergence. (B) Distribution of the four lineages (A, B, C and C2, D) following postglacial dispersal. (C) Nucleotide diversity of sampled areas, in relation to the area formerly inundated by major glacial lakes (shaded area); the height of bars indicates the level of nucleotide diversity. From Bernatchez and Wilson (1998), used with permission.

Figure 17.4

The relationship between nucleotide diversity and latitude for North American freshwater fishes, showing a general trend of reduced genetic diversity in areas that were under glacial ice. Two lines with two different slopes fit the data, with the break between the lines corresponding closely to the 46°N latitude, near the southern limit of the most recent glaciation. Each dot represents a different species. From Bernatchez and Wilson (1998), used with permission.

Figure 17.5

Drainage basins of western North America that support at least one spawning population of Pacific salmon (see Table 17.4). Letter codes correspond to the following ecosystems: A, Georgia Basin; B, temperate rainforest; C, north coast; D, Klamath Mountains; E, northern California; F, southern California; G, Central Valley; H, Willamette/Lower Columbia River; I, mid-Columbia River; J, upper Columbia River; K, Snake River tributaries; L, mainstem Snake River. From Waples et al. (2001), used with permission.

Figure 17.6

A neighbor joining tree (A) and parsimony network (B) based on mtDNA cytochrome *b*, showing the relationships among trumpetfish species across the range of genus *Aulostomus*. The scale indicates 1% sequence divergence. The data indicate a 3–4-million-year-old separation between West Atlantic (*A. maculatus*; haplotypes AM-1 and AM-2) and Indian-Pacific (*A. chinensis*; haplotypes AC-1 to AC-8) species, followed by approximately a 2.5-million-year separation between the Indian-Pacific and the East Atlantic species (*A. strigosus*; haplotypes AST-1 to AST-3). These separations correspond to major vicariant events separating the tropical fauna of each ocean basin (see text). From Bowen et al. (2001), used with permission.

Figure 17.7

Parsimony network for mtDNA cytochrome *b* showing that the Atlantic Goby, *Gnatholepis thompsoni*, is the product of a recent colonization from the Indian Ocean. Populations in the western, central, and East Atlantic are indicated by blue, green, and yellow coloration. The sister species (*Gnatholepis scapulostigma*) is indicated in red (South Africa) and black (Pacific). Breaks in the branches (small circles) indicate mutation events, and unbroken branches indicate a single mutation regardless of length. The size of the circle indicates the frequency of each haplotype. From Rocha et al. (2005b), used with permission.

Figure 17.8

Phylogeny of the most ancient lineages of extant fishes. Previous studies had indicated that lampreys are more closely related to jawed fishes than hagfishes, based on shared primitive traits including features of the nervous system, osmotic regulation, and a lens apparatus in the eye. In contrast, DNA sequence data indicate that the two jawless fish taxa are sister lineages, followed by separation of the elasmobranch from the lineage that gave rise to modern bony fishes (actinopterygians) and tetrapods. The outgroup (Amphioxus) has a notochord but not a true vertebral column, is united with vertebrates in the phylum Chordata, and is considered to be the closest extant relative of the vertebrates (see Chapter 13). This is a maximum likelihood tree based on 35 nuclear gene sequences; the scale bar indicates percent divergence in amino acid composition. Bootstrap support values are indicated above the primary branches. From Takezaki et al. (2003), used with permission.

Figure 17.9

Phylogenetic relationships among actinopterygian fishes based on parsimony analysis of whole mtDNA genomes. The bar below indicates 100 mutational changes. Branch support is by bootstrap (above the branch) and Bremer decay (below the branch). Internal nodes A, B, and C denote the well-supported differentiation of teleosts from the other actinopterygian fishes. Tree topology indicates that the four lineages recognized as the ancient actinopterygian fish (polypteriforms, acipenseriforms, lepisosteids, and *Amia*) occupied the oldest positions in the phylogeny. These data do not support the proposal that the acipensiforms (sturgeons and paddlefish) are the sister group to the neopterygians (lepisosteids, *Amia*, and teleosts; Nelson 1969), but otherwise provide a good fit to previous phylogenetic hypotheses. From Inoue et al. (2003), used with permission.

Figure 17.10

Molecular phylogeny of parrotfish genera based on a maximum likelihood analysis of nuclear and mitochondrial sequences. The jaw dentition for various feeding modes is indicated on the right. This tree shows that the key evolutionary innovation of feeding by excavating and scraping arose twice in the family Scaridae. This is an example of trait mapping (see text) to elucidate the evolution of fish diversity. From Streelman et al. (2002), used with permission.

Figure 17.11

Phylogenetic relationships of bonefish species based on maximum likelihood analysis of mtDNA cytochrome *b*. Bonefish that occupy shallow sand flats were thought to be one species worldwide (*Albula vulpes*), with a second species occupying deeper water (*A. nemoptera*). However, allozymes and DNA studies demonstrate at least 10 evolutionary lineages in the genus *Albula*. Numbers above branches indicate bootstrap support. Some species have yet to be formerly described (species A, B, C, and E), whereas others are only tentatively linked to a branch in the tree (*A. virgata*, *A. oligolepes*) pending DNA sequence analysis from voucher specimens (see Chapter 2). The scale bar indicates 5% sequence divergence. From Bowen et al. (2007), used with permission.

Figure 17.12

The complementary roles of three scientific fields (phylogeneticists, ecologists, and evolutionary biologists) in conservation. The process of conserving fishes begins with phylogenetic studies to identify the products of past evolutionary radiations. Subsequently, ecologists identify the key habitat features that allow fishes to persist in the present. Finally, evolutionary biologists identify the raw materials for future diversification. The black circles represent extinction events. From Bowen and Roman (2005), used with permission.

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.

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.

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).

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.

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.

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).

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.

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.

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.

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.

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.

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.

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).

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.

Figure V *(opposite)*

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

Figure 19.1

Variations on a theme: convergence in morphology among fast start predators. Lurking predators that swim in the water column tend to be elongate with long mouths, sharp teeth, and fins set far back on the body. Examples from six different orders and eight families are shown, including one extinct form. (A) Lepisosteiformes, *Lepisosteus* (Lepisosteidae), gar, 1 m. (B) Characiformes, *Ctenolucius* (Ctenoluciidae), Pike Characid, 1 m. (C) Esociformes, *Esox* (Esocidae), pike, 1 m. (D) Beloniformes, *Ablennes* (Belonidae), needlefish, 1 m. (E) Cyprinodontiformes, *Belonesox* (Poeciliidae), Pike Killifish, 20 cm. (F) Perciformes, *Sphyraena* (Sphyraenidae), barracuda, 1 m. (G) Perciformes, *Luciocephalus* (Osphronemidae), Pikehead, 15 cm. (H) †Osteolepiformes, *Eusthenopteron* (Eusthenopteridae), a Devonian tetrapodomorph, 75 cm. (A–C, G, H) from Nelson (1994); (D) from Collette (1995); (F) from Jordan (1905), used with permission.

Figure 19.2

"Aggressive" mimicry in the frogfish *Antennarius maculatus*. The fishlike lure, or esca, sits at the end of the elongate first dorsal spine, termed the illicium. The resemblance of the lure to a real fish is increased by an anterior eyespot, vertical bars and mottling on the body, and finlike appendages. The lure is waved by movements of the illicium, thereby attracting potential prey fishes. From Pietsch and Grobecker (1978), used with permission.

Figure 19.3

Is this the face of death? (A) The general features of a predatory face that elicit fright responses in prey fishes are a broad head; a wide, downturned mouth; and ringed, broadly elliptical eyes, as shown in drawing on the left. (B) Head-on views of piscivorous reef fishes: 1, *Epinephelus summana*, a seabass; 2, *Cheilinus trilobates*, a wrasse; 3, *Lutjanus kasmira*, a snapper; 4, *Cephalopholis argus*, a seabass; 5, *Epinephelus fario*, a seabass; 6, *Synodus variegatus*, a lizardfish. (A) from Karplus et al. (1982); (B) from Karplus and Algom (1981), used with permission.

Figure 19.4

The use of the hammer during feeding by a Great Hammerhead Shark. A 3 m long hammerhead captured and consumed a l m wide Southern Stingray by knocking it to the bottom with its hammer and then using the hammer to hold the ray against the bottom while the shark pivoted around and fed on the front margins of the pectoral fins. The following sequence is shown: 1, shark chases the ray; 2, shark strikes downward across the back of the ray with the flat underside of its hammer; 3, ray bounces off the bottom from the force of the blow while the shark brakes with its pectoral fins; 4, shark delivers a second downward blow across the back of the ray; 5, shark pivots while holding the ray against the bottom and takes a bite from the front of the left pectoral fin; 6, injured ray attempts to swim off followed by the shark. From Strong et al. (1990); used with permission.

Figure 19.5

Archerfish learn to hit rapidly moving targets by observing other archerfish. Observer archerfish allowed to watch a school member (model) improving its accuracy are almost as accurate on their first shot as the model fish was after more than 1000 shots. Crosshatched bar, initial success of model; open bar, success of model after training; solid bar, average success of observer on its first shot having watched the model. The target was 54 cm above the water and was moving at 5 cm/s. After Schuster et al. (2006).

Figure 19.6

Rotational feeding in American Eels. (1) Grasp: a 50 cm eel grasps the bait (a snapper filet tied to a weight). (2) Initial torsion: the eel develops a twist in its body just prior to spinning. Note that the ventral surface of the head (light coloration) faces the camera and the ventral surface of the posterior half of the body faces upward, whereas the dorsal (dark) region between the head and midpoint of the body face the camera. (3) Spinning: after the first initial rotations, spinning continues with no apparent twisting in the body; internal forces generating the spins are not understood. (4) Withdrawal with food; the eel has removed a piece of food and is backing away from the bait. From Helfman and Clark (1986), used with permission.

Figure 19.7

Barracuda teeth typify those of predators capable of actually dismembering prey via cutting. The teeth are pointed, flattened, and sharpened on the edges. They also fit neatly into sockets in the opposite jaw, which facilitates complete closing of the mouth during a bite, perhaps aiding the severing of prey into pieces. Photo by G. Helfman.

Figure 20.1

The tail region of the plesiopid reef fish *Calloplesiops* (bottom) may intimidate predators by mimicking the head of a moray eel (top), with which it occurs. From McCosker (1977), used with permission.

Figure 20.2

Examples and functions of disruptive coloration in fishes. (A) The Jacknife Fish, *Eques lanceolatus*, may use boldly contrasting, dark and light regions to emphasize those parts of its outline that are not fishlike in appearance, thus momentarily confusing a potential predator. (B) Many lurking predators possess a dark or light interorbital stripe that could disrupt their head outline when viewed head-on, making recognition by prey momentarily difficult. This large (*c*. 45 cm) Japanese Snook (probably *Lates japonicus*) has a distinctive, light colored interorbital stripe. (A) from Cott (1957), used with permission; (B) photo by J. DeVivo.

Figure 20.3

Countershaded fishes disappear in the water column because their graded coloration reflects light in a manner that makes them match natural background light. (A) A *uniformly colored* gray fish illuminated primarily from above (= *natural lighting*) would have a relatively bright dorsum and a relatively dark ventrum. (B) A *countershaded* fish viewed under unnaturally uniform illumination, as in flash photography, is not camouflaged because it contrasts with the gradient of illumination of background light. (C) In a *countershaded* fish viewed under *natural lighting* conditions, the gradual transition from dark dorsum to light ventrum, which is opposite to the actual distribution of background light, has an averaging or canceling effect. In this way the top of the fish is seen as dark against dark, the middle as intermediate brightness against intermediate, and the light belly as light against light. All color-background combinations eliminate the contrast between the fish and its background.

Figure 20.4

Presumed interaction between illumination and reflectivity in countershaded fishes. The "goal" is neutral color with respect to background (= 0 result). +, relatively bright; –, relatively dark; 0, neutral with respect to background. Neutrality is impossible to achieve when viewed from directly below because of the shadow cast by the fish's body.

Figure 20.5

The functional morphology of mirror sides in fishes. (A) A clear plate of glass suspended in water is invisible because background light passes directly through it (extensions of dashed lines X_2 and Y_2 to the observer's eyes); an observer sees no difference between the glass plate and its background. A mirror suspended in water also disappears because light reflected off the mirror (solid lines X_1 and Y_1) is identical to the background light that would pass through the object if it were clear (dashed lines). (B) Cross-section through the body of a Bleak (*Alburnus alburnus*) to show orientation of the reflective platelets in silvery fishes. The platelets are embedded in the skin and scales and are oriented vertically, even along the curved surfaces of the fish. After Denton and Nicol (1965).

Figure 20.6

The advantage to fishes of hovering in shade. On a sunny day in a lake, a shaded observer has a relative visual advantage over sunlit observers. When horizontal visibility is 10 m, a shaded observer can detect sunlit objects 12 m away, which is approximately 1.2 times better visibility than experienced by a sunlit observer viewing a sunlit target (= a 20% advantage over ambient conditions). More significantly, the sunlit observer cannot see an object in the shade until it is 6 m away, which gives the shaded observer a 100% advantage over the sunlit observer. The relative visual advantage decreases on cloudy days, as does the attractiveness of overhead objects. After Helfman (1979b, 1981a).

Figure 20.7

Predator avoidance has shaped body morphology in zooplanktivorous reef fishes. Fishes that feed close to protective structure tend to be more deep-bodied with square or rounded tails, those that forage higher in the water column are more streamlined with forked tails. All these fishes dive for the coral when threatened by predators. Streamlining may also facilitate holding the fish's position in the stronger currents higher above the reef. Lettering on the photograph of the reef indicates the zones where the five different fishes typically feed: (A–C) damselfishes (pomacentrids), (D) *Anthias* (a serranid), (E) *Pterocaesio* (a lutjanid). From Hobson (1991), used with permission.

Figure 20.8

The graded responses of minnows under attack. Responses increase in intensity as the predator's actions become more threatening. The hierarchy of responses begins at the top ("compact") and proceeds clockwise to "flash expansion". From Magurran and Pitcher (1987), used with permission.

Figure 20.9

Balloonfish inflate themselves with water in response to being handled by potential predators. They undergo a three-fold increase in volume, which turns them into a sphere with projecting spines. Extremities that might offer a predator a grasping point, such as the caudal (C), pectoral (P), and other fins, sit largely within the protective framework of the spines when the fish is inflated. Inflation occurs as water is pumped into the stomach, which expands up to 100-fold to fill an unusually large peritoneal space. The spines are embedded in a highly derived, stretchable skin. From Brainerd (1992), used with permission.

Figure 21.1

Parthenogenesis in Mexican livebearers. (A) In gynogenesis, a triploid female (designated MLL, shorthand for *Poeciliopsis monacha-lucida-lucida*) produces 3N eggs that are activated but not fertilized by sperm from a male *P. lucida* (L´). A daughter identical to the mother is produced. (B) In hybridogenesis, a diploid mother (ML, for *P. monacha-lucida*) produces haploid eggs (M) that contain only the maternal genome. Sperm from *P. lucida* (L´) combine to form a diploid daughter (ML´), but this male component will be discarded again during gamete production and all future eggs will continue to have solely *monacha* genes. After Vrijenhoek (1984) and Allendorf and Ferguson (1990).

Figure 21.2

Breeding tubercles in fishes. Males of at least 25 different families develop keratinized bumps on their fins and body during the breeding season that may help maintain contact between spawning fish and stimulate females to spawn. (A) Tubercles on the head of an *c*. 15 cm long male River Chub, *Nocomis micropogon*. The swollen region on the top of the head is also characteristic of male River Chubs during the breeding season. (B) Internal structure of a tubercle from the snout of a gyrinocheilid algae eater. The tubercle consists of an outer cap of epidermal keratin, with concentrations of replacement keratin lying in a pit at the base of the tubercle that will replace the tubercle in the event of its loss. (A) from Jenkins and Burkhead (1993), used with permission; (B) from Wiley and Collette (1970), used with permission.

Figure 21.3

Extreme sexual dimorphism in a male Bluehead Chub, *Nocomis leptocephalus*. This *c*. 20 cm minnow builds pebble nests on stream bottoms and attracts females with its swollen head and distinct breeding tubercles. Photo by P. Vecsei, used with permission.

Figure 21.4

Turbidity-influenced light transmission is causing hybridization and loss of species in Lake Victoria. (A) Species richness and spectral properties at 13 sampling stations in Lake Victoria, showing that where water clarity is greater (upper curves), greater transmission of light at the short and long regions of the spectrum occurs. Where turbidity is high (lower curves), few photons at short and long wavelengths are transmitted. The number of haplochromine cichlids are shown next to the curve for each station. (B) A detectable difference in red and blue colors ("ratio of reflectance") decreases as the width of the transmission spectrum narrows. Red (*Nyererei*) and blue (*Neochromis*) males appear very similar where the spectrum is narrow (left side of graph) but the colors are easier to discriminate where the spectrum is wider (right side). After Seehausen et al. (1997a).

Figure 21.5

Spawning nests or bowers of African cichlids. Male cichlids construct sand structures that vary from simple pits to complex structures, where females deposit eggs just prior to picking them up in their mouths for brooding: (A) *Tilapia* (*Oreochromis*?) *andersonii* and *T. nilotica*; (B) *T. variabilis*; (C) *T.* cf. *macrochir* from Lake Bangweulu; (D) *T.* cf. *macrochir* from Lake Mweru. In the latter, radiating spokes are created by the male plowing through sand with his open mouth from the focal point to the edge. Structures vary from 15 to 150 cm across. From Fryer and Iles (1972), used with permission.

Figure 21.6

Spawning frequently involves multiple males and a single female. (A) California grunion (Atherinopsidae) spawn on beaches at the top of the tide zone, a single female (arrowed) assuming a head-up position in the sand while males encircle her and release milt. (B) Robust Redhorse Suckers (*Moxostoma robustum*, Catostomidae) typically spawn over gravel and cobbles in groups of three, a single female (arrowed) flanked on either side by a male. In this group, the female has one male on her left and two on her right. (A) photo courtesy of M. Horn; (B) photo courtesy of B. Freeman.

Figure 21.7

Fertilization occurs in the mouth of some female African cichlids. (A) Males of many African cichlids have round spots, termed egg dummies, on their anal fins. During spawning, the female repeatedly deposits a few eggs on the spawning site and then immediately takes them up in her mouth. The male spreads his anal fin against the bottom and the female mouths the egg dummies as the male ejaculates. (B) In some species, females instead mouth "genital tassels", which are elongate, orange lobules that grow from the genital region. (C) Other males have greatly elongate pelvic fins with enlarged, conspicuous tips that reach to the cloaca. All such structures and behaviors may facilitate fertilization, assure paternity, and minimize predation on newly laid eggs. From Fryer and Iles (1972), used with permission.

Figure 21.8

Well-developed (near-term) embryos in the ovary of a Mexican goodeid, the Butterfly Splitfin, *Ameca splendens*; 13 embryos are visible. The anterior third of the ovary is not shown. Fingerlike extensions projecting forward from the ovary are trophotaenia, which are epithelial structures that grow from the embryos' anal regions and serve to take up nutrients provided by the mother. Trophotaenia have evolved convergently in goodeids, ophidioids, and embiotocid surfperches. of, oocytes; om, ovarian mesentery; os, ovarian septum, ow, ovarian wall. Regrettably, *A. splendens* is considered to be extinct in the wild, although it is commonly kept and bred in aquaria (IUCN 2006). Drawing by Julian Lombardi, from Wourms et al. (1988), used with permission.

Figure 21.9

A male Nurseryfish, *Kurtus gulliveri*, with eggs attached to his occipital crest. Length about 15 cm. Drawing originally in Weber (1913), reproduced in Berra (2001).

Figure 21.10

Parental care in the Spraying Characin, *Copella* sp. Eggs in this species are deposited on the undersides of overhanging vegetation, out of the water. The male guards the eggs, splashing them periodically with his tail to keep them moist. From Krekorian and Dunham (1972), used with permission.

Figure 21.11

Parental care in cichlid fishes. Two of the more striking forms of parental care exhibited by members of the diverse cichlid family are shown. (A) Provisioning young. Few fishes with external fertilization actually provide nutrition for their young. Many cichlids are suspected of provisioning, but the behavior is best known in the discus, *Symphysodon*. A pair of discus is shown, with the young feeding on the mucus secretions of the female. (B) Mouth-brooding. A female opens her mouth after signaling danger to a shoal of young. Mouth-brooding of eggs is fairly widespread in fishes, but brooding of free-swimming young is relatively rare. (A) from Herald (1961), used with permission; (B) from Fryer and Iles (1972), used with permission.

Figure 21.12

(A) Cuckoo Catfish pairs (darker fish) follow close behind spawning, mouth-brooding cichlids, laying their eggs amongst the fertilized cichlid eggs. The female cichlid picks up the catfish eggs along with her own. (B) In the mouth of the mother cichlid, catfish young hatch earlier and develop faster than cichlids, eating first the yolk sacs and eventually entire cichlid larvae. After Sato (1986) and Barlow (2000).

Figure 21.13

Variations in life history and behavior result in alternative mating tactics in male Bluegill Sunfish and Pacific Salmon. Both species are characterized by large, territorial males that court females and fight other males versus smaller males that interject themselves during spawnings by larger males. (A) Bluegill males occur as: (i) large males that dig nests, spawn, and guard eggs; (ii) small sneaker males that hide in vegetation and dart past spawning pairs, quickly depositing sperm; and (iii) intermediate satellite males that mimic female coloration and behavior and thus gain access to spawning pairs. The life history alternatives for male Bluegill are to mature at a young age and small size and adopt a sneaker and then later a female mimic role, or to mature later at a larger size and adopt a courting and parental role. All females mature at an intermediate size and age. (B) Coho Salmon males occur as large, hooknosed males that fight for access to females in midstream, or as smaller jacks that hide near structure or in shallow water and sneak copulations. Life history alternatives for the salmon are to mature at a young age and small size and adopt a sneaker role, or to mature later at a larger size and adopt a fighting role. All females mature at a relatively large size and old age. Modified from Gross (1984, 1991), used with permission.

Figure 22.1

A nighttime photograph of a male ponyfish, *Leiognathus elongatus*, emitting light from its specialized circumesophageal light organ. The light display is the bright rectangular area just posterior of the pectoral fin. Light emission involves a complex series of structures and behaviors including bacterial light production, internal reflection, and transmission through a muscular shutter in a transparent section of the body wall. Four different light displays have been described in which duration and intensity of light emission are varied. From Sasaki et al. (2003), used with permission.

Figure 22.2

Lateral and frontal displays in fishes. During agonistic interactions, fish may line up parallel, antiparallel, or head-to-head and remain stationary, spread fins or operculae, change colors, and swim in place or circle one another. (A) Typical swimming-in-place lateral display when water currents (arrows) are directed at the head of the opponent, as happens in many cichlids. (B) Lateral display in the clownfish, *Amphiprion*, during which individuals strike each other with their pectoral fins. (C) Head-to-head pushing in the butterflyfish, *Chelmon rostratus.* (A) after Chiszar (1978); (B, C) after Eibl-Eibesfeldt (1970).

Figure 22.3

Exaggerated swimming display of the Gray Reef Shark, *Carcharhinus amblyrhynchos*. When approached by a diver or another shark or a small submarine, or when competing for food, Gray Sharks lift the snout, arch the back, lower the pectoral fins, and swim in a tense, exaggerated manner (exaggerated postures shown on left, comparatively normal swimming postures on right). If the intrusion continues, the displaying shark may attack the intruder. Similar displays, without attacks, have been observed in Galàpagos, Silky, Lemon, and Bonnethead sharks, and a Bull Shark performed exaggerated S-turn swimming before attacking a small boat that had been following it (S. Gruber, pers. comm.). After Johnson and Nelson (1973), used with permission.

Figure 22.4

Color patterns that camouflage the eye in reef fishes. Predators and prey alike focus on the eyes of other fishes, and many fishes have color patterns that tend to mask the eye or call attention away from it. (A) A Blackcap Basslet (Serranidae): the dark eye is contained in a dark area. (B) A Peacock Flounder (Bothidae) and (C) a wrasse (Labridae): numerous false eyes call attention away from the real eye. (D) A frogfish (Antennariidae): a small eye is subsumed in a series of radiating patterns that converge on different points. From Barlow (1972), used with permission.

Figure 22.5

A Fourspot Butterflyfish, *Chaetodon quadrimaculatus*, in the field that has suffered an obvious wound in the region of its posterior ocellus or eye spot. Rare photos such as this one are indirect evidence that ocelli serve as deflective marks that direct the attacks of predators away from more vulnerable head regions. Photo by P. Motta, used with permission.

Figure 22.6

Types and activities of fish aggregations. Shoals contain fish attracted to one another but whose activities are only loosely coordinated. In schools, behavior is synchronized: fish often swim parallel, in the same direction, with fairly uniform spacing (the "polarized school" of many authors). Foraging and spawning groups generally form shoals, whereas predator avoidance often results in highly synchronized schooling activities. In this figure, five common antipredator actions and their relationship to grouping behavior are shown in the smallest circles (see also Chapter 20, Responses of aggregated prey). After Pitcher (1983), used by permission of the publisher Academic Press Ltd, London.

Figure 22.7

Garden eels (Congridae) live in colonies of several hundred individuals on sand bottoms near coral reefs. Individuals feed on zooplankton during the day, often extending just the anterior portion of their bodies out of burrows, the sides of which are cemented with mucus produced by the fish's skin. Withdrawal of one individual into its burrow stimulates withdrawal of all other members of the colony. Photo by G. Helfman.

Figure 22.8

Testing for social learning in juvenile grunts. The twilight migration routes at four experimental sites are shown. "Resident" fish are those with an established migration route. "Transplants" were brought from another location and allowed to follow resident fish. "Control" fish were also transplanted but were released at the resident site after resident fish were removed, hence controls had no opportunity to learn the routes. At sites 1 through 3, transplants adopted the resident route and used it even when residents were absent. Controls never used the resident route. At site 4, residents did not migrate but instead drifted away in different directions. Transplants also drifted away from the resting site, whereas controls underwent a distinctive migration. Adapted from Helfman and Schultz (1984), used with permission; grunt drawing from Gilligan (1989).

Figure 22.9

Typical cleaning activities of a cleaner wrasse, *Labroides* sp., from the tropical Pacific. Cleanerfishes exist in almost all habitats, but only in tropical seas are species relatively specialized for this role. (A) A large wrasse poses in a head-up position while the smaller cleaner inspects it for parasites and necrotic tissue, contacting the host with its pelvic, anal, and caudal fins. (B) The cleaner solicits posing from a potential host by riding it while flicking the host with its pelvic fins. (C) The cleaner is about to remove a parasite or necrotic tissue from the anal fin of a carangid. After Losey (1987).

Figure 22.10

Goby–shrimp symbiosis. Several tropical goby species in the Pacific, Indian, and Atlantic oceans live with burrowing alpheid shrimps. The goby stands guard at the burrow entrance while the shrimp excavates and repairs the burrow. The shrimp, which is often functionally blind, maintains contact with the goby via its antennae. If the goby is removed, shrimp will often seal up the burrow entrance and not emerge until the goby is replaced. After Losey (1978).

Figure 22.11

Anemonefish, *Amphiprion bicinctus*, move among the tentacles of an anemone. Stinging cells in the anemone's tentacles would paralyze other fishes but are not discharged when contacted by a resident anemonefish. Photo by H. Fricke.

Figure 23.1

Day (A) versus night (B) distribution of families in a rocky reef area, Baja California, Mexico. Solid lines show habitat differences of diurnal fishes, dashed lines of nocturnal groups. Diurnal species: 1, benthic damselfishes; 2, Sergeant Major damselfishes; 3, parrotfishes; 4, zooplanktivorous damselfishes; 5, surgeonfishes; 6, butterflyfishes. Nocturnal species: I, squirrelfishes; II, cardinalfishes; III, drums; IV, grunts. After Lowe and Bray (2006), based on Hobson (1968).

Figure 23.2

A daytime resting school of juvenile French and White Grunts hover amidst *Diadema* sea urchins. At dusk, grunts move away from coral areas and feed in sand and grassbed regions, returning the next morning to the same daytime locales. Photo by G. Helfman.

Figure 23.3

Light availability, dark adaptation, species changeover, and predator–prey interactions at evening twilight on a coral reef. (A) Available light (curved line) decreases maximally during the period from 13 to 33 min after sunset. This is the time (stippled area) when (i) diurnal eyes are dark-adapting, (ii) predators are maximally active and successful, and (iii) diurnal and nocturnal prey species abandon the water column, creating the quiet period. Approximate lux values for light units are 10^{14} photons = 10,000 lux, 10^8 photons = 0.0001 lx. (B) Temporal sequence of cessation of activity of reef families at dusk, and onset at dawn. Families are coded by number. B, benthic; Lg, large; Plk, planktivorous; QP, quiet period; Sm, small. (A) after Munz and McFarland (1973), used with permission; (B) after McFarland et al. (1999), used with permission.

Figure 23.4

Endogenous, circatidal activity rhythm of the Shanny, *Lipophrys pholis*, held in a laboratory under continuous light. Activity is indicated by the darkened histograms, times of high tide where the fish was captured are denoted by the vertical dashed lines. The Shanny is normally active at high tide. In the absence of tidal stimuli, the activity cycle "free runs" with a period of 12.4 h, displacing it slightly from predicted high tides with each cycle. In the field, the fish's clock would be recalibrated (reset) by the hydrostatic pressure of high tide, which would keep the fish's activity synchronized with actual tides. After Gibson (1993), after Northcutt et al. (1990).

Figure 23.5

Semilunar spawning cycle of the Grunion. Grunion are small (15 cm) atherinopsids that frequent the nearshore waters of Baja and southern California. They spawn every 2 weeks in the summer during spring tides, when waves sweep farthest up the beaches. Adults ride the waves up the beach, dig in the sand, and deposit and fertilize eggs. Spawning occurs shortly after peak tides, insuring that eggs will not be inundated again until the next spring tide, 10–14 days later, when they are ready to hatch. Fish symbols indicate nights of spawning. Redrawn from Alcock (1989), used with permission.

Figure 23.6

Genetically based, local adaptation in Fraser River Sockeye Salmon. Among stocks (named dots), fish spawn on different dates, and eggs are incubated at different mean temperatures. These differences lead to emergence dates favorable to juvenile feeding. Different spawning dates also help to coordinate migrations among smolts originating at different distances from the sea. After Brannon (1987); sockeye drawing from USDA Forest Service, www.fs.fed.us.

Figure 23.7

Sticklebacks have a daily rhythm of photosensitivity that is maximal about 14–16 h after sunrise. During this maximally sensitive period, exposure to light induces sexual maturation. The photoinducible phase helps the fish determine if day length is increasing, as would happen during spring and summer. Experimental manipulations of daily light/dark cycles can pinpoint the existence and position of the photoinducible phase by providing a 2 h pulse of light at different times after sunrise. The open bars at the bottom indicate when lights were on, the darkened portions when lights were off (0 = sunrise). Light 14–16 h after sunrise would be naturally experienced when days consisted of 16 h of light (L) and 8 h of dark (D), as would happen during summer. Maximum levels of sexual maturity (bar V) are found in this light regime. From Baggerman (1985), used with permission; stickleback drawing from www.seagrant.wisc.edu.

Figure 23.8

The seasonal progression of events for many fishes in large tropical rivers. The dark curved line indicates relative water levels. Seasonal flooding of highly productive gallery forests and swamps opens these areas up to lateral migration, feeding, and spawning by fishes. Many regions show two rainy seasons and both result in lateral migrations. Fat stores increase as fishes capitalize on the food abundance in flooded regions. From Lowe-McConnell (1987), used with permission.

Figure 23.9

Diadromy takes three general forms: anadromy, catadromy, and amphidromy. In anadromy, adults spawn in fresh water, juveniles move to salt water for several years of feeding and growth, and then migrate back to fresh water to spawn. In catadromy, adults spawn at sea, juveniles migrate to fresh water for several years to feed, and return to the sea to spawn. In amphidromy, spawning can occur in either fresh or salt water (but usually fresh), larvae migrate to the other habitat for an initial feeding and growth period, then migrate to the original habitat as juveniles where they remain for additional feeding and growth prior to spawning. B, birth; G, growth; R, reproduction. Modified from Gross (1987).

Figure 23.10

The latitudinal distribution and frequency of different forms of diadromy among major fish groups. The number of species employing each tactic is plotted as a function of latitude, showing: (A) anadromy to be largely a northern, temperate and polar phenomenon; (B) catadromy to be more tropical and subtropical in distribution; and (C) amphidromy to be more bipolar and temperate. Modified from McDowall (1987), used with permission.

Figure 23.11

Characteristic life history of a Pacific salmon, as seen in the Sockeye Salmon, *Oncorhynchus nerka*. At different stages, different orientation mechanisms are likely to come into play to help the developing, growing, or maturing fish find its way to, through, and away from the sea and back to its natal river to spawn. Responses to light, gravity, and current are initially important for recent hatchlings. Later, sun compass and magnetic detection, backed up by other cues, aid a fish moving downstream and into the ocean. Finally, the memory of home stream chemicals on which the juvenile imprinted lead the maturing adult back to its spawning grounds. Redrawn after Quinn and Dittman (1990).

Figure 24.1

Bigger fish produce more eggs, both within and among species. Since fish grow throughout their lives (= indeterminate growth), older fish are usually larger. Within a species, larger individuals generally produce more eggs and often larger eggs. The generalization even holds for pregnant male seahorses, with larger individuals possessing larger pouches capable of holding more embryos (Woods 2005). Values are plotted for a variety of Canadian freshwater species. Redrawn after Wootton (1990).

Figure 24.2

Year class strength in an endangered sucker. The Cui-ui, *Chasmistes cujus* (Catostomidae), presently occurs only in Pyramid Lake, Nevada. Its long life span, approaching 45 years, has probably saved it from extinction. Reproductive failure in most years has resulted from drought and human diversion of water from its spawning habitat in the lower Truckee River. (A) Samples of spawning fish in 1978 indicate that the entire species has been maintained by two year classes, one born in 1950 and the other in 1969. (B) Mortality had all but eliminated the 1950 year class by 1983. (C) A bypass channel built in 1976 gave fish access to the river even at low water levels, and some successful reproduction had occurred in subsequent years (no fish occur in the 0–6-year classes because reproduction does not start until age 6). The inset shows an adult Cui-ui held in a captive propagation facility, Pyramid Lake, Nevada. From Scoppetone and Vinyard (1991), used with permission; photo courtesy of the US Bureau of Reclamation, www.usbr.gov/mp/lbao/endangered_species.html.

Figure 24.3

Four morphs of Arctic Char that differ anatomically, behaviorally, and ecologically can be found in a single lake. Shown here are adults of the four morphs from an Icelandic lake. They are, from top to bottom, the large, benthic feeding morph (33 cm long), the small benthic feeding morph (8 cm), the piscivorous morph (35 cm), and the plantivorous morph (19 cm). Photo by S. Skulason, from Skulason and Smith (1995), used with permission.

Figure 24.4

Foraging guilds of soft bottom fishes on the southern California shelf. Two general groups are recognized: those that swim above the bottom and those that are in contact with the bottom. The actual guilds take into account height above bottom, foraging type (search and capture activities), and time of feeding. From Allen (2006), used with permission.

Figure 24.5

Habitat choice in stream fishes as demonstrated by vertical segregation among cyprinid fishes in a Borneo stream. Habitat choice is one aspect of the niche of a species; species choose habitats according to specific characteristics, and species often differ in one or more quantifiable characteristics of habitat. From Welcomme (1985), used with permission.

Figure 24.6

The characacid Dorado, a popular gamefish of the Amazon Basin, is ecologically convergent with large riverine salmonids. Photo from Rio Paraná, Ayollas, Paraguay, courtesy of www.planetapesca.com.

Figure 24.7

Vertical zonation of fishes in a kelp bed. Species portrayed are the more common fishes found in southern California rocky kelpbed reefs. The assemblage is a mixture of three biogeographic faunal elements, involving tropical- and subtropical-derivative families (chubs, grunts, croakers, damselfishes, wrasses), cool temperate Oregonian families (rockfishes, surfperches, greenlings, sculpins), and cool temperate San Diegan species such as kelp rockfish and black perch. From Stephens et al. (2006), used with permission.

Figure 24.8

Survivorship curves in theory and practice. (A) Three general forms of survivorship (percent surviving at the end of each year or within each age class) are found in natural populations. Because predation tends to be most heavily focused on young and small fishes, populations that display type III survivorship curves are most likely to be regulated by predation, as seen in curves B through D. (B) A grunt (Haemulidae) population in the Virgin Islands. (C) A wrasse (Labridae) population in Panama. (D) A squirrelfish (Holocentridae) population in the Virgin Islands. SL, standard length. After Hixon (1991), used with permission; fish drawings from Gilligan (1989).

Figure 24.9

The various processes that operate to determine the diversity and abundance of fishes on a coral reef. Solid arrows indicate known interactions, dashed arrows possible interactions; the broken arrow between reproductive output and planktonic larvae refers to the uncertainty that reproduction on a reef may influence the number of recruits returning to a reef. From Mapstone and Fowler (1988), used with permission.

Figure 24.10

Priority effects. The foraging behavior of species that settle into an area determine the success of later arrivals. In the Barbados Marine Reserve, adult grunts (dark bars) were much more abundant inside the reserve than in adjacent, non-reserve areas, but recently settled grunts (open bars) were more abundant in adjacent than in reserve habitat. Juveniles (crosshatched bars) were equally abundant inside and outside the reserve. Lack of recruits in the reserve was thought to be the result of predation on settling larvae by resident adult grunts. Data from Tupper and Juanes (1999); grunt drawing from Gilligan (1989).

Figure 25.1

The distribution of prey fishes in shallow streams reflects the risk of predation from various sources. Piscivorous fishes, which are gape-limited, present the greatest threat in deeper water. Wading birds, which can dismember prey and are therefore not gape-limited, present the greatest threat in shallow water. Small prey fishes are safest in shallow water because they can hide from birds among structure, whereas larger prey fishes cannot fit into small spaces. However, larger prey are safer in deeper water because many predators cannot swallow them whole. Adapted from Power (1987).

Figure 25.2

Growth of the predatory dinoflagellate, *Pfiesteria piscicida*, relative to nutrient conditions. Water samples from North Carolina show the dramatic increase in *Pfiesteria* zoospores within 100 m of wastewater discharge sites, where phosphorus and nitrogen compound concentrations exceeded 100 ppb. Left inset, a *Pfiesteria* zoospore. Right inset, deep focal lesions on Menhaden taken from a *Pfiesteria*-induced fish kill, Pamlico estuary, North Carolina. From Helfman (2007), after Burkholder and Glasgow (1997), used with permission; insets courtesy of North Carolina State University Center for Applied Aquatic Ecology, www.waterquality.ncsu.edu.

Figure 25.3

Relative numbers and types of herbivores as a function of latitude. More species and types of herbivores inhabit coral reefs than occur at higher latitudes, although browsing prevails at higher latitudes. Values shown are based on southern hemisphere comparisons, particularly Australia and New Zealand. However, the same or ecologically similar groups and numerical trends hold for northern hemisphere assemblages, e.g., sea chubs have temperate representatives in California (Halfmoon, Opaleye) and pricklebacks are functionally similar to aplodactylids. Exceptions may include the temperate east coasts of North America and southern Africa, which have relatively more browsers among the porgies (e.g., Hay 1986). Redrawn from Choat (1991), used with permission.

Figure 25.4

Food webs involving ciguatera fish poisoning in a reef community. Top predators, including humans, are affected because a single meal can contain significant amounts of a highly potent neurotoxin. *Gambierdiscus toxicus* is the dinoflagellate implicated in most ciguatera poisonings. CTX, ciguatera toxin; ppb, parts per billion. From Helfman (2007), after Lewis 2001; inset photo courtesy of the Florida Marine Research Institute, www.floridamarine.org.

Figure 25.5

Damselfish territoriality leads to high algal species diversity. The diversity of algal species was measured over 1 year outside territories where roving herbivores were abundant, inside cages that excluded damselfish and other herbivores, and inside damselfish territories. Diversity remained low outside of cages and territories. Inside cages, diversity first increased then decreased as a red algal species became dominant. Inside territories, diversity was highest after 1 year because damselfish excluded roving herbivores that often stripped surfaces bare, while feeding by damselfish controlled the competitively dominant algal species. After Hixon and Brostoff (1983); damselfish drawing from Gilligan (1989).

Figure 25.6

Algal productivity increases in relation to density of invertebrate feeding fishes. The relationship between primary productivity and fish density is shown for experimental streams in which Red Shiner density was manipulated. Productivity increased in direct proportion to the number of minnows present. After Gido and Matthews (2001); Shiner drawing from Texas Parks and Wildlife Department, ww.tpwd.state.tx.us.

Figure 25.7

Effects of fish predation on zooplankton assemblage structure. (A) Before predators were introduced. (B) When Blueback Herring were introduced into a small Connecticut lake, size-selective predation by the fish caused the average size of zooplankters to decline. Predation favored smaller individuals within species as well as smaller species. After Brooks and Dodson (1965) and Bigelow and Schroeder (1953b).

Figure 25.8

Ecosystem level implications of overfishing on coral reefs. Overfishing frequently leads to dominance of invertebrates and algae via a series of interrelated pathways. (A) Unfished or lightly fished reefs house a diversity of fishes in several trophic guilds, as well as abundant coral cover. (B) The removal of large piscivores results in the elimination of fishes that feed both on sea urchins and on invertebrates that feed on corals. Herbivorous and coral-eating invertebrates proliferate, which leads to overconsumption of corals or permits algae to overgrow coral. In either situation, overall fish diversity declines because of strong direct and indirect dependence of many fish taxa on live coral cover. Darkness of

lettering denotes changes in relative abundance of trophic or taxonomic group. From Helfman (2007), used with permission.

Figure 25.9

A pictorial summary of ecosystem services provided by fishes to humans and other organisms. Services can be classified as: *regulating* populations and processes (e.g., trophic cascades that regulate population dynamics or nutrient cycling, bioturbation of sediments, carbon exchange); *linking* different parts of the ecosystem via transport of nutrients and energy (e.g., open water to benthos, littoral zone, birds, and terrestrial mammals); *informing* (e.g., indicating and recording past and present ecosystem integrity); and *cultural* (e.g., human interactions and direct benefits via exploitation, recreation, water purification, disease abatement, and aquaculture). After Holmlund and Hammer (1999), used with permission; see www.maweb.org for alternative terminology.

Figure 25.10

Trophic cascades. (A) The various components of a trophic cascade as postulated for a lake or pond over a growing season. Solid lines represent changes in biomass or density resulting from a strong year class or the experimental addition of piscivores; dashed lines show the effects of winterkill or overfishing of piscivores. In North America, piscivores would include salmonids, Pike, black basses, and Walleye; vertebrate planktivores would include herrings, minnows, whitefishes, Bluegill, and Perch; invertebrate planktivores would be copepods and many insect larvae; and most herbivores are crustacean zooplankton. (B) An actual trophic cascade. This is the one producing the outcome in the Eel River, California, depicted in Fig. 25.11. See text for explanation. (A) from Carpenter et al. (1985), used with permission; (B) after Allan and Castillo (2007).

Figure 25.11

Trophic cascades in rivers mediated by fish. (A) During early summertime low flow conditions, filamentous algae develop long turfs on cobble bottoms. (B) By late summer, midges have consumed most of the algae and woven the remainder into small tufts. These midges are eaten by invertebrates and fish fry, which are in turn consumed by larger fish. When large fish are excluded, predators on the midges abound, the midges decline in numbers, and the algae reach abundances more like (A) than (B). Hence algal abundance is determined indirectly by the activities of large predatory fishes. From Power (1990), used with permission.

Figure 25.12

Disruptions of large-scale, oceanic trophic cascades can result in major shifts among interacting species. (A) Landings and abundance index for principal groundfishes and flounders off the northeastern USA. (B) Landings and abundance index for skates and Spiny Dogfish, showing increases in these less desirable species while groundfish declined. From Helfman (2007), after Anderson et al. (1999); fish illustrations after Bigelow and Schroeder (1953b).

Figure 25.13

The relationship between parrotfish grazing and algal growth in a coral reef protected area, Exuma Cays Land and Sea Park, Bahamas. Left-hand bars show grazing intensity of parrotfishes and right-hand bars show percent cover of macroalgae inside (darkened bars) and outside (open bars) the reserve. Grazing was more intense and algal cover less inside the reserve. Redrawn from Mumby et al. (2006); parrotfish photo by G. Helfman.

Figure 25.14

A trophic cascade with unexpected results. Extensive gill-netting of large sharks in the Natal region of South Africa removed large sharks, such as the Bull Shark, *Carcharhinus leucas*, a predator on humans. Primary prey of large sharks, such as juvenile Dusky Sharks, *C. obscurus*, increased in numbers. Abundant small sharks consumed sportfishes (e.g., Bluefish, *Pomatomus saltatrix*). (+) increasing population; (−) declining population. Based on data in Van der Elst (1979); drawings after Bigelow and Schroeder (1948b, 1953a).

Figure 25.15

Salmon-derived nutrients and food webs based on anadromous fishes. The Pacific salmon ecosystem includes oceanic, estuarine, riverine, and old-growth forest components. Aquatic and terrestrial habitats are linked via predators and scavengers that feed on different life history stages. Inset: a decomposing Sockeye Salmon carcass. After Willson et al. (1998).

Figure 25.16

Food webs involving fishes. (A) A relatively simple food web in a temperate North American lake involving humans, predatory fishes (Pike, Walleye), planktivorous fishes (Cisco, Yellow Perch), invertebrate plankton, and algae. The thickness of lines reflects the importance of a food item in a species' diet. (B) A small, lowland forest stream in Costa Rica. (C) A swamp creek in Venezuela. Each numbered point in the webs represents a fish species or a prey taxon eaten by fishes. The base of the food webs is at the bottom and includes detritus, plants, and plant parts. Intermediate levels in the webs represent primary consumers (herbivorous fishes and invertebrates), with predatory fishes at the top. Eleven fish species are involved in food web B and 51 species in web C. (A) after Rudstam et al. (1992); (B, C) from Winemiller (1990b), used with permission.

Figure 25.17

(A) Bite marks on a Pacific coral head from parrotfish grazing. (B) A model depicting the processing of coral fragments into sand as they pass through the mouth, pharyngeal mill, and gut of a parrotfish. Photos by G. Helfman.

Figure VI *(opposite)*

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

Figure 26.1

Extinction rates and causes. (A) Fish extinctions in North America. Extinctions grew steadily over the past century until the latter part, when they apparently slowed down, possibly indicating improved conditions or early elimination of more sensitive forms. Illustrated left to right are the Harelip Sucker (extinguished *c.* 1900), Alvord Cutthroat

Trout (*c.* 1930s or 1940s), and San Marcos Gambusia (*c.* 1980). (B) Major causes of fish extinctions globally. Habitat alteration, introduced species, overfishing, and pollution are the primary agents, but combined factors cause the most extinctions, which is why the summed percentages of all columns exceed 100%. (A) from Helfman (2007), after Stiassny (1999); sucker drawing by J. Tomelleri, trout and gambusia by Sara V. Fink, used with permission of the artists; (B) from Helfman (2007), based on Harrison and Stiassny (1999).

Figure 26.2

Impacts of bottom trawling on gravel (A) and mud (B) habitats, Stellwagen Bank National Marine Sanctuary, Gulf of Maine. Gravel habitats protected from trawling (A1) contain erect sponges; areas open to trawling (A2) lack such biogenic structure (a Longhorn Sculpin, *Myoxocephalus octodecemspinosus*, is visible in the center of photo A2). Mud habitats also contain biological structure such as burrowing anemones (B1), whereas trawled areas (B2) can be devoid of such structure (note trawl gear tracks in B2). Photos courtesy of P. J. Auster, National Undersea Research Center, University of Connecticut.

Figure 26.3

Endangered fishes of the upper Colorado River. Prior to impoundment, the Colorado River experienced exceptionally high flows, >9000 m³/s during winter and spring floods, which redistributed sediments critical to spawning and larval rearing. Several Endangererd Colorado River endemics evolved reproductive habits attuned to this flood cycle. Large native Colorado River species also show marked convergent morphologies, having long, tapered bodies with elongate caudal peduncles, small depressed skulls with predorsal humps or keels, winglike fins that have hardened leading edges, and tiny or absent scales. Humps have been interpreted as providing a hydrodynamic advantage or as a response to gape-limited native predators such as Colorado Pikeminnows. Four of the large, Endangered cypriniforms of the Colorado exemplify these traits: (A) Razorback Sucker (*Xyrauchen texanus*); (B) Bonytail chub (*Gila elegans*); (C) Colorado Pikeminnow (*Ptychocheilus lucius*) and (D) Humpback Chub (*G. cypha*). After Portz and Tyus (2004), used with permission.

Figure 26.4

Commercial catches of Chinook Salmon and Steelhead Trout in the Columbia River over the past century. Soon after commercial exploitation began, catches rose to sustained levels of 20,000 tons annually. After dam construction, catches declined regularly and have been as low as 550 tons. After Williams (2006); inset photo courtesy R. Carlson.

Figure 26.5

Effects of suspended sediments on young fishes. Threatened Spotfin Chub, *Erimonax monachus*, were raised at various sediment concentrations to study the effects on gill morphology and growth. (A) Gill arches and filaments of a young Spotfin Chub reared for 21 days at low (0 mg/L) sediment concentrations. (B) Gills from a similarly aged chub reared at high (500 mg/L) sediment concentrations; note the thickening and fusion of filaments and clogging with mucus. (C) Growth rates of young Spotfin Chub relative to sediment concentration, showing decreased growth at higher sediment loads. The growth rate at the highest sediment level was 1/15th that in clean water. High sediment concentrations tested (500 and 100 mg/L) occur regularly in the wild due to watershed development. Bars with the same lower case letter are not significantly different. From Helfman (2007), after Sutherland (2005), used with permission; chub drawing by A. Sutherland.

Figure 26.6

Natives as well as aliens are involved in faunal homogenization. The progressive changes expected in southern Appalachian streams are depicted, showing how habitat disruption (deforestation, siltation) first favors native generalists over endemic specialists. As habitat disruption continues, even these native invaders are replaced by highly tolerant aliens. From Scott and Helfman (2001), used with permission.

Figure 26.7

Effects of Nile Perch introduction on the food web of Lake Victoria. (A) The food web prior to the introduction of *Lates*. The top predators included piscivorous catfishes and haplochromine cichlids which fed on a variety of prey (including characins, cyprinids, mormyrids, catfishes, haplochromine and tilapiine cichlids, and lungfishes), which in turn fed on a variety of invertebrate prey and algae. (B) The food web after *Lates* eliminated most other fish species. *Lates* feeds on juvenile *Lates*, a cyprinid (*Rastrineobola*), and an introduced tilapiine cichlid. Inset: a large Nile Perch. (A, B) from Ligtvoet and Witte (1991), used with permission; inset photo courtesy of L. and C. Chapman.

Figure 26.8

Experimental evidence of competitive displacement of a native by an introduced species. Sacramento Perch, an imperiled native sunfish of California, alone in aquaria (dark bars) grew more in mass and showed a trend toward greater length increase than when kept with introduced Bluegill Sunfish (shaded bars). After Marchetti (1999); fish drawing by A. Marciochi, in Moyle (2002), used with permission.

Fig. 26.9

Sentiment expressed on a bumper sticker, Burlington, Washington. Photo by G. Helfman.

Figure 26.10

Trends of landings among North Atlantic groundfishes. Most major groundfish fisheries experienced rapid or continual population declines after an upsurge in fishing in the 1960s to 1970s. Species entered the 21st century at or close to all-time low levels. From Sinclair and Murawski (1999), used with permission.

Figure 26.11

Status of the world's fisheries stocks. (A) Most stocks are fully or overexploited, leaving little room for more fishing. Most underexploited stocks occur in the Indian Ocean. Recovering (R), depleted (D), overexploited (O), fully exploited (F), moderately exploited (M), and underexploited (U). (B) Status relative to the relationship between stock biomass and fishing mortality for different exploitation levels. Stocks fished most heavily have been driven to the lowest levels of biomass, which reduces their ability to recover. (A) from Helfman (2007), data from FAO (2000a); (B) from Helfman (2007), redrawn from Botsford et al. (1997).

Figure 26.12

(A) The Gulf of California and a reconstruction of the presumed seasonal migration route of the endangered Totoaba, the world's largest sciaenid: SA, pre-spawning adults; PA, post-spawning adults; FA, adults during fall migration. Numbers indicate life history zones: 1, spring spawning zone and nursery ground of juveniles; 2, summer feeding zone; 3, fall feeding zone. Zone 1 is now largely a biosphere reserve. (B) The relationship between water delivery from the Colorado River and Totoaba population size as calculated from commercial catches. From Cisneros-Mata et al. (1995), used with permission of Blackwell Science; inset Totoaba drawing from Universidad Autonoma de Baja

Figure 26.13

Evolution of body shape in exploited whitefish. Lake Whitefish in Lesser Slave Lake became skinnier over time as a result of gill netting; fat fish were more likely to be captured. Data plotted are condition factors, k ($k = 10^5$ weight/length^3), for male whitefish, 1940–75; females showed similar patterns but were not used because of weight changes caused by egg-bearing. From Helfman (2007), after Handford et al. (1977).

Figure 26.14

Fishing down food webs. Over the past half century, most of the world's marine and freshwater fisheries have been taking species progressively lower in food webs. The mean annual trophic levels of marine fisheries landings are calculated as total landings times the fractional trophic level of species groups (primary producers and detritus = 1, top predators = 4; species that feed at more than one level are assigned fractional values). The decline in trophic levels in the 1960s represents extremely large catches of planktivorous Peruvian Anchoveta, a fishery that collapsed in the early 1970s. A parallel trend exists in freshwater fisheries; the plateau region between 1950 and 1975 probably reflects incomplete information. From Helfman (2007), redrawn from Pauly et al. (1998).

Figure 26.15

Impacts of aquarium collecting on reef fishes, Kona Coast, Hawaii. Underwater surveys at two areas showed significant declines among targeted species at collection locales compared to control sites protected from collecting. Data are given for three aquarium species: Achilles Tang (Pakuikui, *Acanthurus achilles*), Multiband Butterflyfish (Kikakapu, *Chaetodon multicinctus*), and Moorish Idol (Kihikihi, *Zanclus cornutus*). From Tissot and Hallacher (2003), used with permission; line drawings by Helen Randall and Loreen Bauman, from Randall (1981), used with permission.

Figure 26.16

Functions of marine protected areas from a fisheries management perspective. Inside the reserve, the numbers, size, and age of residents increase in response to reduced fishing pressure. This leads to increased reproduction and net export of both adults and larvae into adjacent regions. Diversity can also increase. After Russ (2002).