Fish Ecology

K. O. Winemiller
Texas A&M University

Fish ecology is the study of fishes and their interactions with the physical and living components of their environments. Because fishes are the oldest and most species-rich lineage of living vertebrates, a particularly diverse variety of adaptations and ecological relationships are observed among different species and even among different populations within some species. Fishes are found in a great diversity of habitats, including temporary ponds in arid environments, subterranean waters, mountain streams, lakes, rivers, estuaries, coral reefs, pelagic ocean waters, and oceanic abysses. On a global basis, the greatest number of living fishes occupy marine environments, but the highest species densities (number of species per unit area) tend to occur in fresh waters. These differences in species densities may be related to greater habitat complexity and opportunities for geographical isolation of populations in freshwater ecosystems. Aquatic and estuarine habitats are very sensitive to pollution and human-induced landscape alterations, and as a result the abundance and diversity of fishes have declined in many regions of the world. Despite increased fishing effort and advances in the technology of fishing, the collective annual catch of the world's major marine fisheries has leveled off over the past two decades.

I. INTRODUCTION

Water covers over 70% of the earth's surface, so it is perhaps not surprising that fishes are the most abundant and speciose group of living vertebrates (estimates of the number of living species range between 20,000 and 30,000). Fishes occupy aquatic habitats ranging in elevation from mountain lakes and streams, approximately 5 km above sea level, to deep ocean trenches 11 km below sea level. Fishes are also the oldest vertebrate lineage; the first agnathan fishes originated some 500 million years ago. The long evolutionary history of fishes, coupled with the large quantity and diversity of aquatic and marine habitats, has resulted in tremendous variation in the ecological characteristics of modern species of fishes. This article reviews the relationship between fishes and the living and nonliving components of their environments. Because it is impossible to survey the full range of ecological characteristics of such a large and diverse group of organisms, select species and habitats will be used to illustrate major similarities and differences among taxa and ecological settings.

Fish ecology is greatly influenced by the physical properties of water: density, heat capacity, viscosity, and miscibility as a solvent. Because water is more than 750 times denser than air, fishes need not invest great amounts of matter and energy into the development and maintenance of a massive skeleton to support the body. Most fishes possess a gas-filled swim bladder that allows them to maintain neutral buoyancy over a range of water depths with low energetic cost. A number of benthic fishes that lack functional swim bladders [e.g., sculpins (Cottidae), many darters (Percidae), and gobies (Gobiidae)] use fin movements and body undulations to rise above the substrate. These forays into the water column require large energy expenditures, and as a result they tend to be of short duration, as when feeding or changing locations on the substrate. The high density of water also causes sound to be transmitted much more efficiently than through air. Sound attenuates slowly in water, so that sonic signals can be transmitted over very long distances. Fishes perceive sound with the inner ear and the acousto-lateralis system. The acousto-lateralis system consists of pressure receptors housed in tubes embedded in scales of the head and body flanks. In minnows and suckers (Cypriniformes), tetras (Characiformes), and catfishes (Siluriformes), a chain of small bones, called the Weberian ossicles, transmits sound pressure from the swim bladder to the inner ear. Sound pressure first received by the body wall is transmitted to the swim bladder, which functions as an ear drum. Sounds are produced for intraspecific communication by many minnows and catfishes, plus a variety of fishes from families lacking Weberian ossicles.

Water achieves its maximum density at 4°C and can stratify over relatively shallow depth gradients. Nearly all fishes are ectothermic and can exploit temperature gradients to locate their thermal optima or to increase their efficiency of energy utilization. By reducing vertical or horizontal mixing of water, thermal and density gradients also affect nutrient dynamics and ecosystem productivity. In cold climates, lakes may experience vertical mixing (turnover) when they become isothermal during the spring and fall. This vertical mixing can release nutrients locked in deeper waters into the light penetration layer (epilimnion), where photosynthesis takes place. Blooms of phytoplankton production often follow these seasonal lake turnovers.

Light attenuation occurs much more rapidly in water than in air. Long wavelengths are the first to be absorbed (within the first 25 m), so that objects viewed at great depths appear blue due to reflectance of shorter light wavelengths. Fishes are assumed to have color vision, especially those diurnal species that have flashy species-specific or sex-specific color patterns. The retinal cone receptors have been investigated in several fish species, such as the walleye (*Stizostedion vitreum*) and goldfish (*Carassius auratus*). Many fishes have countershading, darker pigmentation in the dorsal region fading to a light-colored ventral surface. With illumination from above, countershading results in uniform reflectance that masks the normal shading cues that reveal object depth. Countershading is a particularly important adaptation for concealment in pelagic fishes.

Water has a high specific heat, meaning that it must receive or lose more energy than air or rock to change the same number of degrees. Therefore, aquatic and marine habitats are more thermally buffered against sudden climatic changes than adjacent terrestrial environments. Because of its higher density, water also conducts heat more rapidly than air. Fishes are ectotherms, and the time lag between a change in ambient temperature and subsequent change in body temperature is very short.

Because water is more viscous than air, fishes can propel themselves by swimming. Drag influences the energetics of alternative methods of locomotion, with a fusiform body producing less drag than stout or compressed body shapes. Water's high viscosity enhances the efficiency of suction feeding and, to a lesser extent, hinders grasping. Water's high density and viscosity facilitate passive dispersal of buoyant gametes, larvae, and even some adult fishes. The high viscosity of water also affects the architecture of aquatic and marine landscapes via sediment erosion, transport, and substrate scouring.

Water has been called the universal solvent, because it dissolves a great variety of chemical substances, including gases, salts, acids, bases, nutrients (nitrates, phosphates), and biological waste compounds (carbon dioxide, ammonia). Because of the solvency of nutrients in water, the dynamics of nutrient cycling and primary production tend to be faster in aquatic ecosystems compared with terrestrial systems. Partial pressures and diffusion rates of oxygen and carbon dioxide are lower for water than for air. Even so, high CO_2 concentrations can cause severe physiological stress or death in many fishes. Acute or chronic hypoxia (low concentrations of dissolved oxygen) can pose a serious problem for fishes in swamp, lake, and estuarine habitats. Fishes from these habitats have evolved a wide variety of respiratory adaptations, including aerial respiration with lungs (lungfishes), swim bladder (loricariid and clariid catfishes), gut (callichthyid catfishes), skin (some blennies and anguillid eels), gill chamber (synbranchid eels), and suprabranchial chambers (snakeheads and anabantids). During periods of acute hypoxia, many freshwater fishes rise to the surface and skim the oxygen-rich surface film (aquatic surface respiration). The electrical conductivity of water permits several groups of fishes (African mormyriforms, neotropical gymnotiforms) to utilize electrogeneration and reception for navigation, prey detection, and communication. At least three groups of fishes (torpedinid rays, electrophorid eels, and malapterurid catfish) have evolved the ability to produce electrical shocks as mechanisms for subduing prey and for defense.

II. EVOLUTION OF FISHES

A. Phylogenetic Diversity

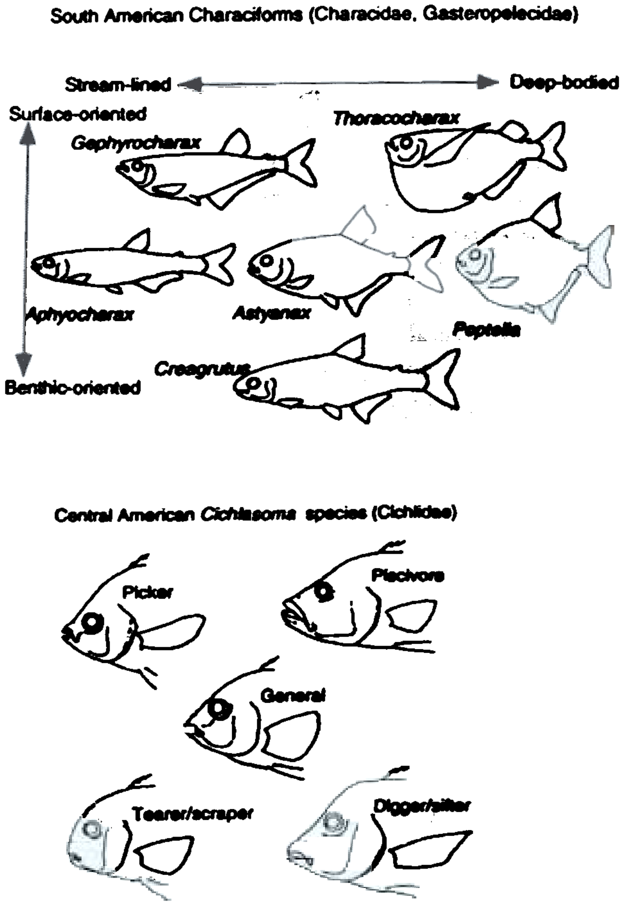
Fishes belong to the phylum Chordata and are derived from a common ancestor with the protochordates (acorn worms, sea squirts). The three groups of living fishes are the Agnatha (jawless cartilaginous fishes), the Chondrichthyes (jawed cartilaginous fishes), and Osteichthyes (bony fishes). Agnatha has by far the fewest living taxa: about 50 species of hagfishes and lampreys of the classes Pteraspidomorphi and Cephalaspidomorphi. The class Chondrichthyes contains about 800 living species of sharks, skates, rays, and chimaeras. The vast majority of Chondrichthyes are restricted to marine habitats, although some species, such as bull sharks (*Carcharinus leucus*) and sawfishes (*Pristis*), regularly enter freshwater habitats where they may reside for extended periods. All the tetrapod vertebrates (amphibians, reptiles, birds, mammals) are derived from a primitive lineage within the Osteichthyes. If all the known undescribed species and estimated undiscovered species were tallied, the total number of bony fishes might be well over 25,000. Of the many dozens of new fish species described each year, the vast majority come from tropical latitudes, especially from freshwater habitats.

Bony fishes inhabit an incredibly wide range of aquatic habitats, including marginal aquatic habitats like thermal springs (North American killifishes of the genus *Cyprinodon*, African cichlids of the genus *Sarotherodon*), underground waters [cavefishes (Amblyopsidae), North American catfish genera *Satan* and *Trogloglanis* (Ictaluridae)], torrential mountain streams [Asian loaches (Cobitidae), South American hillstream catfishes (Astroblepidae)], ephemeral savanna pools [African and South American killifishes (Rivuliidae), lungfishes (Ceratodontidae, Lepidosirenidae)], and tidal mudflats [mudskippers (Periophthalmidae)]. Except for a few special cases, the generation of new fish species (speciation) is believed to have occurred by way of geographical isolation and genetic divergence of populations (allopatric speciation). Freshwater habitats provide numerous opportunities for geographical isolation of populations, and on a global basis the density of fish species in fresh water is much greater than in marine habitats. About 40% of all fishes live in fresh water, which comprises less than 0.01% of the earth's total volume of surface water. Populations can be split into isolated subunits when river drainages are divided by geological and climatic changes, river captures (anastomoses), confinement in separate lake basins, or formation of habitats hostile to dispersal between separate river drainage basins. Species flocks occur in a number of lake basins (cyprinodontids in Lake Titicaca, Peru; atherinids in central Mexico; salmonids in the North American Great Lakes; cichlids in the African Rift Lakes). Evolutionary biologists debate the potential mechanisms of sympatric speciation for generating these species flocks, especially the African cichlids. Most evidence seems to support a hypothesis of allopatric speciation within isolated or partially isolated lake subbasins, or within preferred habitats separated by shoreline regions containing hostile habitat. Geographical isolation of marine populations occurs by a variety of geographical and climatic changes, including formation of isthmuses and islands, tectonic movements of landmasses, zones of freshwater intrusion, and a host of oceanic currents that influence patterns of dispersal.

B. Ecological Diversity

Regions at higher latitudes generally contain fewer fish species than tropical areas, and this pattern holds for both marine and freshwater ecosystems. Likewise, fish diversity tends to be lower at higher altitudes compared with lowland areas in the same biogeographic region. A variety of historical, climatic, and ecological factors interact to produce these gradients of fish species diversity. The basic mechanisms influencing fish biodiversity probably do not differ significantly from models proposed for terrestrial vertebrates. Compared with the tropics, regions at high latitudes and altitudes suffered more species extinctions during glacial epochs, experience more frequent and more severe climatic changes over evolutionary time scales, and generally experience greater habitat changes with season. Consequently, coevolution, ecological specialization, and adaptive radiations are much more apparent in tropical freshwater fish communities than in arctic or temperate communities. Research has documented more morphological variation and ecological strategies in tropical fish assemblages relative to fish assemblages in comparable physical habitats at higher latitudes. For example, arctic and temperate freshwater fish assemblages are dominated by invertebrate-eating and fish-eating fishes, whereas tropical fishes in the same kinds of habitats contain a number of specialized invertebrate- and fish-eating fishes, plus fishes that specialize on algae, detritus, wood, macrophytes, seeds, fruit, fish fins, fish scales, and the external mucus slime layer of other fishes.

Fishes have proven to be a particularly good group for the study of the relationship between functional morphology and ecology (ecomorphology). Body form and the sizes, shapes, and positions of fins determine swimming performance in fishes (Fig. 1). The bodies of benthic fishes tend to be cylindrical or stocky with a flattened belly region, or their bodies are entirely depressed in the dorsoventral plane, as in skates, rays, and many catfishes. Soles, flounders, and other flatfishes are compressed in the lateral


South American Characiforms (Characidae, Gasteropelecidae)

Central American *Cichlasoma* species (Cichlidae)

FIGURE 1 Ecological and morphological diversification of body form and swimming performance in South American characiform fishes (above) and head form and feeding in Central American cichlid fishes (below). (With permission from the National Geographic Society and Kluwer Academic Publishers.)

plane and rest on their sides on the substrate. Midwater fishes that are compressed in the lateral plane can maneuver well in three dimensions. A laterally compressed body and broad fins permit greater stability in water, which is important for fishes that suction feed on small food items in the water column or glean prey from surfaces. North American sunfishes (*Lepomis*), many tropical cichlids, and coral reef damselfishes and surgeonfishes illustrate this ecomorphological strategy. These deep-bodied fishes achieve slow but stable locomotion by sculling their broad pectoral fins. They can also perform rapid swimming by folding their broad fins close to the body (reducing drag) and using undulatory propulsion by laterally flexing the body and caudal (tail) fin.

Tunas, mackerels, salmon, and other fishes that rely on rapid and sustained swimming generally possess fusiform bodies with relatively narrow dorsal and ventral fins. The more elongate, fusiform body reduces drag in these strong swimmers. Drag is further reduced by a narrow caudal peduncle (region between the body and the caudal fin) and a caudal fin that is tall and forked to some degree (high aspect ratio). Pike, barracuda, and other fishes that rely on stealth and a rapid swimming burst to capture prey often have very elongate bodies and medial fins positioned posteriorly. These fishes can accelerate rapidly by bending the body in an s-shape, then shooting off like an uncoiling spring. These burst predators perform sustained swimming by the normal undulating mechanism of lateral flexion of the body and tail. Eels have extremely elongate bodies and reduced fins that permit swimming or burrowing by undulatory locomotion (lateral body flexion). The elongate eel-like morphology has evolved independently in a number of taxa, including anadromous eels, moray eels, and snipe eels (Anguilliformes), neotropical knife fishes (Gymnotiformes), paleotropical spiny eels (Mastacembelidae), and swamp eels (Synbranchidae).

Much can be determined about a fish's feeding behavior by examining its jaw morphology (Fig. 1). Predatory fishes generally have large mouths armed with jaw teeth for grasping, piercing, or cutting the flesh of prey. Some piscivores (fish eaters), like sculpins (Cottidae) and scorpion fishes (Scorpaenidae), use suction feeding rather than grasping. Others, like the tarpon (*Megalops*), use an engulfing mode of prey capture in which the predator passes over its prey with jaws and gill covers (opercula) flared. Some large-mouthed plankton feeders, such as paddlefish (*Polyodon spathula*) and whale sharks (*Rhincodon typus*), use this engulfing feeding mode, but in this case small food items are strained from the water passing through the gill openings using comblike gill rakers. In modern bony fishes like the North American crappie (*Pomoxis*), the Central American cichlid (*Petenia*), the tarpon snook (*Centropomus pectinatus*), and the African thin-face cichlid (*Serranochromis angusticeps*), suction feeding is enhanced by highly protrusible jaws. During jaw protrusion, the premaxillary and maxillary bones of the upper jaw swing forward as the mouth opens and, with the mandible, form a tubular gape. Fishes that primarily use biting or grasping often have less protrusible jaws, and some, like piranhas (*Pygocentrus*) and barracudas (*Sphyraena*), lack significant protrusibility altogether.

Depending on the ecological setting, piscivores that feed on a wide variety of prey often can adopt either grasping, sucking, or biting prey capture modes. North American bass (*Micropterus*) and marine groupers (*Epinephelus*) feed on a wide variety of invertebrate and fish prey using all three feeding modes. Many small-mouthed invertebrate-feeding fishes use a picking (biting) mode to glean insects and small crustaceans from the substrate or vegetation. The same species may also use suction feeding to capture small food items from the water column or to glean surfaces. The jaw elements of sea horses, pipefishes, and trumpet fishes are fused to form a long tubular snout used for suction feeding. In habitats with soft bottom sediments, some fish forage by grabbing a mouthful of sediment and sifting immature aquatic insects from the sediments with their gill rakers or pharyngeal teeth (the latter located on the throat region). These digger/sifters, like "earth-eating" cichlids (*Geophagus, Satanoperca*) and marine mojarras (*Diapterus, Eucinostomus*), usually have long snouts or highly protrusible jaws to reach deep into soft sediments. Cypriniform fishes lack jaw teeth and manipulate prey primarily with their pharyngeal teeth prior to ingestion. Fishes that feed on hard-bodied prey, like corals and molluscs, usually have massive flattened pharyngeal teeth used for crushing.

Herbivorous and detritivorous fishes generally have relatively compact jaws for grasping and tearing plant material. Seed- and fruit-eating fishes usually have multicuspid teeth for tearing and crushing. The relationship between powerful compact jaws, multicuspid teeth, and a frugivorous diet is well illustrated by a large number of neotropical characids, including species of the genera *Astyanax*, *Brycon*, and *Colossoma*. Grazers have flat unicuspid or bicuspid teeth used for scraping algae from the surfaces of rocks, wood, or vegetation. Great diversity in tooth morphology is often observed among sympatric grazers, and different tooth morphologies seem to select for different algae taxa in their diets. Herbivorous and detritivorous fishes usually have long, coiled alimentary canals, and detritivores sometimes have crop and gizzard stomach chambers and pyloric ceca. The muscular gizzard contains sand particles ingested along with detritus that aid the mechanical breakdown of plant cell walls. A long gut and pyloric ceca provide more surface area for digestion of tough plant tissues and absorption of nutrients. Some herbivorous and detritivorous species, like the wood-eating South American catfishes (*Panaque*), have coevolved gut faunas (microbial organisms) that aid the digestion of plant tissues.

III. PHYSIOLOGICAL ECOLOGY OF FISHES

Growth in fishes has been called indeterminate because they exhibit some growth even after attainment of sexual maturation, even though the rate of growth usually declines with size and age. As in any organism, a fish's growth potential is determined genetically, and its realized growth is derived from the interaction between genes and environment (temperature, salinity, food quality and quantity). Fisheries ecologists frequently employ the von Bertalanffy curve to describe growth rates in the following manner:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_t is length at age t, L_∞ is the asymptotic length, t_0 is the hypothetical time when length is zero, and K is the rate of approach to L_∞. Some piscivorous fishes show an accelerated growth rate during the juvenile stage that coincides with an ontogenetic shift from invertebrates to larger, more energy-rich fish prey. Because fishes are ectotherms, each individual has an optimal temperature for food assimilation and growth. The biotic environment can also affect growth, with crowding reducing growth via exploitation competition for limited food or via interference competition for limited space. The relationship between fish weight (W) and length (L) can be described by the equation $W = aL^b$, where a and b are constants. If growth is isometric, with no change in shape with change in size, then b is approximately 3.0. The relationship between fish length and fish size has been used as an index of condition of plumpness in fisheries management. Species-specific standards that describe average or good condition have been derived empirically by regression methods. Fish condition can be influenced by foraging rate, environmental stress, reproductive state, and habitat characteristics.

Fishes can be aged by a variety of methods, all of which involve counting concentric bands that are deposited on hard structures during their growth process. Spines, scales, and otoliths (mineral grains in the inner ear) grow radially at different rates depending on seasonal ecological conditions, maturation, or reproduction. Minerals are deposited as daily layers (circuli) that appear as rings in cross section. During periods of rapid growth, the layers are thicker and the more opaque boundaries between layers are spaced farther apart. During periods of slow growth, as in winter or spawning seasons, the daily rings are tightly compacted and appear as bands. The bands on scales, spines, and otoliths correspond to annual age increments (annuli) in most temperate-zone fishes and many tropical fishes from seasonal habitats. In young fishes, otolith circuli often can be counted under a microscope to estimate their age in days.

Freshwater fishes are hypertonic to their aquatic environment, and marine fishes are hypotonic to marine waters that typically range between 32 and 35 ppt (parts per thousand) solute concentration. Because the epithelia of the skin, mouth, and gills of fishes are permeable to ions and water molecules, freshwater fishes' ions tend to diffuse out and water tends to diffuse into their bodies. Likewise, ions passively diffuse into the body and water diffuses out of the bodies of marine fishes. Freshwater fishes use their kidneys to eliminate excess water in dilute urine and gain lost salts in their diets and by active ion transport in branchial cells of the gill membranes. Marine fishes produce concentrated urine and eliminate as little as 3 ml of urine per kilogram of body weight per day. Up to 90% of nitrogenous wastes may be eliminated through the gills of marine fishes. Cartilaginous fishes in marine habitats have elevated levels of urea in their body fluids, which reduces the diffusion gradient of water. Most fish species live out their entire lives in habitats that experience little variation in salinity. These species are generally stressed by salinity changes of only a few ppt and are intolerant of changes greater than 15–20 ppt. Salmon (*Oncorhynchus*, *Salmo*), American shad (*Alosa*), striped bass (*Morone*), American eels (*Anguilla*), and other diadromous fishes have the ability to make rapid osmotic adjustments by changing urine volumes and the uptake or secretion of ions against diffusion gradients by the gills.

Sex in most fishes is genetically or chromosomally determined, but sexual development in some species is influenced by environmental conditions. Sex ratio in the Siamese fighting fish (*Betta splendens*) is strongly influenced by temperature. A number of marine fishes and a few freshwater species exhibit sex switching with age and size or in response to their social environment. Some groupers (Serranidae) and wrasses (Labridae) mature as males and become females when they are older and larger. This protandrous strategy maximizes lifetime fitness because mating is not highly selective, and a small male can produce large quantities of sperm, but female fecundity is strongly size-dependent. Some reef-dwelling wrasses, such as the cleaner fish *Labroides dimidiatus*, mature as females and later change into males (protogyny), depending on their status in the dominance hierarchy of a social group inhabiting a territory. When the dominant male is removed, the most dominant female rapidly begins to show hormonal and behavioral changes followed by physiological and morphological changes to male characteristics.

Several all-female species (gynogenetic species) have been identified within the live-bearing poeciliid genera *Poeciliopsis* and *Poecilia*, and these appear to have orginated sympatrically via reproductive isolation from genetic mechanisms following hybridization. Some of these all-female species must mate with males of heterospecific species in order for the egg to develop into a genetic clone of its mother. In other species, male genetic material is incorporated in offspring and then subsequently lost during alternate generations, and no significant amount of the male's genetic material enters into the gene pool of the all-female species (hybridogenesis).

IV. LIFE-HISTORY VARIATION

Fishes demonstrate more variation in life-history traits than any other comparable taxonomic group (Table I). For example, clutch sizes range from 1–2 in the longfin mako (*Isurus paucus*), thresher (*Alopias*), and sandtiger sharks (*Eugomphodus taurus*) to over 6×10^8 in the ocean sunfish (*Mola mola*). Even within species, individuals may vary considerably in their sizes and ages at maturity, growth rates, fecundities, and longevities. Fishes have been grouped based on their spawning habitat and method of egg deposition, parental care, or brooding. At one end of the spectrum are nonguarding egg scatterers that usually have external fertilization and group spawning. Pelagic spawners scatter their eggs into the water column. Eggs and early larvae of pelagic egg scatters usually contain oil droplets in the yolk that enhance buoyancy. In freshwater habitats, many nonguarding species scatter their eggs over vegetation, gravel, or stones. Some nonguarding fishes hide their broods. Trout and

TABLE I

Interspecific Variation in North American Fish Life-History Traits

	Age of maturity[a] (years)	Length of maturity[a] (mm)	Longevity (years)	Clutch size[b] (N_{eggs})	Egg diameter (mm)
Freshwater Species					
Polyodon spathula (Polyodontidae)	9–10	2235	30	141,531	3.35
Lepisosteus osseus (Lepisosteidae)	6	1370	30	59,422	2.65
Dorosoma cepedianum (Clupeidae)	2	486	14	543,912	0.75
Salmo clarki (Salmonidae)	4	663	7	4,420	4.70
Salvelinus namaycush (Salmonidae)	8	1240	41	18,051	5.50
Umbra limi (Umbridae)	1–2	85	4	1,489	1.60
Esox lucius (Esocidae)	3	1296	24	226,000	2.80
Notemigonus crysoleucas (Cyprinidae)	1–2	259	9	200,000	1.25
Pimephales promelas (Cyprinidae)	1	74	2	1,136	1.30
Ictiobus bubalus (Catostomidae)	3–4	909	19	427,880	5.00
Ictalurus punctatus (Ictaluridae)	4	976	14	70,000	3.75
Amblyopsis spelaea (Amblyopsidae)	3–4	113	7	70	2.15
Lepomis macrochirus (Centrarchidae)	2	384	9	81,104	1.20
Pomoxis annularis (Centrarachidae)	2	505	8	213,000	0.89
Etheostoma spectabile (Percidae)	1	80	3	320	1.42
Stizostedion vitreum (Percidae)	5	790	14	400,000	1.75
Marine Species					
Acipenser oxyrhynchus (Acipenseridae)	20	2743	60	3,755,745	2.55
Anguilla rostrata (Anguillidae)	8	740	40	2,561,000	1.00
Alosa pseudoharengus (Clupeidae)	3–4	352	9	466,701	0.90
Anchoa mitchilli (Engraulidae)	<1	100	2	2,100	0.80
Oncorhynchus tshawytscha (Salmonidae)	4–5	1490	5	13,619	6.50
Osmerus mordax (Osmeridae)	2	310	5	69,600	0.95
Arius felis (Ariidae)	?	355	8	68	16.0
Merluccius productus (Gadidae)	4	910	11	496,000	1.12
Lycodopsis pacifica (Zoarcidae)	?	460	5	52	2.00
Gasterosteus aculeatus (Gasterosteidae)	1	102	3	150	1.70
Katsuwonus pelamis (Scombridae)	2	870	7	1,900,000	1.05
Ammodytes americanus (Ammodytidae)	2	210	9	1,313	0.83
Pomatomus saltatrix (Pomatomidae)	2	710	14	195,000	1.05
Haemulon aurolineatum (Pomadasyidae)	3	289	9	83,000	0.93
Scianops ocellatus (Scianidae)	4–5	1986	33	3,500,000	0.93
Lagodon rhomboides (Sparidae)	1	437	7	39,200	1.02
Centropristis striata (Serranidae)	1–2	550	11	1,050,000	0.95
Lutjanus campechanus (Lutjanidae)	2	906	13	9,300,000	0.82
Morone saxatilis (Percichthyidae)	4–5	1245	17	4,010,325	1.78
Microgobius gulosus (Gobiidae)		71	3	567	1.14
Sebastes caurinus (Scorpaenidae)	4	570	20	640,000	0.95
Ophiodon elongatus (Hexagrammidae)	5	1520	16	500,000	3.50
Paralichthys dentatus (Bothidae)	2	445	10	4,190,000	0.98
Pseudopleuronectes americanus (Pleuronectidae)	4–5	570	12	3,329,000	0.81

[a] Average for a population near the center of a species range.
[b] Maximum clutch size reported for a population near the center of a species range.

salmon use their caudal fins to bury their eggs in gravel (create spawning redds), and European bitterling (*Rhodeus sericeus*) deposits their eggs in the gills of unionid clams. Brood-guarding occurs in a variety of forms. Ovoviviparity (live-bearing without maternal nutritional contribution during gestation) and viviparity (live-bearing with maternal nutritional contribution during gestation) are common in a variety of fish taxa, including many sharks, skates, rays, guppies and other poeciliids

(Poeciliidae), surfperches (Embiotocidae), and the coelacanth *Latimeria chalumnae*. The coelacanth gives birth to 1–5 very large, advanced offspring that gain nutrition during gestation within the oviduct by consuming unfertilized trophic eggs and perhaps even smaller less-advanced siblings.

Male guarding of the nest and brood is perhaps the most common form of parental care in fishes. Most cichlids have biparental care, but a few species, like the dwarf cichlids (*Apistogramma*), have maternal care. External-bearing and mouth and gill chamber brooding are other forms of parental care in fishes. Males of several South American aspredinid and loricariid catfishes brood their embryos on the surface of their bellies, and male pipefishes and sea horses (Syngnathidae) carry their eggs and larvae in a belly brood pouch. Males of the Australian nursery fishes (*Kurtus*) carry their developing embryos on a hook that protrudes from their foreheads. The developing embryos hang on either side of the head in small clusters suspended by a twisted cord made from egg membranes looped through the eye of the hook. Oral brooding occurs in a number of freshwater and marine families, including the ariid catfishes (Ariidae), bony tongues (Osteoglossidae), cichlids (Cichlidae), and cardinal fishes (Apogonidae) [*See* LIFE HISTORIES.]

Life-history strategies result from trade-offs among attributes, such as clutch size and egg size, that have either direct or indirect effects on reproduction and fitness. For example, one way to achieve a larger clutch is to partition the biomass available for reproduction into smaller eggs. This functional constraint contributes to the negative correlation between clutch size and egg size frequently observed among fish species. Larger clutches can also be attained by delaying reproduction and growing to a larger body size. Comparing both within and across species, larger fishes tend to produce more eggs per batch than do smaller fishes. Yet, exceptions to this rule are common. Many fishes with parental care, like the mouth-brooding gaftopsail catfish (*Bagrus marinus*), have much smaller clutches than those of smaller species that scatter their eggs, like anchovies (*Anchoa mitchilli*) and dace (*Rhinichthys atratulus*).

Comparative life-history studies of fishes have repeatedly identified associations of large adult body size with delayed maturation, long life span, large clutches, small eggs, and few spawning bouts during a short reproductive season. Fishes with well-developed parental care tend to have larger eggs and often have longer reproductive seasons and serial spawning. Three primary life-history strategies define the end points of a continuum derived from comparisons of diverse ecological and taxonomic groupings of fishes worldwide (Fig. 2). At one end point, *periodic-strategists* have delayed maturation, mature at intermediate or large body sizes, produce large clutches of small eggs, tend to spawn in annual episodes, and tend to exhibit rapid growth during the first year of life. *Opportunistic-strategists* mature early at small sizes, produce small- to medium-sized clutches of small eggs, have multiple spawning bouts each year, and grow rapidly as larvae. *Equilibrium-strategists* may be any size, but tend to produce small- or medium-sized clutches of relatively large eggs, and often have brood guarding or maternal provisioning of nutrients to developing embryos.

Fishes near the periodic region of the life-history continuum probably reap two major benefits from delayed maturation and large adult body size: capacity to produce large clutches and enhanced adult survival during periods of suboptimal environmental conditions, like winter and periods of reduced food availability. Fishes with large clutches frequently spawn in synchronous bursts that coincide

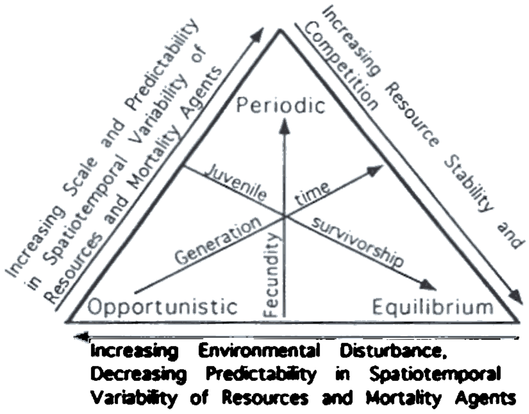


FIGURE 2 Schematic representation of the triangular continuum of primary life-history strategies in fishes and environmental factors associated with selection gradients. [Based on K. O. Winemiller and K. A. Rose (1992). *Canad. J. Fish. Aquat. Sci.* 49(10), 2196–2218.]

either with migration into favorable habitats or with favorable periods within the temporal cycle of the environment, like the spring or rainy season. Cod, cobia, mackerels, tunas, and other marine fishes with tiny pelagic eggs and larvae also have among the highest fecundities. These species cope with large-scale spatial variation in the marine pelagic environment by producing huge numbers of tiny offspring, at least some of which are bound to thrive once they encounter favorable strata or patches. On average, larval survivorship is extremely low among highly fecund fishes in the marine environment, and the average larval fish probably dies during the first week of life. Fast larval growth rates reflect successful exogenous feeding by the lucky survivors that encounter areas of relatively high prey density.

At higher latitudes, large-scale and cyclic temporal variation in environmental conditions is a major factor selecting for the timing of reproduction. Highly fecund fishes can exploit predictable patterns in time or space by releasing massive numbers of progeny in phase with periods in which environmental conditions are most favorable for larval growth and survival. Selection favors physiological mechanisms that enhance a fish's ability to detect cues that predict the periodic cycle (photoperiod, ambient temperature, solute concentrations). In tropical marine pelagic environments, large-scale variation in space may represent a periodic signal as strong as the seasonal variation at temperate latitudes. Research in physical oceanography has shown patchy distributions for a variety of physical parameters (salinity, temperature), primary production, and zooplankton due to upwellings, gyres, convergence zones, and other currents.

Many periodic-type species are migratory. Anadromous American shad (*Alosa sapidissima*) show more repeat spawning and devote a greater portion of energy to migration at higher latitudes where environments are more variable and less predictable. Anadromous sticklebacks (*Gasterosteus aculeatus*) have more periodic-type life-history traits (larger clutches, larger size at maturity) compared with conspecific freshwater populations. By adopting anadromy, adult fishes can find favorable environments for the development and survival of their larvae. In contrast, the reproductive success of marine broadcast spawners depends on rates of larval encounters with suitable zones or patches. Massive clutches of small pelagic eggs undoubtedly enhance dispersal capabilities of wide-ranging marine fishes during the early life stages. In a stable population, losses due to settlement in hostile habitats (called *advection*) ultimately are balanced by the survival benefits derived from the passage of some fraction of larval cohorts into suitable regions or habitats.

The opportunistic life-history strategy is associated with rapid population turnover rates and a high intrinsic rate of population increase (*r*, an index of the potential for exponential growth). By having among the smallest rather than largest clutches, opportunistic-type fishes differ markedly from the traditional model of *r*-strategists. Yet because of their small size, the *relative* reproductive effort of opportunistic strategists is actually high, despite the fact that *absolute* clutch size and egg size are small. In these small species, serial spawning sometimes results in an annual reproductive biomass (i.e., annual fecundity) that exceeds the female's body mass. Small fishes with early maturation and frequent spawning are well equipped to repopulate habitats following disturbances and to sustain their numbers when faced with continuously high mortality during the adult stage. Given their high intrinsic rates of increase, opportunistic-strategists are relatively efficient colonizers of disturbed habitats. A relative opportunistic-strategy is observed in the bay anchovy (Engraulidae), silversides (Atherinidae), annual killifishes (Rivuliidae), marsh killifishes (Cyprinodontidae), and mosquito fishes and other freshwater live-bearers (Poeciliidae, Goodiidae). These small fishes often maintain dense populations in marginal or constantly changing habitats and persist in the face of high predation mortality during the adult stage. Extreme examples of the opportunistic-strategy appear to be more common in tropical fresh waters than in the temperate zone, and in shallow marginal habitats than in deeper freshwater and marine habitats.

An equilibrium life-history strategy in fishes corresponds largely with the suite of traits associated with the traditional *K*-strategy of adaptation to life in resource-limited or density-dependent environments (delayed maturation, large body size, clutches containing few large offspring). Large eggs and parental care yield larger or more developmentally advanced juveniles at the onset of independent life. Live-bearing sharks and rays that bear relatively large, advanced offspring would lie near the equilibrium end point of the life-history spectrum. Among bony fishes, marine ariid catfishes (egg diameters 16–20 mm, oral brooding of eggs and larvae) and amblyopsid cave fishes (branchial brooding of small clutches of relatively large eggs) illustrate relatively extreme forms of this equilibrium-strategy. Cave fishes inhabit among the most stable and resource-limited of aquatic habitats. Parental care tactics (including long gestation in live-bearers) tend to be more highly developed and widespread in tropical fresh waters and among certain reef-dwelling marine fishes, such as sea horses, surfperches, and sharks.

Of course most fishes are associated not with a particular end point strategy, but rather with intermediate strategies within the triangular gradient of primary life histories. Some of the largest periodic-type fishes, the sturgeons (Acipenseridae) and paddlefish (Polyodontidae), have relatively large eggs, which reduces their theoretical maximum clutch size. Salmon and trout possess even larger eggs (4–6.5 mm diameter) and smaller clutches than fishes exhibiting the extreme periodic-strategy. Yet among populations of coho salmon (*Oncorhynchus kisutch*), egg size declines and clutch size increases with increasing latitude. Selection seems to favor local optima in egg size with clutch size adjustments resulting from physiological constraints and ecological performance. Relative to periodic-strategists with larger clutches and smaller eggs, salmon and trout apparently have evolved a more equilibrium-strategy of fewer but larger offspring at the onset of independent life. In eutrophic ecosystems, a pulse of primary and secondary production during short summers probably favors a periodic-type strategy at high latitudes. Studies of several fish species with large ranges along the eastern North American coast show that juvenile growth rates are actually faster for fishes at higher latitudes where the growing season is shorter. Yet, the growing season at high latitudes may be so short that brood guarding is not a viable tactic for large fishes in oligotrophic systems. Data from arctic char (*Salvelinus alpinus*) indicated that the growing season at high latitudes probably constrains age at maturity and the frequency of spawning. Migration to special spawning habitats and burial of fertilized eggs (brood hiding) by salmon, char, and trout are forms of parental investment that carry large energetic and survival costs in relation to future reproductive effort. Senescence associated with semelparity in Pacific salmon might have evolved as a consequence of the survival cost of returning to the sea after energetically costly upstream runs to fluvial habitats that enhance larval survivorship. By comparison, freshwater whitefishes (*Coregonus*, *Prosopium*) exhibit a perennial periodic-strategy that involves large clutches, small eggs, and annual spawning bouts.

A number of intermediate-sized fishes have seasonal spawning, moderate clutch sizes, and nest guarding (North American ictalurid catfishes and sunfishes, *Lepomis*). Rockfishes of the eastern Pacific (Scorpaenidae) have large clutches and small eggs and bear living young. All of these fishes lie between periodic and equilibrium end points of a triangular gradient. Small fishes with rapid maturation, small clutches, large eggs relative to body size, and a degree of parental care (minnows of the genus *Pimephales*, madtoms, darters, sticklebacks, pipefishes, and sculpins) lie between opportunistic- and equilibrium-strategists. Similarly, small fishes with seasonal spawning, moderately large clutches, small eggs, and only one or a few bouts of reproduction per season lie between opportunistic and periodic extremes of the gradient. It is important to note that fishes with divergent life-history strategies frequently coexist in the same habitats. Each species' morphology and feeding niche determine the nature of the resource variation and predation that it experiences; and morphological constraints, including features involved in feeding within particular microhabitats, restrict the evolution of life-history features. In addition, phylogenetic constraints will result in varying degrees of adaptive divergence or evolutionary convergence toward a given adaptive suite of life-history traits.

V. POPULATION REGULATION

The study of population regulation in fishes has been dominated by the search for density-dependent recruitment in commercial stocks. Several simple models describe density-dependent relationships between stock abundance (expressed as either spawning adults or egg cohorts) and the abundance of recruits (expressed as age 1 fishes, or cohorts when they enter the fishery or become vulnerable to sampling gear). These include the well-known Ricker and Beverton–Holt stock/recruitment models. By and large, data from large marine and lake fisheries conform very poorly to density-dependent, stock-recruit models. This has spurred greater examination of potential density-independent factors that influence recruitment, such as climatic fluctuations and seasonal changes in marine currents. Evidence for density-dependent population dynamics has been obtained from a variety of sources, including studies of local population dynamics, niche relationships, and predator- or resource-regulated community dynamics. [*See* POPULATION REGULATION.]

In terms of life-history strategies, fitness can be estimated by either V_x, the reproductive value of an individual or age-class, or by r, the intrinsic rate of natural increase of a population or genotype. Each of these fitness measures can be expressed as a function of three essential components: survivorship, fecundity, and the onset and duration of reproductive life. In the case of reproductive value,

$$V_x = m_x + \sum_{t=x+1}^{\omega} (l_t m_t)/l_x$$

where for a stable population m_x is age-specific fecundity, l_x is age-specific survivorship, and ω is the last age-class of active reproduction. When x is equal to α, the age of first reproduction, reproductive value is equivalent to the lifetime expectation of offspring, and contains survivorship, fecundity, and timing components. The intrinsic rate of population increase can be approximated as $r \simeq \ln R_0/T$, where R_0 is the net replacement rate, T is the mean generation time, and $R_0 = \Sigma\, l_x\, m_x$, resulting in $r \simeq \ln (\Sigma\, l_x m_x)/T$. The relative rate of population increase is directly dependent on fecundity, timing of reproduction, and survivorship during both immature and adult stages. Averaged over many generations, the three parameters (l_x, m_x, T) must balance, or populations would decline to extinction or would grow to precariously high densities and eventually crash.

The three end point life-history strategies of fishes referred to previously are associated with trade-offs among age at maturation (α positively correlated with T), fecundity, and survivorship. The periodic-strategy corresponds to high values on fecundity and age at maturity axes (the latter is a correlate of population turnover rate) and a low value on the juvenile survivorship axis. The opportunistic-strategy of high population turnover rate via rapid maturation corresponds to low values on all three axes. The equilibrium-strategy corresponds to low values on the fecundity axis and high values on the age of maturity and juvenile survivorship axes.

Clearly, the periodic-strategy maximizes age-specific fecundity (clutch size) at the expense of optimizing turnover time (turnover times are lengthened by delayed maturation) and juvenile survivorship (maximum fecundities are attained by producing smaller eggs and larvae). Large body size enhances adult survivorship during suboptimal conditions and permits storage of energy and biomass for future reproduction. Iteroparity permits a fish to sample its environment several times until, sooner or later, reproduction coincides with favorable conditions and strong recruitment occurs. Virtually all ecosystems exhibit either spatial or temporal variation that is to some degree predictable. This may be especially true in freshwater and marine environments, because batch spawning of large clutches is predominant among bony fishes worldwide. Spawning by these periodic-type fishes is usually annual and synchronous, so that generations are often recognized as discrete annual cohorts. Yet, correlations between parental stock densities and densities of young-of-the-year recruits have been shown to be negligible in these fishes. Recruitment often depends on climatic conditions that influence water currents, larval retention zones, productivity of prey patches, and a host of other environmental factors that determine early growth and survival. Accurate predictions of recruitment by periodic-type species in large marine ecosystems require understanding of physical oceanography plus the ability to forecast weather conditions. Because weather cannot be predicted over long time intervals, fisheries projections often rely on short-term estimates of juvenile cohort strength several weeks or months following spawning, rather than long-term estimates based on parental stocks.

Many periodic-type fishes spread their reproductive effort over many years (or over large areas), so that high larval/juvenile survivorship during one year (or in one area) compensates for the many bad years (or areas). For example, anadromous female striped bass (*Morone saxatilis*) live up to 17 years on average and produce an average clutch of 4×10^6 eggs every year or two. This requires survivorship of roughly 3×10^{-8} during the egg to maturation interval to maintain a stable population. Most years probably result in a larval survivorship approaching zero for most females. For an individual female, the fitness payoff comes only during one or two spawning acts over the course of a normal life span. In species like striped bass, the variance in larval survivorship that serves as input for population projections lies well beyond our ability to measure differences in the field. Management of exploited populations of long-lived, highly fecund fishes requires the maintenance of critical densities of adult stocks and the protection of spawning habitats during the short spawning season. Because recruitment is largely determined by unpredictable interannual environmental variation, this critical density is impossible to determine with any degree of precision. And because most larvae never recruit into the adult population even under pristine conditions, it follows that some spawning must proceed unimpeded each year if strong recruitment is to occur during the exceptional year.

The opportunistic life history maximizes the intrinsic rate of population growth (r) through a reduction in the mean generation time (T). Fishes exhibiting an opportunistic-type strategy are often associated with shallow marginal habitats. These edge habitats are the kinds of environments that experience the largest and most unpredictable changes on small temporal and spatial scales. Changes in precipitation and temperature induce major alterations in water depth, substrate characteristics, and productivity in shallow aquatic habitats. Population density estimates for small fishes in shallow marginal habitats, like headwater streams and salt marshes, has shown large monthly variation. In the absence of chronic intense predation and resource limitation, opportunistic-type populations can quickly rebound from localized disturbances.

Because they tend to be small and occur in shallow marginal habitats, opportunistic-type fishes are not usually exploited commercially. Some important commercial species, like gulf menhaden (*Brevoortia patronus*), are intermediate between opportunistic- and periodic-strategies. Yet, small fishes are often the most important food resources for larger piscivorous species. Bay anchovies (*Anchoa mitchilli*) and silversides (*Menidia menidia*) inhabit relatively stable habitats, yet they suffer high adult mortality from predation. Given the capacity for opportunistic-strategists to sustain losses during all stages of life spans that are typically rather short, one of the keys to their management is protection from large-scale or chronic perturbations that eliminate important refugia.

The equilibrium-strategy in fishes is roughly equivalent to the traditional *K*-selection model of evolution in density-dependent and resource-limited environments. For example, some stream-dwelling darters (*Etheostoma*) and madtoms (*Noturus*) probably have fewer refuges in shallow riffles during periods of reduced stream flow. If refuges are limited, individuals may be forced to compete for depleted food supplies in areas immediately surrounding refuges. In the East African rift lakes, many brood-guarding and mouth-brooding cichlids have home ranges that cover only a few square meters. In the marine environment, parental care is most frequently seen in small fishes associated with the benthos or structure (damselfishes, pipefishes, sea horses, eelpouts, some gobies). Compared with opportunistic- and periodic-strategists, equilibrium-strategists ought to experience lower temporal variation in population density and conform better to stock-recruit models.

Because equilibrium-strategists produce small numbers of offspring, early survivorship must be relatively high for these populations to avoid local extinction. When parental care is involved, survivorship during early life stages depends on both the condition of adults and their nesting habitat. Relatively few equilibrium-type fishes are commercially exploited on a massive scale. Sev-eral species exploited by sport fisheries exhibit brood guarding and are intermediate between equilibrium- and periodic-strategies, including lingcod (*Ophiodon elongatus*) and the North American sunfishes. Management of exploited stocks of equilibrium-type fishes requires the maintenance of undegraded habitats and adult stock densities that promote surplus yields that can be fished and replaced via natural compensatory mechanisms.

VI. ECOLOGICAL INTERACTIONS

A. Predation

Predation has a major influence on fish evolution, population dynamics, and community structure. The diversity of feeding mechanisms of fishes is derived from the mechanical trade-offs involved in harvesting different kinds of food resources. In the absence of stable food resources and interspecific competition, generalized feeding is often favored. Many fishes show seasonal diet shifts, in which a greater variety of prey is consumed during periods of prey abundance. In diverse fish assemblages, predatory fishes usually exhibit divergence in feeding tactics and diet. Piscivores may feed by a sit-and-wait tactic (flounders, scorpion fishes), stealth and rapid pursuit (barracudas, pikes), solitary active searching (snappers, black bass), or actively searching in schools (tunas, piranhas). Divergence in piscivore foraging tactics has coevolved with an equivalent amount of evolutionary and ecological divergence in prey escape tactics. Prey species avoid predation by crypsis, mimicry, hiding, schooling, spines, bony plates, and aggression. Small fishes, like anchovies and killifishes, often have few specialized defenses against predators (other than hiding and schooling), yet their populations thrive owing to their rapid population turnover times and high growth potentials.

Piscivores can have major effects on the density, population structure, and behavior of their prey. The addition of piscivores (largemouth bass, *Micropterus*) to North American lakes has been shown to decrease the abundance of small planktivorous fishes (minnows), which in turn leads to wholesale changes in zooplankton, phytoplankton, and nutrient dynamics. Because mouth gape and the diameter of the throat limit the size of prey ingested, piscivores that swallow their prey whole are often very size selective. Size selectivity can alter the size and age structure of prey populations. For example, small gizzard shad are more vulnerable than larger conspecifics to predation by largemouth bass and other piscivorous fishes. Shad populations in predator-dense habitats tend to be dominated by older age-classes comprising larger individuals. In Europe, the size/age structure of roach (*Rutilus*) populations is often influenced by predatory perch (*Perca*). Piscivores can also influence the competitive interactions between prey species. Walleye (*Stizostedion*) are efficient predators of both young-of-the-year perch (*Perca*) and gizzard shad (*Dorosoma*). In temperate lake ecosystems, young perch compete with shad for zooplankton. If shad densities are high, competition can cause a competitive bottleneck for perch recruitment into older age-classes. At high densities of gizzard shad, young perch grow more slowly and remain vulnerable to walleye for a longer period of time.

Effects of piscivores on aquatic ecosystems are clearly demonstrated by introductions of exotic predators. The predatory sea lamprey has contributed to the decline of a number of fishes of the Laurentian Great Lakes, including lake trout and endemic whitefishes (*Coregonus*). The introduction of peacock bass (*Cichla*) into Lake Gatún, Panama, resulted in major changes in the aquatic food web and local extirpation of several native fish species. In Africa, the introduction of predatory Nile perch (*Lates*) into Lake Victoria ranks among the most devastating exotic species introductions in history. Prior to the introduction of Nile perch, the lake's fish community was dominated by more than 400 species of endemic haplochromine cichlids. Lake Victoria is now dominated by Nile perch, a native minnow, and an introduced species of tilapia (a detritivorous/herbivorous cichlid), and a great number of haplochromine cichlids are now extinct. The complex food web supported by the ecologically diverse haplochromines has been replaced by a simple food web linking detritus–shrimp, tilapia, minnows–Nile perch. Recent evidence indicates that the entire lake ecosystem's nutrient dynamics may have been destablized by the replacement of haplochromine biomass and diversity with shrimp, minnow, and tilapia biomass.

By influencing the behavior of their prey, piscivorous fishes can have subtle effects on ecosystem structure and function. Recent studies have demonstrated that fishes are able to perceive predation risks in different habitats, and that they alter their use of habitats in accordance with the relative costs and benefits of foraging gains versus predation risks. Experiments have shown that algae-feeding stone rollers (*Campostoma*) will avoid stream pools containing largemouth bass. As a consequence, pools that contain bass develop and maintain more benthic algae than pools without bass. In North American streams, dace (*Rhinichthys*) will avoid pools that containing large piscivorous creek chubs (*Semotilus*). Stream areas containing higher concentrations of food induce dace to take greater predation risks. Similarly, in the presence of largemouth bass (*Micropterus*), bluegill sunfish (*Lepomis*) spend more time foraging in vegetation than in open water areas of ponds where foraging is more profitable.

B. Competition

Competition occurs when the supply of resources is insufficient to meet the demand of two or more conspecific consumers (intraspecific competition) or consumer populations (interspecific competition). Food and habitat have been identified as the resources that most often limit individual fitness and population densities. Historical competition is frequently inferred from comparisons of species characteristics within natural assemblages. Diverse fish assemblages in the tropics show more interspecific variation in ecomorphology than assemblages from comparable habitats at higher latitudes. Resource segregation in response to interspecific competition is a likely causal factor for this pattern. In a study of four tropical fish assemblages, fishes were clustered into feeding guilds and species within guilds were segregated in their use of food resources more than would be expected by chance. Many studies have shown high levels of resource segregation, particularly in fishes' use of habitat. Considerable diet and habitat overlap have been observed during early stages of ontogeny and during seasonal increases in resources in many different aquatic and marine ecosystems. Declines in fish diet or habitat overlap during periods of natural resource depression provide comparative evidence for interspecific competition.

Interspecific competition has been inferred from observed niche shifts in response to species introductions in natural and experimental systems. The introduction of planktivorous alewife (*Alosa pseudoharengus*) into Lake Michigan resulted in native bloaters (*Coregonus hoyi*) shifting to forage in deeper waters on larger and more benthic invertebrate prey. The bloater's shift in ecology was accompanied by a reduction in the length and number of gill rakers formerly used for straining plankton from the water column. In experimental ponds, bluegill sunfish (*Lepomis macrochirus*), green sunfish (*L. cyanellus*), and pumpkinseed sunfish (*L. gibbosus*) use a similar range of habitats and food resources when stocked as single species. When all three are stocked together, bluegills feed more in open water on zooplankton, green sunfish feed more in the vegetation on aquatic insects, and pumpkinseeds feed more on benthic invertebrates. The growth rates of each species are slower in multispecies ponds compared with similar single-species ponds, offering further evidence of interspecific competition for resources.

VII. COMMUNITY PATTERNS AND BIODIVERSITY

In general, regional fish diversity is positively correlated with drainage basin area and negatively correlated with latitude. South American fresh waters contain the highest regional freshwater fish diversity, and the southwestern Pacific Ocean contains the greatest diversity of marine fishes. Within freshwater families having little or no salinity tolerance, species and populations show conservative biogeographic patterns in which recently divergent taxa are restricted to disjunct drainage basins. On a longer time scale, distributions of fish families reflect dispersal across continental landmasses via stream captures and freshwater intrusions into coastal marine habitats. For example, catastomid suckers range from eastern Asia across the Bering Strait into North America and south to central Mexico; and centrarchid sunfishes are restricted to eastern, central, and southern portions of North America. Minnows, carp, and other cyprinid fishes are found on all continents except South America, Australia, and Antarctica. Marine taxa have distributional patterns that reflect biogeographical processes on different scales. The Central American isthmus separates recently divergent sister species of numerous coastal marine taxa. Several marine families have circumglobal distributions that are restricted by latitude, such as the anadromous salmonids in the Northern Hemisphere and their sister clade, the anadromous argentiniids in the Southern Hemisphere [*See* BIODIVERSITY.]

At a local level, fish species composition results from both historical regional processes and contemporary ecological processes. Analyses of lake assemblages in Canada showed that geographical distance explained the level of fish assemblage similarity more than local habitat conditions. In contrast, streams located only a few kilometers apart, but with different habitats, may share only a very small fraction of their species. For example, some tropical freshwater fishes are restricted to "blackwater" streams that flow through regions containing nutrient-poor soils. Other species inhabit only nutrient-rich "whitewater" rivers that support high aquatic primary production and biomass of invertebrates and fishes. Species composition of these assemblages correlates more with habitat conditions than geographical distance. Several studies have used multivariate statistical methods to examine fish assemblage composition in relation to habitat gradients. Stream systems in many different regions of the world show clear patterns of faunal change and species turnover in relation to longitudinal fluvial gradients. Many small species are restricted to headwater tributary streams, where stream flow is highly variable and habitats are very dynamic. As one moves downstream into larger, more stable, and more productive habitats, a few of the headwater species are retained and new species are added.

Fish biodiversity is threatened by a number of factors. The introduction of exotic species can eliminate native species directly via competition and predation or indirectly via alteration of the food web. On a global basis, the tiny North American mosquito fish (*Gambusia affinis*) and herbivorous African tilapias (*Tilapia, Sarotherodon, Oreochromis*) may be the most widespread and damaging exotic species. Carp (*Cyprinus carpio*), largemouth bass (*Micropterus salmoides*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo salar*) have been introduced worldwide for sportfishing. The effects of these introductions on native species have varied greatly, but in most areas the full impact on the native fauna is unknown. Exotic introductions can result in genetic contamination of locally adapted fish populations, as when hatchery salmon are introduced to rivers containing native stocks. Overfishing and environmental degradation from a variety of agents have caused the decline of fish populations and species diversity in virtually all major aquatic and marine ecosystems. Fluvial and estuarine ecosystems are among these most affected by pollution and other anthropogenic perturbations in regional landscapes. Deforestation and plowing cause increased soil erosion, runoff, and sedimentation, all of which degrade fish habitat. Trace contaminants like lead and PCBs can attain high concentrations in fish tissues through the process of bioaccumulation. Elevated nutrient levels from pollution and agricultural runoff increase primary productivity of aquatic ecosystems, which frequently leads to higher biomass of less desirable species like carp and gar and declines in game fishes like largemouth bass. In arid regions, fragile aquatic habitats have been completely destroyed by removal of subsurface water for irrigation, industry, and municipalities. When they block movement to critical spawning habitats, dams can eliminate local populations of migratory fishes in little more than a single generation. [*See* MARINE BIOLOGY, HUMAN IMPACTS.]

Fishes can serve as sensitive indicators of water quality and ecosystem health. Small species that adjust well to laboratory conditions, such as the fathead minnow (*Pimephales promelas*) and the medaka (*Orizias latipes*), are used extensively in toxicological research. Species that have broad geographical ranges and are highly sensitive to habitat degradation are useful as bioindicators. For example, many North American stream-dwelling darters (Percidae) require oxygen-rich water flowing over hard substrates. These species are among the first eliminated from habitats degraded by pollution, siltation, and other landscape perturbations. In addition, the structure of local fish communities has been used as an indicator of ecosystem stress. Under normal conditions, diverse fish faunas will contain a mixture of detritivorous, insectivorous, omnivorous, and piscivorous fish species. Oftentimes, piscivores will be supported by greater numbers and a greater variety of fishes at lower trophic levels. An index of biotic integrity was developed to evaluate ecosystem change as a result of anthropogenic perturbations. This index compares the structure of fish communities in degraded habitats with the structure of communities in similar but unperturbed habitats from the same biogeographic region.

Glossary

Anadromous Of or pertaining to species that spend most of their lives in the sea and migrate to fresh water to breed.

Assemblage Group of species populations coexisting in a local area, usually pertaining to species belonging to the same higher taxonomic grouping (e.g., fish assemblage, minnow assemblage, trout assemblage).

Benthic Of or pertaining to the bottom or substrate region of freshwater and marine environments. Category of fishes that inhabit the bottom region (e.g., many catfishes, sculpins, darters).

Catadromous Of or pertaining to species that spend most of their lives in fresh water and migrate to the sea to breed.

Demersal Of or pertaining to the deep-water regions near the bottom or substrate of aquatic and marine environments.

Diadromous Of or pertaining to species that migrate between fresh water and the sea.

Fluvial Of or pertaining to flowing freshwater ecosystems such as streams and rivers.

Iteroparity Condition of performing repeated episodes of reproduction over the lifetime.

Marine Of or pertaining to oceanic or coastal environments, typically containing solute concentrations greater than 30 parts per thousand.

Pelagic Of or pertaining to the open-water region of freshwater and marine environments.

Pharyngeal teeth Throat teeth that occur on pads on various gill arch elements in many fishes.

Semelparity Condition of performing a single bout of reproduction during the lifetime.

Stock Local population of fishes, usually referring to one that is exploited as a commercial or recreational resource.

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