

Functional Innovations and the Conquest of the Oceans by Acanthomorph Fishes

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The world's oceans are home to many fantastic creatures, including about 16,000 species of actinopterygian, or ray-finned, fishes. Notably, 85% of marine fish species come from a single actinopterygian subgroup, the acanthomorph or spiny-rayed fishes. Here, we review eight functional innovations found in marine acanthomorphs that have been instrumental in the adaptive radiation of this group in the marine realm. Jaw protrusion substantially enhances the suction feeding mechanism found in all fish. Fin spines serve as a major deterrent to predators and enhance the locomotor function of fins. Pharyngognath, a specialization of the second pair of jaws in the pharynx, enhances the ability of fishes to process hard and tough prey. Endothermy allows fishes to function at high levels of physiological performance in cold waters and facilitates frequent movement across strong thermal gradients found in the open ocean. Intramandibular joints enhance feeding for fishes that bite and scrape prey attached to hard surfaces. Antifreeze proteins prevent ice crystal growth in extracellular fluids, allowing fish to function in cold waters that would otherwise freeze them. Air-breathing allowed fishes at the water's edge to exploit terrestrial habitats. Finally, bioluminescence functions in communication, attracting prey and in hiding from predators, particularly for fishes of the deep ocean. All of these innovations have evolved multiple times in fishes. The frequent occurrence of convergent evolution of these complex functional novelties speaks to the persistence and potency of the selective forces in marine environments that challenge fishes and stimulate innovation.

Introduction

Marine environments dominate our planet. They cover about 70% of the surface of Earth and make up about 99% of the volume of aquatic habitats [1]. So, it may at first seem surprising that only half of actinopterygian fish species live in the oceans [2], with the other half inhabiting brackish and freshwater (Figure 1). Species accumulate more slowly in the marine realm, apparently because the fractured nature of freshwater habitats provides ample barriers to gene flow and is associated with higher rates of speciation [3–5]. Nevertheless, ray-finned fishes are by far the dominant vertebrate radiation in the oceans. Marine habitats are extraordinarily diverse and present a wide array of challenges to fishes, ranging from fast and turbulent water flow, vast distances and depths, extremely cold temperatures and a potential prey resource that encompasses most animals, many plants as well as a vast diversity of prokaryotes. The success of ray-finned fishes in the oceans is a story about how the challenges presented by this ecological opportunity were met.

Marine fish are not spread evenly across the actinopterygian tree of life. About 85% of the roughly 16,000 marine species are found within one subclade, the acanthomorph, or spiny-rayed fishes (Figure 1). Thus, the success of actinopterygian fishes in the modern oceans is largely a story about the success of acanthomorphs. This group originated just after the Jurassic–Cretaceous boundary 150 million years ago and have achieved levels of diversity never before seen in marine actinopterygian fishes [6–8]. Acanthomorphs make up the vast majority of fish species on coral reefs, temperate reefs, sandy shores, polar seas and the surface regions of the open ocean. Marlin, tuna, mackerels, flatfishes, triggerfishes, puffers, ocean sunfish, anglerfishes, surgeonfishes, mahi,

snappers, croakers, butterflyfishes, seahorses, stickleback, sculpin, rockfishes, pricklebacks, icefishes, trevallies, wrasses, parrotfishes, flying fishes, mullet, damselfishes, clownfishes, blennies, gobies and many other well-known marine fishes are acanthomorphs. Nevertheless, there are some important marine groups that are not acanthomorphs. These include eels and their relatives, that account for 6% of marine species. Additional diversity is found in deep sea habitats and a significant number of these species are not acanthomorphs, including members of Myctophiformes (lanternfishes), Aulopiiformes (lizardfishes), Ateleopodidae (jellynose fishes) and Stomiiformes (dragonfishes) that together make up 5.8% of marine species [6].

In order to achieve widespread success in the oceans, acanthomorphs have had to adapt to and dominate a huge diversity of habitats. This includes fertile, rich habitats that support extremely high biodiversity such as coral reefs, as well as challenging habitats such as the open ocean and polar regions with extremely cold water. Success in all of these habitats has been influenced and facilitated by a series of functional innovations that enhance the ability of fishes to perform in extreme environments, compete and dominate in the ecosystems with highest biodiversity, and take on novel life-histories that might not otherwise have been possible. Below, we examine the extraordinary conquest of modern oceans by ray-finned fishes and review eight major functional innovations that have enabled acanthomorphs to dominate the world's oceans.

Jaw Protrusion

The ability to protrude the upper jaw toward prey during feeding is a major innovation in the feeding mechanism of fishes

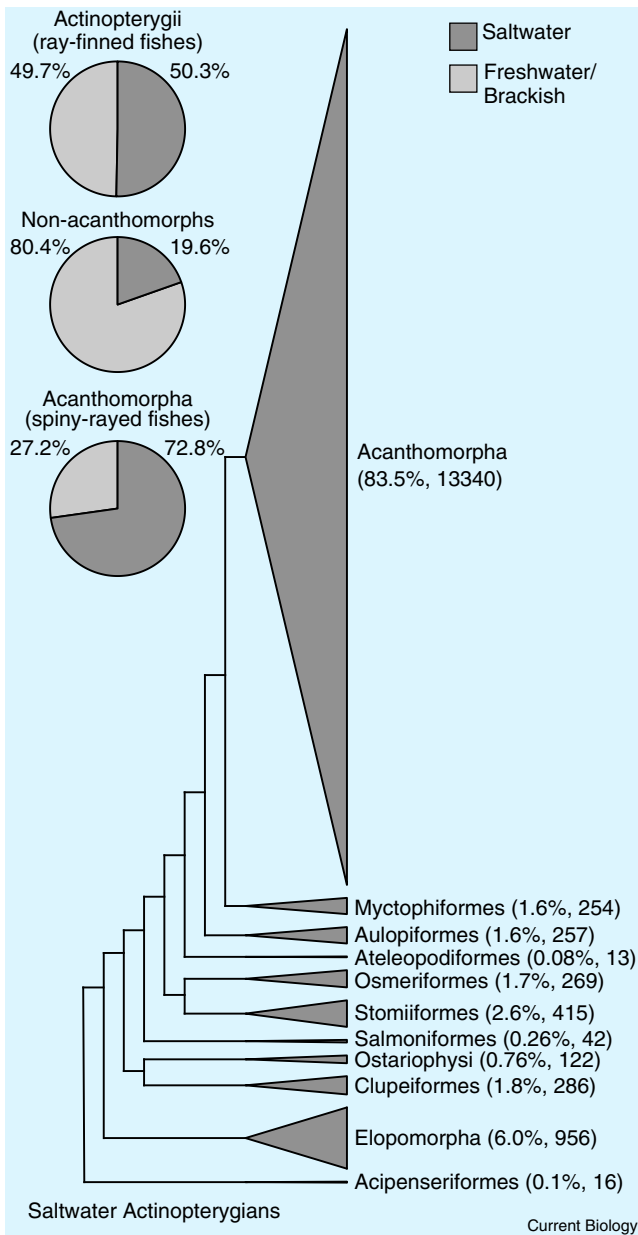


Figure 1. The phylogenetic make-up of marine actinopterygian fishes.

About half of all actinopterygian fishes, roughly 16,000 species, are marine. But 84% of these are acanthomorphs, or spiny-rayed fishes. Among the major non-acanthomorph marine fishes is a significant elopomorph radiation that includes eels, several deep-sea groups and the herrings and anchovies. Data taken from fishbase [2].

(Figure 2). Jaw protrusion enhances feeding performance in several ways, but the most widespread and general benefit is its use during suction feeding [9–11]. Suction feeding is the most commonly used means of prey capture in all fishes, including acanthomorphs [11]. Suction feeding involves the rapid expansion of the mouth and buccal cavity by a series of evolutionarily highly conserved movements and mechanisms. As the buccal cavity is expanded in as little as three to four milliseconds, water is aspirated and draws the prey into the mouth [10,12].

Protrusion of the jaws toward the prey during suction feeding causes the velocity of the suction flow around the prey to increase more quickly than it would without protrusion, thus increasing hydrodynamic forces due to fluid acceleration and induced drag [13]. One estimate indicated that the hydrodynamic force exerted on prey is increased by up to 35% because of jaw protrusion [9]. Thus, there is a very substantial enhancement of suction feeding performance as a result of jaw protrusion, in addition to other benefits [14].

Jaw protrusion is a shared derived trait of acanthomorph fishes [15,16]. Although it has been secondarily lost several times in marine acanthomorphs (such as tetraodontiforms and acanthurids), it is found in most species. Interestingly, jaw protrusion has evolved independently at least five times in actinopterygian fishes [11].

Spiny Fins

Acanthomorphs share a second major innovation. The anterior skeletal elements that support the dorsal, anal and pelvic fins of acanthomorphs are formed by strong, sharp spines that function to deter predators [17,18]. Spines in the median fins are oriented with the dorsal-ventral axis of the fish and function synergistically with a deep-bodied shape to exceed the gape width of predators, and indeed among ray-finned fishes that possess spines, deeper bodies and longer spines are positively correlated [19]. Median fin spines are very apparent in many marine acanthomorphs, in some cases accounting for a considerable fraction of skeletal mass (Figure 3). Spines tend to be best developed and most effective in predator defense in deep-bodied taxa, while in some slender-bodied marine acanthomorphs, such as mullet and flying fish, they are probably not effective against predators. Spines in the median fins (the dorsal and anal fin) also enhance swimming performance by providing rigidity and stiffness to the leading edge of the fin, resulting in greater control and functional compartmentalization of the dorsal fin.

Fin spines, the trait that gives spiny-rayed fishes their name, are also a shared-derived trait for acanthomorph fishes, but, as with jaw protrusion, fin spines have evolved independently multiple times, in acanthomorphs and in two predominantly freshwater radiations, carps and catfishes [19].

Pharyngognathy

Actinopterygian fishes possess two sets of jaws (Figure 4): the oral jaws formed by the familiar mandible and upper jaw (maxilla and premaxilla) and a second set of jaws unique to ray-finned fishes that is formed from modified gill arch elements, called pharyngeal jaws [20]. In the majority of ray-finned fishes the pharyngeal jaws are composed of paired, left and right toothed upper and lower jaw bones [20] and the major biting action involves a rotation of the epibranchial bone that presses the upper jaw bones against the lower jaw bones (Figure 4) [21]. Pharyngognathy is a derived condition of the pharyngeal jaw that involves three major modifications to the widespread primitive condition: a fusion of the left and right lower jaw bones into a single jaw bone, a muscular sling that suspends the lower jaw from the neurocranium and provides a direct biting motion, and well-developed joints between the upper jaw bones and the underside of the neurocranium that support the upper jaws when the lower jaw is pulled against them by the muscular sling [22,23].

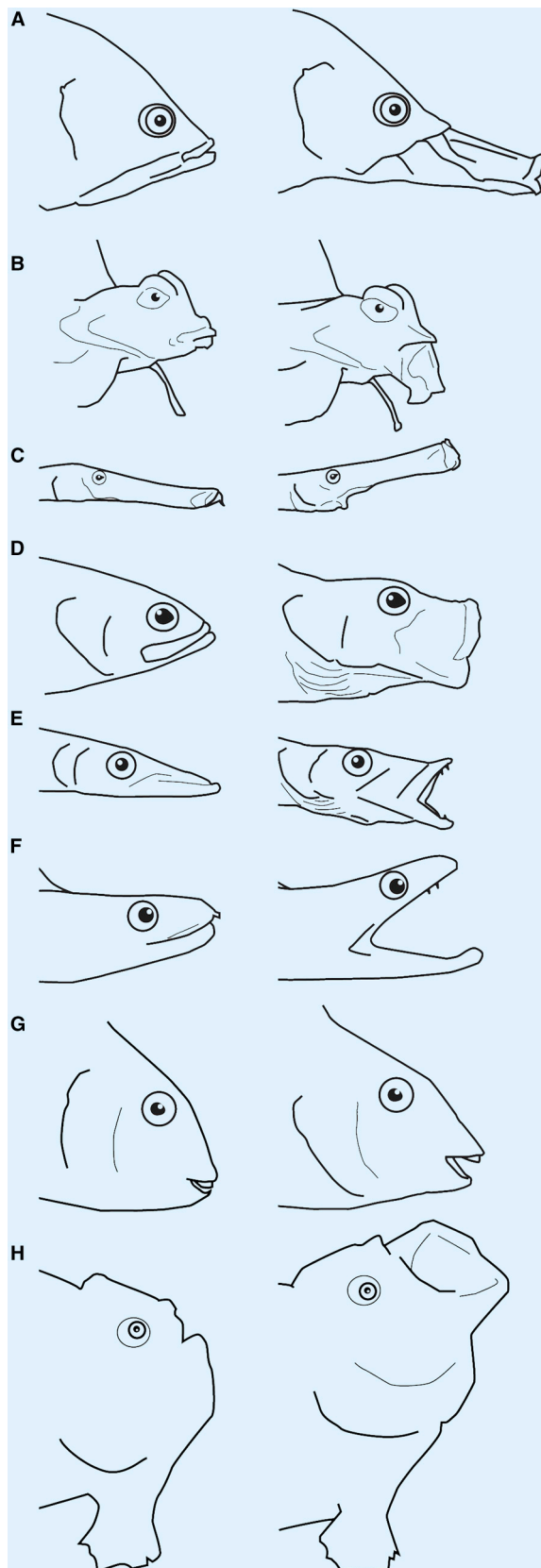


Figure 2. The diversity of upper jaw protrusion in marine fishes.

Each pair of figures is taken from a high-speed video recording of feeding and shows the fish at the onset of a strike and at the time of maximum mouth opening. Jaw protrusion is a shared derived characteristic of acanthomorphs, so is not found in marine fishes outside this group such as the moray eel (F). Species vary considerably in how protrusible the upper jaw is and the direction of protrusion. Most fish use protrusion to enhance suction feeding, but in some biting taxa, like parrotfish, protrusion is employed during substrate biting. Fish strikes and jaw protrusion are very quick. Species illustrated and the elapsed time between images: (A) *Epibulus insidiator*, 47 ms; (B) *Dactylopus dactylopus*, 27 ms; (C) *Aulostomus maculatus*, 32 ms; (D) *Epinephelus ongus*, 21 ms; (E) *Sphyræna barracuda*, 67 ms; (F) *Gymnothorax* sp., 1066 ms; (G) *Ceto-scarus bicolor*, 100 ms; (H) *Antennarius hispidus*, 20 ms.

Pharyngeal jaws in general allow the functions of prey capture and prey processing to be delegated to distinct muscle-skeleton systems [24]. Pharyngognathy represents a major advance in the capacity of the pharyngeal jaws to process hard or tough prey, such as mollusks, heavily armored crustaceans, echinoderms or algae and other plants [22,25]. It has been shown that pharyngognathous lineages of acanthomorphs have evolved a diet of hard or tough prey significantly more often than non-pharyngognathous lineages [26].

Pharyngognathy has recently been shown to have evolved independently at least six times in acanthomorphs [22,27]. Although it is a complex set of three major morphological traits, it is found in Labridae (wrasses and parrotfish), Pomacentridae (damselfishes), Embiotocidae (surfperches), some Beloniformes (needlefish, flying fish, halfbeaks), Centrogeniidae (false scorpioidfish), and Cichlidae. The impact of pharyngognathy on the diversification of cichlids has been discussed extensively [24,28–30]. It is interesting that labrids and cichlids are two immensely successful groups of acanthomorph fishes, labrids being the largest family of coral reef fishes and arguably the most important to reef ecosystem function, while cichlids dominate many tropical freshwater habitats. Both groups are extremely diverse ecologically and feature many species that feed on hard or tough prey.

Intramandibular Joint

Coral reefs and other hard-bottom habitats present fishes with a wide range of attached prey that, in contrast to the majority of prey caught by suction feeding, must be removed by scraping, nibbling and other biting actions. Several fish lineages that bite the substrate when feeding have evolved an intra-mandibular joint that allows flexion, not only in the usual location at the articular-quadrato joint, but also in the middle of the mandible, between the articular and dentary bones [31,32]. In marine angelfishes, the Pomacanthidae, the double jointed lower jaw allows fish to bite while the lower jaw is depressed and the upper jaw protruded [32]. Here the joint is used while these fish tear off pieces of sponges. In fish that scrape hard substrates an intra-mandibular joint may allow a longer scrape per bite [31,33,34], thus enabling fish to take more material with each bite. In other benthic grazers, the joint may enhance the dexterity of biting, allowing the jaws to better conform to the surfaces they feed on [34,35].

An intramandibular joint has evolved several times independently in marine acanthomorph fishes [31]. It is found in one lineage of parrotfishes (the lineage made up by *Scarus*, *Chlorurus* and *Hipposcarus* [33]), many butterflyfishes [31],



Figure 3. Dorsal and anal fin spines in the butterflyfish (*Chaetodon unimaculatus*).

Median fin spines are a shared derived characteristic of acanthomorph fishes that provide considerable protection from gape limited predators and stiffen the leading edge of the fins, allowing for greater control during swimming. Specimen length: 114 mm. Photo courtesy of Steve Huskey.

most pomacanthids [31], the acanthurid genus *Ctenochaetus* [34], Drepanidae, Siganidae, Girellidae [36] and at least one lineage of blenny [31]. The question of how many times this trait has evolved in acanthomorphs has not been addressed in the light of recent major advances in phylogenetics, but there are at least four origins, and maybe ten or more [31]. Indeed, the question is not which substrate-biting reef fishes have an intramandibular joint, but rather which do not. Some of those that lack the intramandibular joint, such as some parrotfishes and members of the Tetraodontiformes, are robust excavators that exert high forces and show reduced jaw mobility as an adaptation to stabilizing the jaws while delivering strong bites [31].

Endothermy

Endothermy is the ability to elevate body temperature above ambient temperatures and to defend that temperature. Thus, it involves mechanisms for both generating and retaining heat. By elevating temperatures above ambient and maintaining a relatively constant temperature, endotherms are able to operate at temperatures that allow relatively high levels of performance while also allowing physiological systems to become more specialized for function at a narrower range of temperatures. Endothermy has evolved at least three times independently in marine acanthomorphs [37–39], in tunas, billfishes and the opah (*Lampris guttatus*) (Figure 5). In all of these cases, the fish show regional endothermy, as only part of their body retains heat. All three lineages possess specialized tissue or muscle to heat the blood that infuses the part of the brain containing the optic nerves. A warmer brain and optic nerve ensure high performance of these organs when these fishes cross thermal

gradients that are encountered during deep dives. In addition, some tunas and opah also possess body endothermy, in which countercurrent heat-exchanging modifications to the circulatory system allow these fish to retain heat generated by the repeated contraction of swimming muscles. Tunas show a gradation in the degree of endothermy with some species being able to elevate the temperature of axial musculature and the brain, while the more specialized bluefin and albacore tuna also heat regions of the abdominal viscera [37]. Regional endothermy in these taxa is associated with an extensive suite of morphological and physiological specializations that have received considerable attention from comparative biologists [39–44].

Endothermic acanthomorphs are all large, extremely active, pelagic species that often migrate vertically within the water column during which they encounter a wide range of water temperatures [37,38]. Tunas and billfish evolved from fast-swimming tropical or warm-temperate surface dwellers and appear to clearly expand their thermal niche to allow them to access deeper, colder water on feeding forays. By contrast, opah are a member of a lineage of inhabitants of the mesopelagic zone (200 to 1000 m), and their endothermy appears to allow them to operate more continuously in cold water while maintaining elevated physiological performance [38].

Antifreeze Proteins

Among the success stories of marine fishes is the invasion of the coldest regions of our planet. Seawater at high latitudes can often be more than 1°C colder than the freezing point of fish body fluids [45]. Numerous lineages of acanthomorphs have evolved antifreeze proteins that bind to and halt the growth of ice crystals, lowering the freezing point of extracellular body fluids that are otherwise at risk of freezing. How these proteins are absorbed into ice crystals is not fully understood. Antifreeze proteins have evolved numerous times and are notably diverse in molecular structure, with five major types recognized [46]. While they appear to have evolved from numerous progenitor proteins, antifreeze proteins are all formed by 4 to more than 50 tandem repeats of Ala–Ala–Thr with the disaccharide galactosyl-N-acetyl-galactosamine attached at each threonine [45]. Some antifreeze proteins seem to be produced in the liver and distributed through the body by the circulatory system, while others are produced in skin and gills [47–49].

Antifreeze proteins are found in many branches of the tree of life, including bacteria, fungi, plants, arthropods and fishes. In all cases, they expand the thermal niche of the lineages that have evolved them. Within marine acanthomorphs, they appear to have evolved at least five times — in notothenioids, flatfishes, labrids, cods, and sculpin — and likely more [45,48,50]. While these proteins clearly expand the niche of the fish that have them by providing access to colder environments that other groups cannot access, relatively little is known about the broader macroevolutionary consequences of this innovation. In part, this may be due to the recent origin of antifreeze proteins in some lineages [45,50]. However, antifreeze proteins have been proposed to be a key to the success and dominance of notothenioid fishes in antarctic seas, as they evolved in this group 25–40 million years ago, at the base of the lineage that underwent a significant acceleration of net diversification that led to the radiation of this group throughout the cold Southern Ocean surrounding

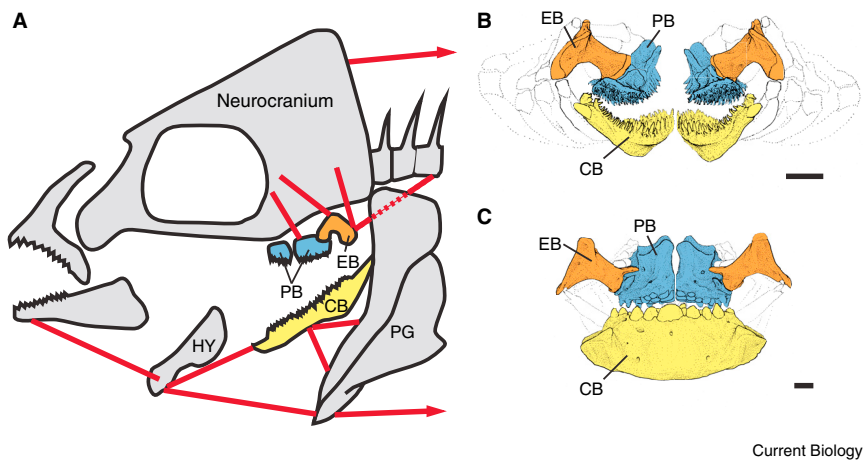


Figure 4. Pharyngeal jaws and the pharyngognathous condition.

(A,B) The generalized pharyngeal jaw apparatus of actinopterygian fishes. Actinopterygian fishes have a second set of jaws, the pharyngeal jaws, derived from gill arch elements (A). In posterior view, as illustrated by *Lepomis punctatus* (B), the generalized pharyngeal jaw shows that the lower jaw bones are separate and large epibranchials dorsal to the upper jaw play an important role in biting motions. (C) Pharyngognathy, as illustrated by the labrid *Halichoeres garnoti*, involves fusion of the paired lower jaw elements into a single lower jaw bone, a muscular sling between the neurocranium and the lower jaw (not shown), and a joint between the underside of the neurocranium and the upper jaw bones. This complex innovation renders the pharyngeal jaws stronger and allows fish better access to hard and tough prey, such as mollusks, many crustaceans, echinoderms, and plants. Abbreviations: CB, fifth ceratobranchial (lower jaw bone); EB, epibranchial bone; PB, pharyngobranchial bone (upper jaw bone). Scale bars: 1 mm.

Antarctica [51]. This innovation originated in notothenioids at around the same time as the emergence of the Southern Ocean, an extensive region with very cold water. Notothenioids are by far the most successful lineage of ray-finned fishes in the Antarctic region [52,53].

Air-breathing

The intertidal zone, at the ocean–land interface, is among the most highly productive marine habitats [54]. Fish that occupy this habitat have given rise to lineages that made the transition to an amphibious lifestyle, thereby presenting them with a very different landscape of opportunities and threats. Many of these species breath air after emerging from water. Marine air breathers respire across the skin, gills and oral epithelium and in some cases have evolved accessory respiratory organs in the pharynx [55]. In addition to physiological modifications [55–57], morphological modifications include reduction in the extent that scales cover the body, reduction in the size of the gill filaments, and smaller body size [58–61].

Over 70 species of intertidal marine fishes, all acanthomorphs, have been shown to be able to breath air [59]. At least 12 families of marine acanthomorphs have independently evolved a highly amphibious lifestyle [59,62], and there may be as many as seven independent origins within Blenniidae [62]. Air breathing and the use of terrestrial habitats allow some lineages to avoid large marine predators and exploit exposed food resources.

Bioluminescence

About 1,500 species of marine fish are bioluminescent — they have the ability to emit light that is produced by a biochemical reaction between luciferin and luciferase [63]. Some bioluminescent fish generate light endogenously while others harbor symbiotic vibriionacean bacteria that make the light, often in discrete organs in the skin [64]. Light production is used in camouflage, to lure prey, to confuse predators and to communicate with conspecifics, particularly in the context of mating. Bioluminescence is found in fish from all depths of the ocean but is particularly well represented in deep-sea fish where the scarcity of ambient light enhances the value of light production [65]. The multiple functions

of bioluminescence indicate that it is a versatile innovation with multiple adaptive causes in fishes that are active at night or inhabit the poorly lit regions of the deep ocean (for more on the deep sea, see the primer by Roberto Danovaro and colleagues in this issue).

Among marine ray-finned fishes, bioluminescence has been acquired independently at least 27 times [63]. Of these 27 origins, there are at least five independent instances of the evolution of intrinsic light production, while the others appear to involve the acquisition of bacteria to generate the light. Different groups with intrinsic light production have evolved only four different luciferins, while the luciferases and photoproteins used in the mechanism tend to be unique in each group [65,66]. It appears that luciferins are often taken up from prey, helping to explain the broad phylogenetic distribution of specific luciferin types [65,67]. There is also growing evidence from marine fishes and other groups of metazoans that bioluminescent lineages that use light production during courtship show increased rates of species accumulation compared to non-luminous relatives [63,68,69]. It is unclear whether this effect is due to the role of light emission in competition between members of the same sex or more accurate species recognition in low-light habitats.

The Impact of Innovations

The innovations listed above have played an important role in the success of marine acanthomorph fishes. While there are other significant innovations in fishes, these are particularly well studied and illustrate the role that key functional modifications can have on the ability of fishes to access novel resources. Their impacts vary and reflect the diversity of ways in which innovations can be important in macroevolutionary dynamics. A classic view of evolutionary innovations is as novelties that significantly enhance performance and thus move the lineage across a threshold into a new adaptive zone where subsequent diversification may be facilitated by a scarcity of other lineages [70,71]. Among the innovations reviewed here, this is best illustrated by antifreeze proteins that were key to allowing diversification in the newly formed Southern Ocean by notothenioid fishes. In this relatively depauperate landscape, notothenioids subsequently underwent a significant radiation into different habitats,

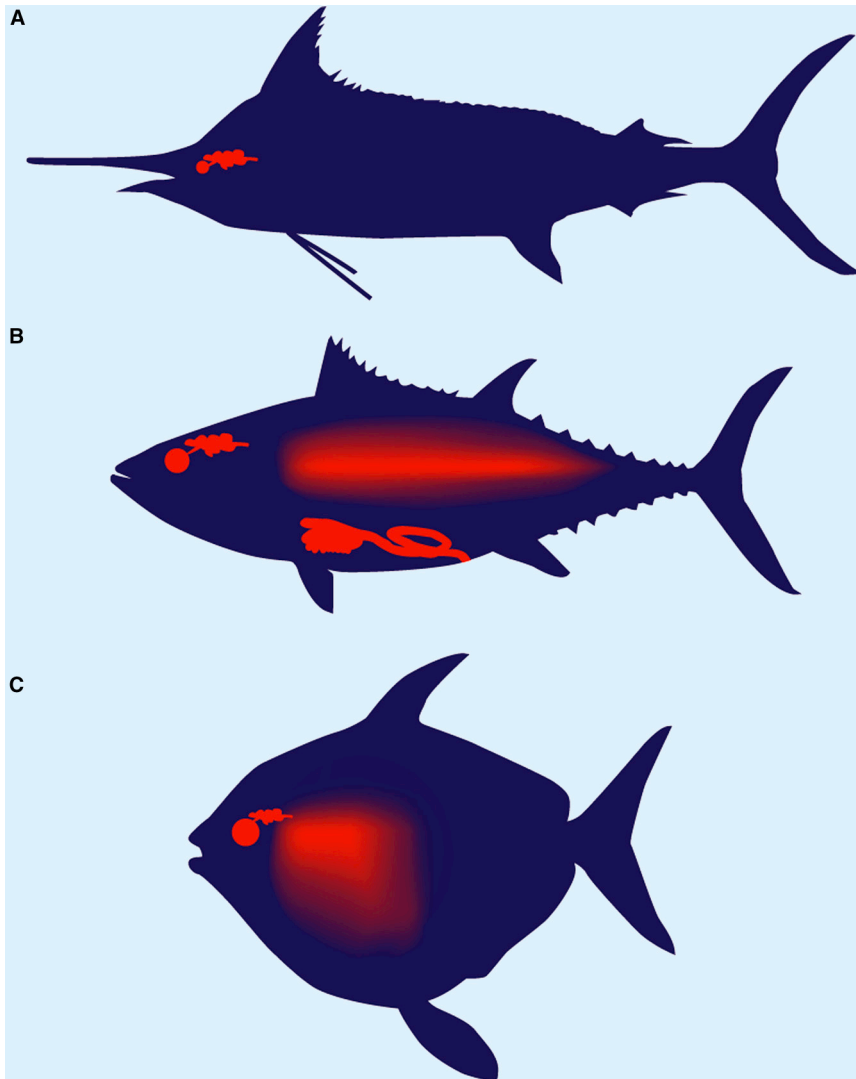


Figure 5. Three evolutionarily independent origins of endothermy in marine acanthomorph fishes.

Marlin and their relatives (A) have brain endothermy, some tunas (B) have brain, body and visceral endothermy, while opah (C) have brain and body endothermy. All three instances of endothermy are associated with significantly enhanced physiological performance in colder water allowing these very active predators to expand their thermal niche.

oceans. Both of these innovations evolved in the earliest acanthomorphs and have subsequently been modified and diversified among marine lineages. For example, jaw protrusion has been enhanced to extreme levels in the sling-jaw wrasse (*Epibululus insidiator*) and in several species of chaetodontids in which additional novel joints have evolved that permit the fish to not just depress the lower jaw, but also protrude it [72,73]. In addition, some lineages, such as parrotfishes and marine angelfishes, use upper jaw protrusion during scraping or biting behaviors, rather than suction, and thereby extend the utility of this innovation beyond its initial context [31,74]. There is also evidence that the presence and diversification of jaw protrusion resulted in major changes in the nature of benthic predator-prey interactions [75]. Fin spines have become secondarily elaborated in some groups, for example lionfish and sailfish, such that they support a very extensive dorsal fin that can be retracted and deployed depending on context.

degrees of buoyancy and trophic position [51,52]. The relative scarcity of non-notothenioid fishes in the Southern Ocean suggest that either this region was relatively free of competitors and predators to counter icefish diversification, or that the onset of icehouse conditions led to extinctions of other lineages. Pharyngognathous results in a stronger pharyngeal jaw and permits access to structurally defended prey, including mollusks, armored crustaceans, various echinoderms and the matrix of algae and detritus imbedded within hard surfaces. Because prey are crushed in the pharyngeal jaws, the oral jaws are free to specialize for prey capture mechanics, which also increases feeding versatility [24]. Among pharyngognathous fishes there has been a higher rate of the evolution towards feeding on these hard and tough prey items, compared to fishes without this modification [26], and in labrids and cichlids the innovation appears to have been a significant factor in trophic diversification [22].

Jaw protrusion and fin spines both represent innovations that appear to have fundamentally enhanced performance in feeding, locomotion and predator avoidance. They may help explain the dominance of the entire acanthomorph radiation in modern

Other innovations have made entry into novel habitats or novel life-styles possible but are associated with less extensive radiations. Examples of this may be found in the non-notothenioid lineages that have evolved antifreeze proteins, the endothermic fishes, bioluminescence and air-breathing. For instance, the stark contrast in the macroevolutionary impacts of antifreeze proteins between Antarctic notothenioids and Arctic cod, despite their surprising degree of convergence in the ability to retard ice growth, illustrates that increased performance does not automatically lead to an evolutionary radiation. Other factors that influence the dynamics of adaptive radiation are important, such as the diversity of resources made available by the innovation and the abundance of competitors, as well as historical and climatological events [76]. Indeed, while pharyngognathous is associated with trophic diversification in multiple major fish radiations [11], the price that pharyngognathous fishes pay, in terms of poorer fish-eating performance, appears to underlie the mass extinction of pharyngognathous cichlids in Lake Victoria following the introduction of Nile perch [26].

One of the most interesting aspects of the eight innovations reviewed here is that each of them has evolved independently multiple times. Convergent evolution is a striking and common feature across the tree of life but the ubiquitous presence of convergence in major complex functional innovations in marine fishes suggests that the selective forces that shaped these innovations are strong, persistent features of the marine landscape that have repeatedly stimulated marine fishes to arrive at similar solutions to the challenges they face.

The observation that the solutions of different fish lineages to these challenges have so often been so similar indicates that the intersection of the raw material that fishes have to work with in their body plan, genome and physiology, and the nature of these environmental challenges, has resulted in repeated evolution of the same solution to each problem. This pattern may not be unique to marine fishes. Many striking examples of convergence in complex functional systems are known in terrestrial vertebrates, such as powered flight or body elongation and loss of limbs in squamates that live underground. Like the functional innovations discussed here in marine fishes, these innovations reflect the powerful attraction of some major adaptive zones that are common on Earth. Biologists recognize that adaptive landscapes depend on community make-up and are ever-shifting, so that the history of life would be unlikely to repeat itself precisely if it were replayed [77]. However, it seems that natural selection in marine fishes nonetheless often produces similar solutions to major challenges, and that this is an important and widespread phenomenon in organismal diversification.

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