

CHAPTER 3

Evolution

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Introduction

Attempts to understand determinants of species composition in animal communities generally have been limited to current influences on existing communities (e.g., MacArthur, 1969; Paine, 1966; Sale, 1977, 1991). Evolutionary history is routinely ignored, often because key issues can be examined only by inference. But more than 45 years of experience with marine communities has convinced me that major determinants of species structure lie in evolutionary processes that greatly transcend the current scene.

The conclusions developed in this chapter draw from my widespread studies of marine communities of California, most in collaboration with Tony Chess. Our efforts in the south were concentrated at Santa Catalina Island (e.g., Hobson and Chess, 1976, 1986, 2001; Hobson et al., 1981), whereas most in the north were along the Mendocino Coast (e.g., Hobson and Chess, 1988; Hobson et al., 2001). The chapter also incorporates a perspective gained through intensive studies of communities elsewhere, particularly in the tropical eastern Pacific (e.g., Hobson, 1968) and on tropical coral reefs of the central and western Pacific (e.g., Hobson, 1972, 1974; Hobson and Chess, 1978). Topics discussed here were the basis of two papers, Hobson (1994) and Hobson and Chess (2001).

Most California coastal fishes are teleosts of the superorder Acanthopterygii (as defined by Nelson, 1994), which are characterized by skeletons of bone and fins supported by spines. This group includes the vast majority of modern fishes other than sharks and rays. Most of California's marine teleost fishes represent a subset (series) of acanthopterygians, the Percomorpha (Nelson, 1994). More specifically, visual assessments of fish communities near the California coast invariably find more than 95% of the fishes—species as well as individuals—representing the percomorph orders Perciformes, Scorpaeniformes, or Pleuronectiformes (e.g., Ebeling et al., 1980; DeMartini and Roberts, 1990; Stephens and Zerba, 1981). According to Nelson (1994), these are three of the four most recently evolved orders of fishes. To understand the nature and basis of their dominance, one should consider certain features of teleost history.

The account of teleost history that follows draws from a problematic body of knowledge, simplified here for more effective presentation. Much of the evidence comes from the

fossil record, which is notoriously incomplete and at least to some extent controversial on virtually every point. I integrate published interpretations of the data to develop a cohesive synthesis, while declining to pursue various inconsistencies and unresolved conflicts in peripheral issues that would unnecessarily cloud essential points.

Relevant Features of Teleost History

Acanthopterygian teleosts represent advanced levels in the evolution of actinopterygian ("ray-finned") fishes, which, according to Schaeffer and Rosen (1961), evolved based mainly on improvements in feeding related capabilities. They stated (p. 187), "In the main stream of actinopterygian evolution from paleoniscoid to acanthopterygian, there has been progressive improvement in a fundamentally predaceous feeding mechanism." They also cited changes in the structure and placement of fins that improved their ability to swim and therefore to capture prey or evade predators. The history of these fishes, therefore, can be considered an evolution of feeding-related adaptations.

The main evolutionary line leading to modern acanthopterygian teleosts has been described as a succession of generalized carnivores, with each major advance producing a diverse array of specialized offshoots (Gosline, 1960). If actinopterygian evolution has been driven by trophic relations, it would follow that the "diverse array of specialized offshoots" resulted mainly from proliferation of ways to obtain food or thwart predators.

The major evolutionary advances and production of specialized offshoots referred to by Gosline can be related to the global episodes of mass extinction–resurgence that have been so prominent in the history of life on the earth (Stanley, 1987).

Impact of Extinction–Resurgence Episodes

The major episodes of global mass extinction–resurgence have followed a common pattern. Each has begun with a catastrophic

event, at least some the impact of an immense asteroid or comet (e.g., Alvarez et al., 1980; McLaren and Goodfellow, 1990; O'Keefe and Aherns, 1989; Ward et al., 2001; Ellwood et al., 2003). These events created environmental conditions intolerable to significant proportions of existing species and resulted in global extinctions that led to collapse of ecosystems that had been stable for tens of millions of years. Immediately following the extinctions and loss of ecosystems have been periods of limited community development lasting some millions of years, which Fagerstrom (1987) referred to as ecological and evolutionary vacuums. Eventual resurgence from this condition has involved surviving representatives of the main evolutionary line that, though generalized in form, embodied specific highly adaptive features. These features, most involving mouth and /or fin structure, have promoted proliferation of diverse forms that filled developing niches during widespread biological resurgence toward new ecosystems.

Other surviving actinopterygians failed to radiate in the new environment because they lacked the potential of mainstream species to diversify. Some of these were well adapted to specific ecological circumstances, however, and managed to persist along distinct evolutionary lines where conditions favorable for them continued to exist. We return to these later in the chapter, but for now we focus on the main line.

Consider the record. It is generally recognized that there have been five major episodes of global extinction–resurgence since late in the Ordovician Period (Raup and Sepkoski, 1982), and all can be related to major advances in actinopterygian evolution, as identified by Long (1995). The extinctions that closed the Ordovician about (~) 440 million years ago (mya) may have influenced actinopterygian origins. The earliest records of these fishes—bone fragments, scales and teeth are from Silurian deposits dated ~30 million years after the Ordovician extinctions. Lacking substance and precision, this evidence can only suggest a possible connection, but relations become clearer as the fossil record improves. The second period of major extinctions came late in the Devonian (~350–375 mya) and could have promoted the radiation of paleoniscoids—the dominant actinopterygians of the late Paleozoic. This dominance lasted until the end of the Permian (~245 mya), when the greatest of all global extinctions brought the Paleozoic to a close by eliminating an estimated 80 to 95% of marine species (Erwin, 1994). Resurgence from this catastrophic episode involved radiation of early neopterygians, which dominated until the fourth major episode of extinctions closed the Triassic (~208 mya). The actinopterygian radiation that followed the end-Triassic extinctions brought advanced neopterygians into prominence. Among these were teleosts, which have become the most successful of modern fishes. The fifth major episode of extinctions came at the end of the Cretaceous (~65 mya), and can be linked to the radiation of percomorph lines that now dominate among fishes in California and elsewhere.

It is significant that forms involved in postextinction radiations had been established as minor elements of communities decimated by the extinctions. Paleoniscoids, for example, are known from the Silurian and were a minor presence among other more dominant forms (e.g., placoderms and acanthodians) throughout the Devonian “Age of Fishes.” They radiated only after the late Devonian extinctions eliminated all or many members of the dominant groups. Similarly, there were early neopterygians in Permian communities, but radiation came

only after mass extinctions ended that period. And though teleosts (which are advanced neopterygians) originated midway through the Triassic (Greenwood et al., 1966), their proliferation during the Jurassic (Gosline, 1971) came after the end-Triassic extinctions. The pattern has persisted to recent times; some percomorph lines that dominate among modern fishes can be traced back into the Cretaceous but did not radiate until some time after mass extinctions and collapse of ecosystems closed the Mesozoic (Gosline, 1960; Patterson, 1964).

In addition to the five major episodes of global mass extinction–resurgence, there have been at least 27 lesser episodes (Sepkoski, 1986). One that decimated reef communities at the Jurassic–Cretaceous boundary (~145 mya; Scott, 1988) has been implicated in the advance of the teleost main line to the acanthopterygian level of development (Hobson, 1994).

Certainly not all extinctions and originations have occurred during episodes of mass extinction and subsequent resurgence. To the contrary, extinction and origination have been continuous throughout the history of life on the earth, probably most during intervals between global episodes. Nonetheless, in making this point, Wood (1999) went on to elaborate (p. 165): “mass extinctions are disproportionately significant in that they . . . by virtue of their speed, unpredictability and magnitude—are capable of removing dominant taxa and their habitats, which can lead to the collapse of whole ecosystems.” The removal of dominant taxa and habitats would seem the key because the continuous extinctions of ordinary times are most likely to concentrate on removing misfits during comparatively minor changes in local conditions that do not represent global threats to the environment.

Because ecosystems that developed after episodes of extinction have been derived from distinctive combinations of survivors, each has been unique. Consider the involvement of actinopterygian fishes. If one accepts the proposition that actinopterygian evolution has been driven mainly by trophic relations, it follows that radiation of forms during ecosystem resurgence has been largely a proliferation of diverse feeding types and defensive structures. This means that there must also have been concurrent and rapid evolution of form and behavior among the organisms that interacted with these fishes as predator or prey. In drawing this conclusion earlier (Hobson, 1994), I reasoned that (p. 63) “. . . evolution of feeding adaptations in predators is inseparable from the evolution of defensive adaptations in prey, the two in combination representing a developing system of coevolved offenses and defenses (Hobson, 1979). The effect . . . would spread far beyond interactions between any two organisms to include, modify and expand the trophic system.” It has been concluded that the trophic system is the primary basis for community species-structure (Hobson and Chess, 2001), which leads to the conclusion that resurgence from collapsed ecosystems to a large extent has involved trophic interactions among developing species. One would expect, therefore, strong affinities between specific ecosystem components.

Teleost–Scleractinia Connection

Teleostean fishes concurred with scleractinian coral reefs in time and place of both first record and subsequent radiation, which suggests a common history. The earliest records of both are fossils laid down during the mid-Triassic at margins of the

Tethys Sea, and their subsequent radiation during the Jurassic was part of a biological resurgence that followed the end-Triassic extinctions (Greenwood et al., 1966; Gosline, 1971; Newell, 1971; Wood, 1999). These and later concurrences led me to propose that the main teleost line has been linked to scleractinian coral reef communities from their beginnings (Hobson, 1974).

The Tethys involvement had a powerful influence on teleost-scleractinia connections, as well as on other facets of teleost evolution. An earlier manifestation of this ancient sea, surrounded on three sides by the supercontinent Pangaea, had been a major feature of the Paleozoic; however, Pangaea began to break apart midway through the Triassic—at about the time teleosts and scleractinians deposited their initial traces—and Tethys became an equatorial seaway that ultimately connected the ancestral Pacific, Indian, and Atlantic oceans (Dietz and Holden, 1970; Stanley, 1989). Remaining that way through the rest of the Mesozoic, Tethys covered much of what are now southern regions of Asia and Europe, with east-west shores that would have contained the evolution of its fauna, including teleost fishes and scleractinian corals, at lower latitudes.

An opposing view held that preacanthopterygian teleosts were maladapted to reef conditions and that teleosts became reef fishes only after acquiring features that advanced the actinopterygian line to the acanthopterygian level during the Cretaceous (Smith and Tyler, 1972). This position was based mainly on the absence of fishes among fossils from early Mesozoic reefs, but Newell (1971) attributed this absence (and the absences of arthropods, polychaetes, and other organisms expected on coral reefs) to their skeletal remains being (p. 6) “systematically removed by scavengers that abound in this strongly oxidizing environment.” In contending that coral reef communities have always included fishes and certain other organisms missing in the fossil record, Newell stated (p. 6), “The history of coral reef crabs and fishes and some other groups must be inferred from the evidence provided by other preserved groups and by the circumstantial evidence of inferred relationships.”

Scleractinian coral reefs thrived during most of the Jurassic but suffered extinctions late during that period and into the Cretaceous (Scott, 1988). Although fishes were not part of the fossil record that marks the decline of Jurassic reefs, it can be assumed that they were among the organisms eliminated during the process. As the corals and other organisms that had structured Jurassic reefs declined, they were replaced as dominant forms in shallow water by rudistids, a diverse group of mollusks (Kauffman and Johnson, 1988). Despite these replacements, however, teleosts remained poorly represented in the fossil record until after scleractinian corals re-established dominance on the seaward margins of reefs ~15 to 20 million years into the Cretaceous (Newell, 1971).

The first evidence of resurgence among teleosts comes from the mid-Cretaceous, ~100 mya, and involved the earliest known percomorph acanthopterygians, representatives of the order Beryciformes (Patterson, 1993). As elements of the main teleost line, preadapted to niches characteristic of coral reef communities, these were primed to diversify when conditions suitable for the expansion of coral reefs developed.

Beryciforms developed in ways similar to development at previous stages of the main actinopterygian line. Apparently their early evolution was rapid because their initial appearance in the fossil record is as a diverse group representing ~25% of that period's marine fishes (Patterson, 1993).

Perpetuating a pattern established during earlier resurgences from mass extinctions, the diversity among them was based largely on enhanced abilities to capture prey, defend against predators, or increase maneuverability—all trophic-related adaptations (Patterson, 1964).

The proliferation of beryciforms produced many species that resembled modern coral reef fishes, including serranids, carangids, kyphosids, chaetodontids, acanthurids, and balistids (Patterson, 1964). The similarities were strong enough to be considered by some as evidence that modern members of these families represent lines independently derived during the Cretaceous from different lines of beryciforms (e.g., Greenwood et al., 1966). Others, however, have argued that the similarities are superficial and not indicative of phyletic relations (e.g., Gosline, 1966). No matter which view is correct, it would mean Cretaceous reef communities were shaped by the same evolutionary processes that have shaped modern communities. Despite the diversity and great success of beryciforms, most perished with the global extinctions that decimated reef communities at the close of the Mesozoic (Patterson, 1964; Gosline, 1971).

Percoids at Last

At some point prior to the end-Cretaceous extinctions, a combination of minor structural changes in one or more lines of generalized beryciforms resulted in the next major advance in actinopterygian evolution—the percoid level of development (Patterson, 1964; Gosline, 1971). These changes were passed on to bass-like early “percoids,” at least some of which represented basal elements of the perciform suborder Percoidei (Patterson, 1964). The evolutionary advances evident at the percoid level were refinements of those same trophic-related features that had made beryciforms better adapted than their progenitors to reef conditions. The early percoids, therefore, represented an extension of the main actinopterygian line of generalized carnivores, which had radiated as beryciforms at an earlier evolutionary stage.

The actinopterygian mainstream continued into the Tertiary as elements of the percomorph order Perciformes, but apparently it was some time before the adaptive potential of the percoid condition was realized. There is little evidence of diversity among actinopterygians through the 10 million years of the Paleocene (Patterson, 1993)—a period also characterized by lack of coral reef development (Newell, 1971). The earliest evidence of increasing diversity among actinopterygians is from late in that period and early in the Eocene (~55 mya; Patterson, 1993). If perciform percoids extended an evolutionary line with adaptive potential linked especially to coral reefs, one would expect that they lacked diversity during times lacking such reefs.

In assessing the diversity among actinopterygian fossils in early Cenozoic deposits, Carroll (1988) and Choat and Bellwood (1991) concluded that the perciform radiation began during the Cretaceous and made major advances throughout the Paleocene. Although it is likely that various lineages originated during the Paleocene, I question whether there could have been a major radiation of forms during a period of limited community development. In the resurgence scenario proposed above, explosive radiation of species is inseparably linked to expanding communities. Furthermore, it could have been predicted that up to 10 or more millions of years would pass after the end-Cretaceous extinctions before there would

be such proliferation because that has been a facet of major extinction–resurgence episodes from the beginning. A gap in the fossil record could explain the apparent absence of community development and perciform radiation during the Paleocene, but terrestrial deposits from that period provide a much better record than marine deposits, and they too lack evidence of modern vertebrates (Romer, 1966).

The critical unknown is the rate at which evolution proceeds during resurgence from ecosystem collapse. Considering that beryciforms, too, were diverse when they first appear in the fossil record, probably evolution proceeds rapidly under conditions that favor ecosystem resurgence.

Actinopterygians regained prominence when perciforms radiated coincident with expanding coral reef communities during early to mid-Eocene (~40–50 mya), and the result was a variety of forms characterized by features that continue to define modern coral reef fishes (Choat and Bellwood, 1991; Bellwood, 1996). The expansion of reef communities at that time also produced many new scleractinian corals, and by the Period's end, all modern scleractinian¹ families had appeared (Wood, 1999). Thus, present-day coral reef communities are extensions of communities that developed during that time. Other aquatic communities must have been stabilizing then as well, because by the close of the Eocene all major families of modern fishes had come to exist (Berg, 1940).

Although the highly variable Cenozoic environments that followed had profound effects on origination, extinction, and distribution at the levels of genera and species, the major variations in morphology and presumably behavior that characterize modern teleost fishes at the family level had been set. Thus, in pondering the derivation of modern species, one can focus on developments during the Eocene and on the evolution of form and behavior as expressed in present-day representatives of the various families. Although the species (and most genera) used as examples in the following synthesis did not evolve until later in the Cenozoic, they embody the features under discussion and so serve as effective stand-ins for their poorly known progenitors.

Derivation of Modern Teleost Fishes

The derivation of modern teleost fishes can be examined based on circumstances involved in their divergence from the main evolutionary line. We begin by characterizing mainstream feeding relations. Mainstream species, as perceived here, are those generalized carnivores that Gosline (1960) and Schaeffer and Rosen (1961) envisioned having the essential actinopterygian features but lacking specialized adaptations to contemporary settings. Current mainstream actinopterygians are among species included in the perciform suborder Percoidei, which has been described as “. . . the basal evolutionary group from which other perciform groups . . . have been derived” (Nelson, 1994, p. 331). The Percoidei, however, are widely recognized as an unnatural group (e.g., Lauder and Liem, 1983; Johnson, 1993) and as usually constituted (e.g., Nelson, 1994), include species considered in this chapter and elsewhere as divergent from the main line.

¹Throughout the rest of this chapter, the terms “coral reef(s)” and “reef coral(s)” refer mainly to scleractinians; they have remained the major reef-building corals up to the present.

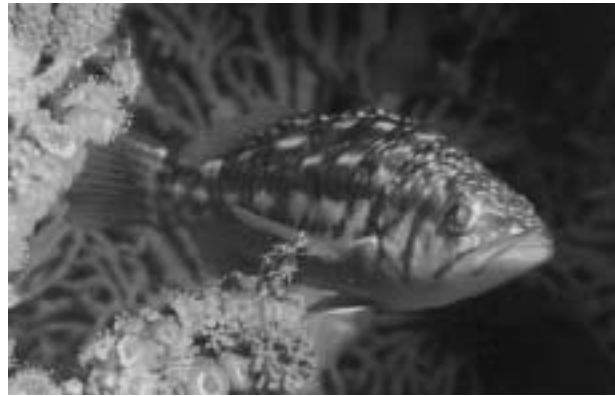


FIGURE 3-1 Kelp bass, *Paralabrax clathratus*.



FIGURE 3-2 Broomtail grouper, *Mycteroperca xenarcha*, surrounded by senioritas, *Oxyjulis californica*.

Feeding Relations in the Mainstream

Although the main actinopterygian line has produced periodic radiations of specialized offshoots from its inception, the generalized carnivores at its core have remained conservative (Gosline, 1960). There have been progressive improvements in jaw and fin structure, along with other minor changes, but most basic features have remained as before. This constancy led to my suggestion that mainstream teleosts probably have attacked the same types of organisms in the same way throughout their history (Hobson, 1974, 1979).

Modern representatives of the teleost mainstream include serranids of the subfamilies Serraninae and Epinephelinae; the former (which includes the California kelp bass, *Paralabrax clathratus*, fig. 3-1) are considered the stem of the family; the latter (which includes the broomtail grouper, *Mycteroperca xenarcha*, fig. 3-2) is an early derivative (Kendall, 1976). Certain key trophic features of serranine and epinepheline serranids have been identified (Hobson, 1968, 1979; Hobson and Chess, 2001; Shpigel and Fishelson, 1989): They have large, generalized mouths and use vision to target organisms in daylight (especially twilight) that are fully exposed to direct attacks. In these attacks, they ambush, run down, or stalk prey that are large enough to grasp and entrap, yet small enough to manipulate and swallow whole. Their prey also lack heavy armor, spines, and other noxious components that an unspecialized digestive system cannot process.

Probably, these trophic features have described mainstream predators and their prey at least throughout most of actinopterygian history. Certainly during this long evolution, potential prey acquired ways to defend against offensive capabilities characteristic of such predators, and, just as certainly, predators countered with modified feeding morphologies and/or behaviors. I suggest that these interactions between predator and prey have been the basis of divergences from the teleost mainstream.

Divergences From the Mainstream

Although the adaptive potential of the percoid condition was most evident in the explosive radiation of perciforms as coral reef communities expanded during resurgence from the end-Cretaceous extinctions, there have been major divergences from the main line for which there is no evidence of comparable radiation or of coral reef involvement. The distinction can be related to whether the departures were based on *adaptations that increased the effectiveness of an existing mode of feeding* or on *adaptations in response to specific prey defenses that enabled new modes of feeding*. These two categories of divergence are considered next.

Divergences Based on Increased Effectiveness of an Existing Mode of Feeding

The main feeding tactics of generalized predators—the ambush and the straightforward rush (Hobson, 1979)—probably have always been the primary means of attack by mainstream actinopterygians, and it is evident that each has keyed major divergences from the main teleost line.

AMBUSHERS

Divergences based on adaptations that improved performance as ambushers were particularly significant because they involved basal elements of the percomorph orders Scorpaeniformes and Pleuronectiformes (rockfishes and flatfishes). Distinguishing features of both—sedentary habits and highly cryptic features—make them more effective ambushers. Modern species clearly adapted to launch attacks from ambush include the ling cod (*Ophiodon elongatus*: family Hexagrammidae, fig. 3-3a), a scorpaeniform, and the California halibut (*Paralichthys californica*: family Paralichthyidae, fig. 3-3b), a pleuronectiform.

It is generally agreed that scorpaeniforms and pleuronectiforms evolved from basal percoids (Hubbs, 1945; Gosline, 1971; Chapleau, 1993), some place the origin of pleuronectiforms with the earliest percoids or even prepercoids (Amaoka, 1969; Li, 1981). Furthermore, modern representatives show evidence of their ancestry in that the most primitive representative of both orders—species of the scorpaeniform family Scorpaenidae and of the pleuronectiform family Psettodidae—are characterized by serranid-like feeding mechanisms, and it is known or inferred that they attack from ambush (Norman, 1934; Harmelin-Vivien and Bouchon, 1976).

Although there is no evidence of explosive radiation when scorpaeniforms and pleuronectiforms departed the teleost mainstream, both orders have since diversified greatly. Furthermore, though their origins seem unconnected to coral reef expansion and their subsequent evolution has progressed mainly in other habitats, both orders were represented among

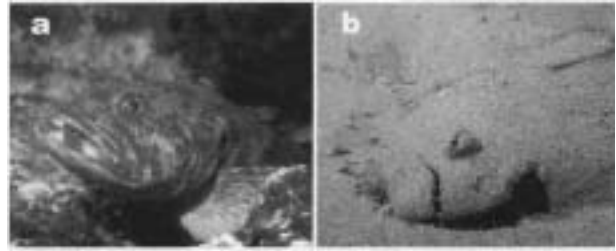


FIGURE 3-3 (a) Ling cod, *Ophiodon elongatus*. (b) California halibut, *Paralichthys californicus* (from Hobson and Chess 1986, with permission from Springer Science and Business Media).



FIGURE 3-4 Grass rockfish, *Sebastes rastrelliger*.



FIGURE 3-5 An aggregation of blue rockfish, *Sebastes mystinus*.

coral reef fishes of the Eocene (Blot, 1980; Bellwood, 1996) and at present include coral reef specialists (e.g., Hobson, 1974).

Modern scorpaeniforms and pleuronectiforms in California coastal communities include variations from their generalized progenitors. Consider, for example, the scorpaeniform genus *Sebastes* (family Scorpaenidae), which includes the majority of rockfishes. Though most that have retained sedentary habits continue to attack prey mainly by ambush, for example, the grass rockfish (*S. rastrelliger*, fig. 3-4), there are varied modes of feeding among others that have abandoned sedentary habits for activities in the water column. Thus, the shortbelly rockfish (*S. jordani*) coordinates its feeding with diel vertical movements of various planktonic crustacea (Chess et al., 1988), whereas the bocaccio (*S. paucispinis*) feeds from an early juvenile stage on smaller fishes in the water column. The blue rockfish (*S. mystinus*, fig. 3-5) feeds largely on gelatinous zooplankters—

a major departure from the standard rockfish diet of crustacea and small fishes (Hobson and Chess, 1988). That planktivorous scorpaenids have greatly reduced versions of the head spines so prominent in basal representatives of the family indicates that feeding in the water column is a derived feature.

There may be at least one ambusher among those scorpaenids that forage in the water column, the kelp rockfish (*S. atrovirens*, fig. 3-6), a nocturnal planktivore that hovers above the bottom at night and strikes at prey that may be detected through bioluminescence in surrounding turbulence (Hobson et al., 1981).

Many of the differences that distinguished early scorpaeniforms from their percoid progenitors, and upon which the divergence of the scorpaeniform line from the teleost mainstream was based, have been lost or variably suppressed by convergences that have developed among modern representatives. For example, the olive rockfish (*Sebastes serranoides*) was named from its similarity to the kelp bass, a serranid perciform (fig. 3-7).

Other California scorpaeniforms show that in retaining the trophic features of generalized predators, it helps to be small. Smallness enables them to feed on microcrustacea, an exceptionally rich source of food. By remaining small, the snubnose sculpin (*Orthonopias triacis*: family Cottidae, fig 3-8), is able to feed throughout life on amphipods, which are exceedingly numerous on reefs (Chess and Hobson, 1997; Hobson and Chess, 2001).

Variations among modern pleuronectiforms are less obvious, mainly because their distinctive flattened bodies overshadow other features. Nevertheless, from the primitive condition, as represented by the large mouth, long pointed teeth, and short, uncomplicated digestive tract of the psetotids (Norman, 1934), their feeding-related morphologies have diversified greatly. Differences in diet define three types of feeding: crustacean feeders, fish feeders, and polychaete-mollusk feeders (DeGroot, 1971). Representatives of all three types commonly occur on sediment along the California coast. The speckled sand dab (*Citharichthys stigmaeus*: family Paralichthyidae, fig. 3-9) feeds mainly on crustacea throughout life, whereas the California halibut, introduced above, feeds on crustacea as a juvenile, but on fishes as an adult. And the C-O sole (*Pleuronichthys coenosus*: family Pleuronectidae, fig. 3-10) feeds on crustacea as a subadult, but later switches to polychaetes and mollusks (Haaker, 1975; Hobson and Chess, 1986).

A number of perciform lines have developed much like scorpaeniforms and pleuronectiforms as sedentary species that ambush prey from positions at rest on specific substrata. Included are the stargazers (family Uranoscopidae), gobies (family Gobiidae), sleepers (family Eleotridae), sand stargazers (family Dactyloscopidae), triplefins (family Tripterygiidae), clinids (family Clinidae), labrisomids (family Labrisomidae), pricklebacks (family Stichaeidae), and gunnels (family Pholidae). Many are similar to scorpaeniforms; for example, the stargazers and sand stargazers resemble stonefishes (family Synanceiidae), and many of the others are like sculpins in both appearance and in being small enough to continue feeding as adults on the exceptionally abundant microcrustacea (Hobson, 1994). The habitats of these species are mostly inorganic reefs, algal turf, or sediment, and though there are both tropical and temperate forms in all suborders represented (except the zoarcoids, which are strictly temperate), few are more than peripherally associated with coral reefs (Hiatt and Strasburg, 1960; Feder et al., 1974, Thomson



FIGURE 3-6 A kelp rockfish, *Sebastes atrovirens*, hovering in midwater at night.

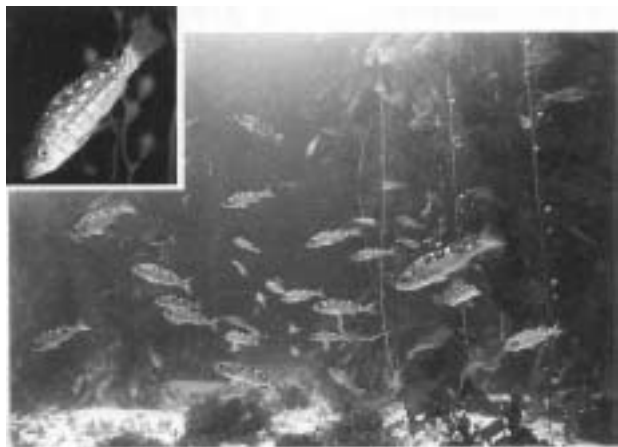


FIGURE 3-7 A group of sub-adult olive rockfish, *Sebastes serranoides*, at the edge of a kelp forest. Inset: a kelp bass of about the same age and size.



FIGURE 3-8 Snubnose sculpin, *Orthonopias triacis* (from Hobson 1994, with permission from Springer Science and Business Media).

et al., 1979). Prominent representatives in California reef communities include the blackeye goby (*Rhinogobiops* (= *Coryphopterus*) *nicholsii*: family Gobiidae, fig. 3-11), the spotted kelpfish (*Gibbonsia elegans*: family Clinidae, fig. 3-12) and the island kelpfish (*Alloclinius holderi*: family Labrisomidae, fig. 3-13).

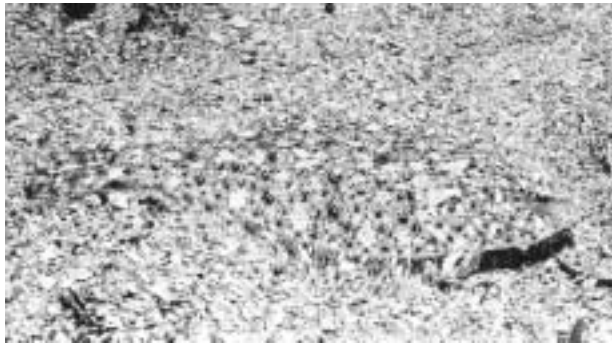


FIGURE 3-9 Speckled sand dab, *Citharichthys stigmaeus*.

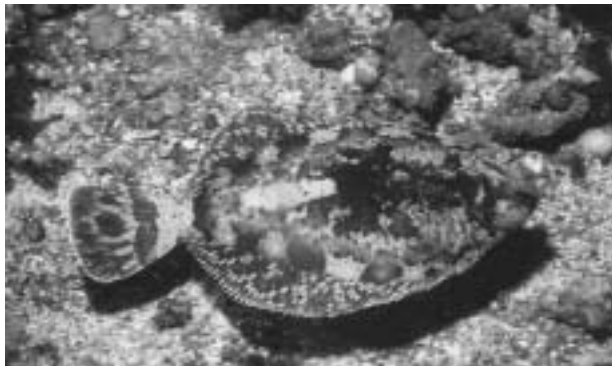


FIGURE 3-10 C-O sole, *Pleuronichthys coenosus* (from Hobson and Chess 2001, with permission from Springer Science and Business Media).



FIGURE 3-11 Blackeye goby, *Rhinogobiops* (= *Coryphopterus*) *nicholsii* (from Hobson and Chess 2001, with permission from Springer Science and Business Media).

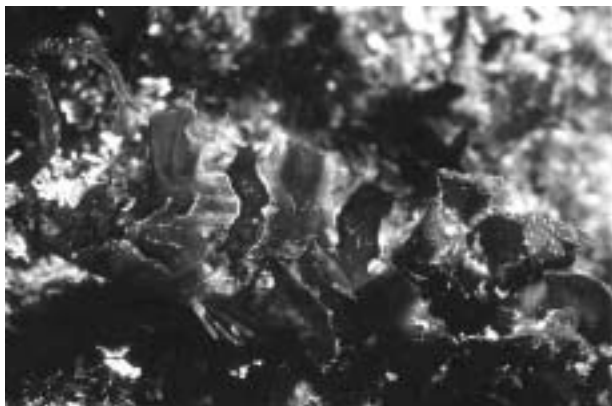


FIGURE 3-12 Spotted kelpfish, *Gibbonsia elegans*.



FIGURE 3-13 Island kelpfish, *Alloclinus holderi* (from Hobson 1994, with permission from Springer Science and Business Media).



FIGURE 3-14 Blue-banded goby, *Lythrypnus dalli* (from Hobson and Chess 2001, with permission from Springer Science and Business Media).

Exceptional is the blue-banded goby (*Lythrypnus dalli*: family Gobiidae, fig. 3-14). Unlike virtually all other small sedentary fishes that prey mainly on microcrustacea on or near the seabed, this species is brightly hued and thus readily visible. It would appear there is no need to avoid being detected by prospective prey, which may be the case. The blue-banded goby feeds mainly by darting up from resting positions on the bottom to capture zooplankters at the base of the water column (Hartney, 1989), and because zooplankters have evolved in a pelagic environment, they may not recognize threats from the benthos (Hobson, 1991).

STRAIGHTFORWARD RUSH

The divergences based on improved performance in capturing prey with a straightforward rush have been based on tendencies toward streamlining, development of body musculature, and other features that promote rapid swimming and therefore an ability to run down prey. These characteristics are most adaptive in pelagic predators, which can take full advantage of speed in open water. Among modern teleosts, they are best developed in the perciform suborder Scombroidei, as defined by Nelson (1994). Representatives of this group common in California waters include tunas (family Scombridae) and billfishes (family Xiphiidae), which are strictly open-water predators. At least one scombroid, however, regularly occurs close to southern California reefs, the California barracuda (*Sphyræna argentea*, family Sphyrænidae). Also defined by features that

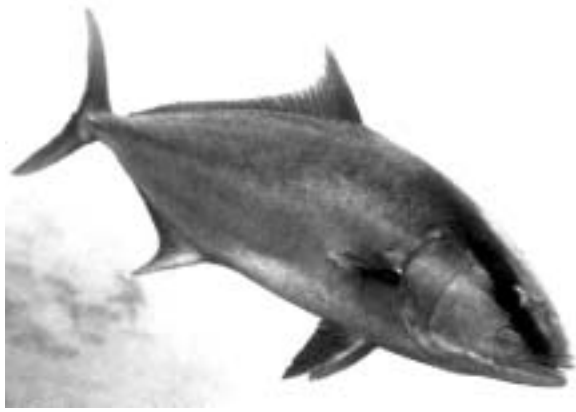


FIGURE 3-15 Almaco jack, *Seriola rivoliana*.

improve a straightforward rush are species of the family Carangidae, which is represented off southern California by the almaco jack (*Seriola rivoliana*, fig. 3-15) and the yellowtail (*Seriola lalandi*), both common near reefs and known to consume reef fishes (Randall, 1967; Craig, 1960). Carangids have long been included among the Percoidei (for example, by Nelson, 1994), but Johnson (1993) recommended placing them in a separate suborder, the Carangoidei, which is consistent with regarding them as divergent from the main line (Hobson, 1994).

Divergences Based on New Modes of Feeding

The radiation of perciforms with expanding coral reef communities early during the Tertiary demonstrated the adaptive potential of the percoid condition. I suggest that this profusion of forms was part of the resurgence from mass extinctions and ecosystem collapse that had ended the Mesozoic. The restructuring of a devastated ecosystem is a process that has been repeated a number of times during the history of life on the earth, as recounted before. Ecosystem stability depends on highly evolved complexes of established interspecific relations. It has become clear that sudden removal of a large proportion of the interacting species by an episode of mass extinction is certain to disrupt the system; the extent of disruption is related to the proportion removed. Resurgence from the end-Permian extinctions, which are estimated to have removed up to 90% of marine species (Erwin, 1994), must have involved a broad restructuring of the system! Although the end-Cretaceous crisis was less severe, the resurgence process clearly was extensive.

The discussion presented above led to the conclusion that ecosystem resurgence from mass extinctions begins with trophic relations among generalized survivors. It has become evident that this process centers on the trophic characteristics of mainstream predators and proceeds as adaptive responses to these characteristics among potential prey. Four basic ways that prey defend against mainstream predators have been identified (Hobson and Chess, 2001): (1) *smallness*, which presents difficulties to predators with large and simply constructed feeding mechanisms; (2) *dissemblance*, which results in going unrecognized by diurnal visual hunters; (3) *inedibility*, which is attained by incorporating materials that an unspecialized digestive system cannot process, and (4) *nocturnality*, which results in avoiding diurnal predators altogether.

An examination of the way predaceous fishes have responded to each of these prey defenses identifies many of the processes that have diversified modern fishes.

SMALLNESS

That smallness protects organisms against mainstream predators can be inferred from changes in the diet of kelp bass as they grow. Individuals shift from a diet of zooplankton to one of benthic microcrustacea before attaining lengths of about 10 cm and from benthic microcrustacea to fishes before attaining about 30 cm. It has been widely reported that serranids shift from crustacea to fishes as they grow; the shift is based on increasing size of prey. These reports have come from the Caribbean (Randall, 1967), the Gulf of California (Hobson, 1968), the South Pacific (Randall and Brock, 1960) and the Indian Ocean (Harmelin-Vivien and Bouchon, 1976). Obviously the trait is widespread among serranids, as probably it is among at least most generalized carnivores of the teleost mainstream.

There seems to have been a consensus that these shifts to larger prey are adaptive as means to meet nutritional needs of their own growth. It has long been recognized that fishes tend to consume the larger of available prey (e.g., Ivlev, 1961), and experimental studies have shown that organisms taken as prey tend to be, on average, larger among gut contents than in the environment (e.g., Brooks and Dotson, 1965; Werner and Hall, 1974). The usual conclusion is that larger prey are preferred and that predation on them is more efficient (Eggers, 1982; Zaret, 1980). It has been argued, however, that the main reason kelp bass and other generalized carnivores shift to larger prey as they grow is that it becomes increasingly difficult for them to capture the smaller ones (Hobson and Chess, 2001). It is questionable whether the shifts would occur if kelp bass were able to continue feeding effectively on the smaller prey because each shift involves turning to organisms that are less numerous and less accessible and also more difficult to capture. This is evident in that the incidence of empty stomachs increases greatly as the fish continues to grow. Furthermore, the way these predators stalk and attack individual prey would become inefficient as the increased nutritional needs of their own growth required them to consume smaller prey in greater numbers. Kelp bass were found to cease feeding on zooplankton upon attaining a size of about 10 cm and then to cease feeding on the larger but still small microcrustacea of the benthos when about 20 cm. It is significant that kelp bass usually attain this size in their third year and they can live at least 33 years (Love et al., 1996). Clearly, being small offers protection from such predators.

The need to shift to larger prey as they grow deprives mature mainstream predators of exceedingly rich sources of readily available prey. Probably, it is in response to this that some of the most successful evolutionary lines diverged from the mainstream based on adaptations that provide life-long access to minute prey. The key has been relative mouth size. If increasing mouth size forces kelp bass and other mainstream predators to turn elsewhere for food, an obvious solution would be to acquire a mouth that remains small relative to the size of prey.

Teleosts have solved the problem in two ways: by evolving smaller adult size or through modification of head and jaw structure that results in a mouth that is small relative to the size of their bodies. The first is the more straightforward and widespread. As noted above, many of those that attack from ambush have acquired life-long abilities to feed on microorganisms by

evolving as smaller predators. Here we are most concerned with those that have reduced relative mouth size through changes in head and jaw structure. (Many of these have also acquired smaller adult size, thus increasing the effect.)

Diurnal planktivores are prominent examples in which structural changes in head and jaws permit relatively large individuals to feed on minute prey. Virtually every major family of modern coral reef fishes includes species specialized as planktivores, and they have become major components of coral reef communities (Hobson, 1974, 1991; Davis and Birdsong, 1973). Furthermore, one planktivore, the blacksmith (*Chromis punctipinnis*, family Pomacentridae, fig. 3-16), may be the most numerous fish species in reef communities of southern California (Bray, 1981; Hobson and Chess, 1976). The blacksmith's mouth is typical of reef fishes specialized for planktivory (fig. 3-17). In addition to being small, its upturned orientation results in a shortened snout and the ability to train both eyes on prey close enough to entrap, and its highly protrusible jaws can be thrust forward to add even more precision to the strike.

Probably, the diurnal planktivores referred to here represent lines that diverged from the mainstream as benthivorous carnivores (Hobson, 1994). It is clear that adaptations for planktivory are highly evolved because their occurrence in species representing diverse families has resulted in a convergence that has tended to obscure family characteristics (Davis and Birdsong, 1973).

The highly specialized trophic features typical of reef planktivores demonstrate the adaptive capabilities inherent in the protrusible jaw of advanced actinopterygians. This feature made its initial appearance in early acanthopterygians and has since been the primary key to success in modern teleosts (Alexander, 1967; Gosline, 1971; Motta, 1984). As Gosline (1981, p. 11) stated, "The acanthopteran (acanthopterygian) system of premaxillary protrusion . . . appears to form part of the inheritance of all higher teleosts." According to Schaeffer and Rosen (1961, pp. 198–199), "It is largely the acanthopterygian mouth that has given rise to the enormous variety of specialized . . . feeding mechanisms for which teleosts are so well known". Although jaw protrusion is particularly well developed among diurnal planktivores, most of the variety of feeding mechanisms referred to here are adaptive features of perciforms specialized to consume organisms characteristic of the coral reef benthos.

A coral reef is a living surface of incredibly diverse organisms that, despite their great abundance and accessibility, are unavailable as food for generalized predators of the teleost mainstream. Only predators with highly specialized trophic capabilities find food on the reef's surface, with each limited to just a narrow and distinctive selection of the organisms present. Virtually all benefit from a small adaptive mouth, but many—such as the abundant labrids—have diets that require additional capabilities and so are more appropriately considered in the next section. Here we concentrate on predators with feeding adaptations developed mainly for prey smallness. Examples include butterflyfishes, which represent the perciform family Chaetodontidae and are widely recognized as characteristic of coral reefs (e.g., Burgess, 1978). Many heavily armored organisms on coral reefs have parts vulnerable to a precise snip by a tiny, manipulative mouth—a weakness that butterflyfishes are equipped to exploit. For example, the pebbled butterflyfish (*Chaetodon multicinctus*) uses its small mouth and pointed snout to pluck coral polyps from their armored encasements. And the long-nose butterflyfish (*Forcipiger flavissimus*) uses its exceptionally



FIGURE 3-16 Feeding aggregation of blacksmith, *Chromis punctipinnis*.

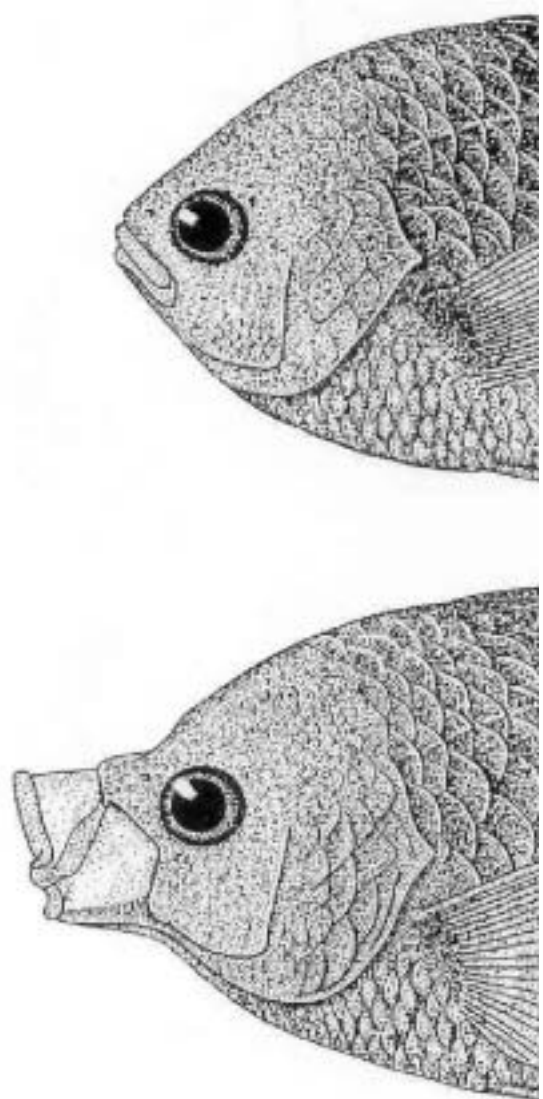


FIGURE 3-17 The protrusible upper jaw of the blacksmith is a widespread feature among diurnal planktivores. (Drawings by Ken Raymond, Southwest Fisheries Science Center; from Hobson 1991, with permission from Elsevier.)

long snout and small mouth to reach among spines of echinoids to pluck podia and pedicellaria (Hobson, 1974).

Perhaps more than any other group, butterflyfishes demonstrate the versatility inherent in the acanthopterygian mouth, which argues strongly against the current practice (e.g., Nelson, 1994) of including them in the basal perciform suborder Percoidei. Surely a close examination would distinguish butterflyfishes at a major taxonomic level apart from the more generalized members of that heterogeneous assemblage.

The advantages gained from a small, adaptive mouth extend beyond the ability to pluck minute organisms from the benthos or water column, however. In fact, the adaptive potential of an advanced acanthopterygian mouth in exploiting the vast store of potential prey among the benthos has been the major force in diversifying modern fishes. This conclusion is implicit in the findings of Gosline (1987) and Kotrschal (1988) that advanced acanthopterygian evolution has been a progression from large mouths that take mobile prey by suction (as do serranids and other mainstream predators) to smaller mouths that take benthic organisms by biting (as do labrids and many other derivative acanthopterygians).

DISSEMBLANCE

A visual assessment of the seabed in the clearest sunlit water is unable to detect the vast majority of the microcrustacea that rest there fully exposed. Some are visible by closer inspection, such as the abundant caprellid amphipods on bryozoans and algae, but most remain unseen even under careful scrutiny (Hobson and Chess, 2001) because they are either transparent or have hues and/or textures that match the underlying substrate. Generally, the match to substrate features defines the distribution of these organisms in the environment; the more abundant match the most widespread substrata (Chess and Hobson, 1997). Clearly, fishes must find prey far more difficult to detect on the seabed than in the water column.

As important as cryptic morphology is in making benthic crustacea difficult to discern, it is clear that they must remain motionless to escape detection. This became clear with repeated observations of kelp bass about 10 to 20 cm long hovering motionless for long periods, their attention clearly fixed on a substrate directly ahead, and only infrequently darting forward to snap prey (e.g., Hobson and Chess, 2001). It was evident that this predator attacked when organisms previously unseen became visible momentarily. Based on my own experience that benthic microcrustacea generally become visible only when they move, I surmise that it was prey movement that elicited the attacks. Although such organisms cease movement when predators approach, they may relax their guard and eventually move if the predator shows no further aggression (Hobson, 1979).

There must have been strong selection for increased visual acuity among predators that would habitually feed on benthic microcrustacea, so it is not surprising that species of the labroid family Labridae have acquired exceptionally sharp vision (McFarland, 1991). Prey taken by the rock wrasse (*Halichoeres semicinctus*; family Labridae, fig 3-18) from southern California reefs are mostly microcrustacea plucked "from a substrate after close visual scrutiny" (Hobson and Chess, 2001, p. 425). Two other California reef fishes of the labroid family Embiotocidae, the black perch (*Embiotoca jacksoni*; fig. 3-19) and the rubberlip perch (*Rhacochilus toxotes*, fig. 3-20) have solved the problem of prey dissemblance by ingesting mouthfuls of sediment/turf algae without distinguishing targets and winnowing edibles from inedibles only after ingestion (Drucker and Jensen, 1991).



FIGURE 3-18 Rock wrasse, *Halichoeres semicinctus* (adult male; from Hobson and Chess 2001, with permission from Springer Science and Business Media).



FIGURE 3-19 A group of black perch, *Embiotoca jacksoni*. (Photo: Tony Chess.)



FIGURE 3-20 Rubberlip perch, *Rhacochilus toxotes*.

INEDIBILITY

Being inedible may be the best defense. A wide variety of highly visible prey are readily accessible on many reefs but are protected by armored exteriors or toxic/noxious interiors from all but certain predators equipped with specialized feeding capabilities. They include sessile forms such as sponges, hydroids, anthozoans, bryozoans, and ascidians, as well as mobile mollusks and echinoids. In addition, marine plants,

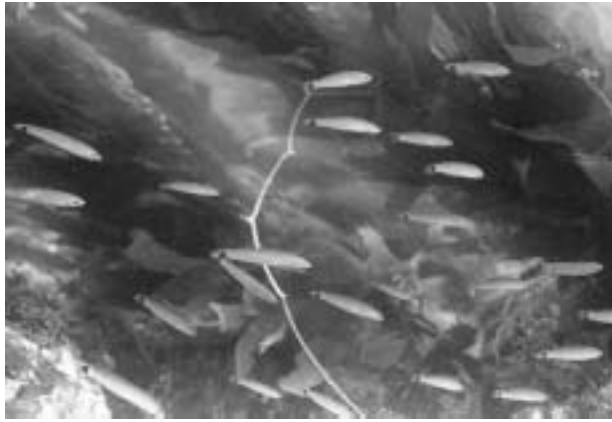


FIGURE 3-21 School of senioritas, *Oxyjulis californica*.



FIGURE 3-22 California sheephead, *Semicossyphus pulcher* (adult male).



FIGURE 3-23 Garibaldi, *Hypsypops rubicundus*.

which have combinations of structural and chemical defenses, deter feeding fishes (Hay, 1991).

Predators able to circumvent the defenses of such organisms to snip off vulnerable parts, such as butterflyfishes, are discussed above. Here we consider predators adapted to deal directly with these defensive structures. Especially prominent are the various benthivores of the perciform suborder



FIGURE 3-24 A pair of pile perch, *Rhacochilus vacca* (from Hobson and Chess 2001, with permission from Springer Science and Business Media).

Labroidei. In addition to having relatively small mouths, labroids are characterized by highly developed pharyngeal dentition that can crush ingested shelled organisms being passed from mouth to gut. This capability has enabled labroids of the families Pomacentridae and, especially, Labridae to share dominance with butterflyfishes among benthivores in coral reef communities.

Benthivorous labroids dominate the reef communities of southern California. Especially prominent are species of the family Labridae, which (in addition to the rock wrasse, introduced above) is represented by the seniorita (*Oxyjulis californica*, fig. 3-21) and the California sheephead (*Semicossyphus pulcher*, fig. 3-22). The family Pomacentridae is represented among benthivores on California reefs by the garibaldi (*Hypsypops rubicundus*, fig. 3-23), and the family Embiotocidae by (in addition to the black perch and rubberlip perch, introduced above) the pile perch (*Rhacochilus vacca*, fig. 3-24).

Species that have acquired features enabling herbivory represent a highly adaptive departure from the mainstream. Marine plants offer an immense trophic resource unavailable to mainstream species, but it is evident that adaptations related specifically to herbivory in coral reef herbivores developed in lines that had diverged from the mainstream as benthivorous carnivores (Hobson, 1994). In suggesting similar derivations for coral reef herbivores and diurnal planktivores, I stated (Hobson, 1994, p. 79), "Certain features that adapt fishes to feed on benthic animals are also adaptive in feeding on zooplankters and plants." Considering these features as preadaptations, I commented in regard to herbivory (p.79), "Benthic plants are like sessile invertebrates in possessing an array of structural and chemical defenses that deter feeding fishes (Hay, 1991), so adaptations that allow benthivorous carnivores to deal with these defenses should also be adaptive in herbivory." It was suggested that herbivory developed among benthivorous carnivores that acquired the means to access nutrients encased in cellulose, a rare substance in animal tissue but a major component of plant cell walls.

The previous remarks are limited to the derivation of coral reef herbivores because the major herbivores in California's reef communities—the opaleye (*Girella nigricans*, fig. 3-25) and the halfmoon (*Medialuna californica*, fig. 3-26)—are from a different evolutionary line. Both represent the family Kyphosidae, which has an uncertain origin. Generally, kyphosids are included among the more primitive perciforms in the suborder Percoidei (e.g., by Nelson, 1994), but certainly they are far removed from the bass-like percoids of the teleost



FIGURE 3-25 A group of opaleye, *Girella nigricans*.



FIGURE 3-26 Aggregation of halfmoons, *Medialuna californiensis*, under the canopy of a kelp forest. (Photo: Tony Chess, from Hobson 1994, with permission from Springer Science and Business Media.)

mainstream. Patterson (1964) suggested they might have been independently derived from kyphosid-like beryciforms of the Cretaceous. In contrast, species considered here as coral reef herbivores are widely considered (e.g., by Nelson, 1994) among the more highly evolved perciforms.

The relatively few kyphosids among modern fishes lack obligate ties to coral reefs, and there is no reason to suspect that such ties existed among earlier kyphosids. The family was not reported among fossils recovered from coral reef deposits of the early Tertiary (Blot, 1980; Patterson, 1993; Bellwood, 1996), so may not have been represented among perciform lines that radiated with expanding coral reef communities during the Eocene. The more typical coral reef herbivores scrape fine algae from the surface of rocks or dead coral, whereas the opaleye and halfmoon feed largely on foliose forms—often as fragments adrift in the water column (Hobson, 1994; Hobson and Chess, 2001). Furthermore, they are more omnivorous, with benthic invertebrates frequently included in their diets (Quast, 1968). The halfmoon differs further in feeding regularly on planktivore feces, which are consumed as these drift through the water column (Hobson and Chess, 2001).

NOCTURNALITY

An effective defense against visual predators is to be sheltered when most visible. This would explain why so many organisms vulnerable to generalized predators occur in exposed positions only at night. These are organisms “large enough to

grasp and entrap, yet small enough to manipulate and swallow whole” and which “lack heavy armor, spines and other noxious components that an unspecialized digestive system cannot process” (Hobson and Chess, 2001, p. 454 and above). Among them are species of amphipods, isopods, and other crustacea that kelp bass capture from the benthos during the day and that rise into the water column only at night (Hobson and Chess, 1976; Chess and Hobson, 1997).

There are varied reasons why organisms that are benthonic by day become planktonic at night (Hobson and Chess, 1976, 1986; Chess and Hobson, 1997). Some disperse in the nocturnal water column to hunt prey, as do certain mysids; others are there to reproduce, as are epitokous nereids. Some, including caprellids and certain myodocopid ostracods, remain at lower levels of the water column, but most are like those isopods that range widely in open water. Some, including certain ostracods, isopods, and amphipods, rise through the water column to concentrate at the water’s surface. For whatever reasons these organisms need to enter the water column, probably they do so at night because in reduced light they are less conspicuous as visual targets.

The protection that these organisms gain by limiting their excursions into the water column to periods of darkness is only relative, however, because many predators have acquired abilities to detect prey in dim light. For most, this has involved increased visual sensitivity; many that have acquired this feature have been enormously successful. Some, including species of the perciform families Lutjanidae and Haemulidae, school in large numbers at the edge of reefs while inactive during the day, and then spread out to forage on organisms that emerge from sediments in surrounding areas at night (Hobson, 1968). Others, including species of the perciform families, Apogonidae and Priacanthidae, shelter in reef caves and crevices by day and forage above the reef at night on crustacea and other prey that are in the water column there only after dark (Hobson, 1974).

It is clear that abilities to function at low levels of illumination are highly adaptive. This is evident in that of the great variety of beryciforms that were so dominant during the Cretaceous, the relatively few present-day survivors are specialized for activity in dim light. These few, however, include some highly successful species. The very abundant squirrelfishes and soldierfishes of the nocturnal family Holocentridae are prominent components of reef communities throughout the present tropics (Randall, 1967; Hobson, 1974; Sano et al., 1984). The only other beryciforms in modern reef communities are small, inconspicuous flashlight fishes, family Anomalopidae, and pinecone fishes, family Monocentridae (Kotlyar, 1985; McCosker and Rosenblatt, 1987), but the order is well represented in the dimly lit deep sea. Among such beryciforms are the roughies (family Trachichthyidae; Nelson, 1994), including the orange roughy (*Hoplostethus atlanticus*), a major commercial food fish exported from New Zealand.

There are no beryciforms near California shores, but nocturnal perciforms are prominent there, especially in the south. Like their close relatives in the tropics, the sargo (*Anisotremus davidsoni*, fig. 3-27) and the salema (*Xenistius californica*, fig. 3-28), both of the grunt family Haemulidae, school above or near southern California reefs during the day and forage on emergent crustacea and other small organisms in surrounding open areas at night (Hobson and Chess, 1976; Chess and Hobson, 1997). The same behavior describes the queenfish (*Seriplus politus*, family Sciaenidae, fig. 3-29) and

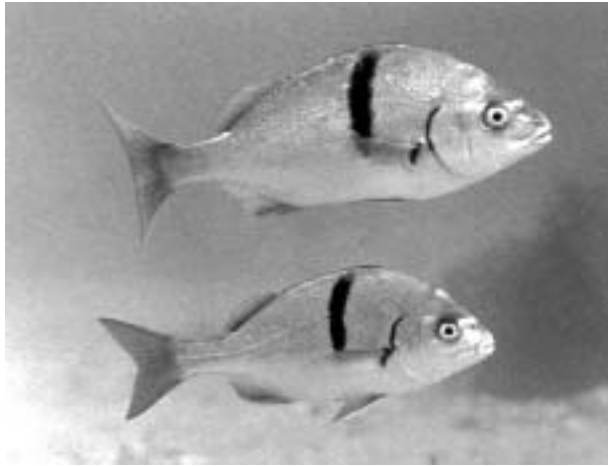


FIGURE 3-27 Pair of sargo, *Anisotremus davidsoni* (from Hobson 1994, with permission from Springer Science and Business Media).



FIGURE 3-28 Salema, *Xenistius californiensis*.



FIGURE 3-29 School of queenfish, *Seriphus politus* (from Hobson 1994, with permission from Springer Science and Business Media).

the walleye surfperch (*Hyperprosopon argenteum*, family Embiotocidae, fig. 3-30), except that the latter occurs abundantly off central and northern California as well (Eschmeyer et al., 1983).

Nocturnal predators that forage over sand at the base of the water column, such as the sargo, tend to have smaller eyes than predators that forage high in the water column, such as the salem and walleye surfperch, probably because ambient

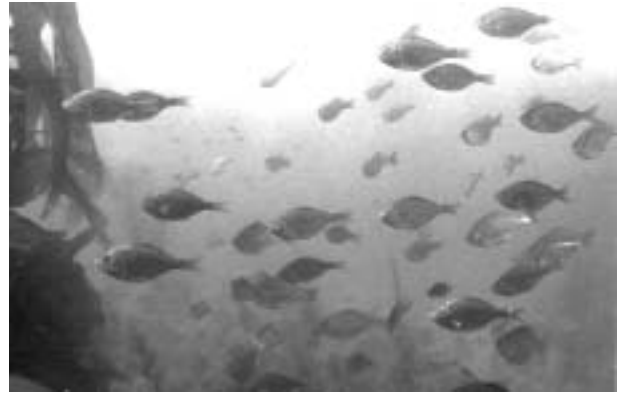


FIGURE 3-30 School of walleye surfperch, *Hyperprosopon argenteum*.



FIGURE 3-31 Treefish, *Sebastes serriceps*.



FIGURE 3-32 Black-and-yellow rockfish, *Sebastes chrysomelas*.

light increases near the seabed by reflected moonlight and/or starlight (Hobson et al., 1981).

Nocturnal foraging is widespread among species of the scorpaeniform family Scorpaenidae. Some, for example, the treefish (*Sebastes serriceps*, fig. 3-31) and the black-and-yellow rockfish (*Sebastes chrysomelas*, fig. 3-32), find their prey close to the sea bed; others, such as the kelp rockfish, feed in the water column close to columns of giant kelp (*Macrocystis*). Consistent

with circumstances among the nocturnal perciforms, as noted above, kelp rockfish (fig. 3-5) have larger eyes (even though treefish typically feed among rocks, not over sand).

Like *smallness*, *dissemblance*, and *inedibility*, therefore, *nocturnality* has promoted specialized feeding adaptations characteristic of certain evolutionary lines. But though the others involved osteological features, with major change in external appearance, nocturnality has elicited mainly sensory features, especially increased photic sensitivity. So while predators adapted to prey smallness, dissemblance or inedibility have acquired distinctive morphological features, predators adapted to nocturnality have remained morphologically similar to their progenitors—at least in features used to assess phylogeny. The result has been that nocturnal predators tend to occupy basal positions in phylogenetic classifications (e.g., Nelson, 1994); thus, both the salema and sargo (as haemulids) and the queenfish (as a sciaenid) generally are placed in the basal perciform suborder Percoidei, whereas treefish and kelp rockfish are placed in the basal scorpaeniform family Scorpaenidae (Gosline, 1971; Nelson, 1994). This chapter, however, considers species specialized as nocturnal predators to be classified as divergent from the mainstream, much like labroids and others generally advanced teleosts. They differ mainly in that their divergence is based on sensory and behavioral features that cannot be properly assessed by procedures ordinarily used in studies of phylogeny.

Cenozoic Influences on Distributions, Extinctions, and Originations

Although basic features of modern reef ecosystems were established with resurgence from the end-Cretaceous extinctions early in the Tertiary, evolution of these systems has continued to evoke change through the present. Conditions under which teleosts diversified, as recounted above, varied in ways that greatly influenced subsequent extinctions, originations, and distributions.

It has been suggested, however, that certain broad features based on trophic relations were in place at the outset (Hobson, 1994). Early Tertiary seas were warm far to the north and south of the present tropics (Newell, 1971), so the temperature barriers to poleward expansion, so prominent today, were not a feature of that period. Of the two types of divergence from the evolutionary mainstream defined above, lines based on advances in existing modes of attack—the ambush and the straightforward rush—should have had more poleward mobility. This would follow if, as suggested, lines based on new modes of feeding developed mainly as elements of expanding coral reef communities. Certainly the ambush and straightforward rush would have been more adaptive in a wider range of settings than modes of feeding associated with specific environmental features.

Distribution at Higher Latitudes

Based on criteria identified above, poleward mobility should have been widespread among scorpaeniforms and pleuronectiforms, as well as among gobioid and blennioid perciforms. Furthermore, once established at higher latitudes, representatives of these groups would have been positioned to evolve as temperate species as the seas there cooled. Consistent with this scenario, coastal communities at high latitudes today, including those off northern California, are dominated by such forms (Hobson, 1994).

Cooling developed at higher latitudes with the progressive isolation of Antarctica. When Australia and South America separated from Antarctica late in the Eocene, 40–45 mya, the southern high latitudes were opened for the Circumpolar Current. This cut off the southerly flow of warm water from tropical latitudes that had maintained relatively high sea temperatures in that region (Stanley, 1989). By mid-Miocene, the condition had progressed to the extent that an icecap covered Antarctica and seas had cooled everywhere, both north and south of the equator, except in the sun-warmed surface waters of the tropics (Newell, 1971).

Distribution at Lower Latitudes

Lines that proliferated with expanding coral reef communities diversified far more than lines distributed at higher latitudes, discussed above, but they were limited in extending their distributions poleward. This limitation has been attributed to low sea temperatures at higher latitudes (e.g., Mead, 1970), but, as noted above, high-latitude seas were warm during the perciform radiation. It is more likely that exclusion of coral reef perciforms from high latitudes related to limits on the distribution of reef-building corals. According to Ziegler et al. (1984), poleward distribution of reef corals has depended more on sun angle than on water temperature. Their findings indicate that sunlight penetrating to the sea bed since Mesozoic time has been insufficient for the coral's symbiotic algae beyond about 36° latitude, which would have made this the poleward limit for reef-building corals and also for organisms with obligatory connections to coral reef communities.

Although limited in distributions poleward, coral reef fishes had great success extending their lineages west and east. It is believed this expansion originated in the region of what is now the Indo-Malay Archipelago (Ekman, 1953) and that from there reef fishes spread through all tropical seas of the world. Westward expansion would have progressed along the shores of the Tethys Sea, and eastward expansion would have progressed from island to island into the Pacific.

When teleosts diversified early in the Eocene, Tethys had been narrowed by northward movement of southern continents, but nonetheless remained a pantropical seaway. Subsequent global developments, however, created major barriers to trans-Tethys distributions. Of particular significance was closing of the seaway between what is now the Indian Ocean and the Mediterranean Sea. This occurred when Africa collided with Eurasia during the Miocene (14–18 mya; Stanley, 1989), blocking passage between the region now encompassing the Indo-Malay Archipelago and what had been the western reaches of Tethys.² Tropical reef fishes had gone this way in extending their lines to the ancestral Atlantic, Caribbean, and—as the Isthmus of Panama had not yet connected North and South America—the eastern Pacific. The Caribbean–Pacific connection closed with formation of the Isthmus of Panama during the Pliocene (3–4 mya; Stanley, 1989), and since then tropical eastern Pacific shore fishes have developed without further input from the east.

² Fishes to the east of this barrier continued to evolve as components of what is now recognized as the Indo-Pacific fauna. Today this diverse complex of species extends from the coast of east Africa (and the Red Sea) eastward across the Indian and western Pacific Oceans to Polynesia, with some elements in the eastern Pacific.

Although it has been over three million years since closure of the Atlantic–Pacific connection between North and South America, the vast majority of fishes near shore in the tropical eastern Pacific today have their closest relatives in the Caribbean and tropical Atlantic, which shows where their affinities lie (Ekman, 1953; Walker, 1960; Rosenblatt, 1967). Relatively few are products of eastward distribution of Indo-Pacific species from the west. There have been no land barriers to impede progress from that direction, but the broad expanse of open ocean that separates mid-Pacific islands from the Americas, which Ekman (1953) termed the East Pacific Barrier, is considered to have blocked passage of most coastal marine organisms (e.g., Grigg and Hey, 1992). It may be, however, that this barrier is less an obstacle to coastal fishes (and certain other organisms, including reef corals) than is generally supposed; an argument can be made that the main reason for few Indo-Pacific reef fishes (and reef corals) in the eastern Pacific at present is that habitats there generally are unfavorable for them.

The marine environment near shore in the tropical eastern Pacific today is mainly one of isolated rocky reefs separated by extensive expanses of sand and/or mud. A broad assortment of tropical reef fishes inhabits the rocky areas (Allen and Robertson, 1994), but forms that inhabit the broad areas of sand and/or mud are more typical of the region. Examples include representatives of the perciform families Haemulidae and Sciaenidae—the grunts and croakers. Grunts generally favor areas of sand, including reef sand-patches (Hobson, 1968), while most croakers favor areas of sand/mud, which tends to draw many to the vicinity of river outflows, including estuaries (Allen and Robertson, 1994).

The first grunt on record is represented by a fossilized otolith from a mid-Eocene coral reef (Patterson, 1993), which would connect the early history of its line with the perciform radiation and resurgence of coral reef communities early in the Tertiary. From this, it would follow that the line evolved with adaptations that enabled feeding on organisms in sediment within and adjacent to coral reefs. Croakers may have evolved in a similar way, but there is lack of evidence that would support this possibility. Although today there are grunts and croakers among eastern Pacific reef fishes that forage in reef sand-patches (Hobson, 1968; Allen and Robertson, 1994), many more of both families occur over the expanses of sediment that lie off most mainland shores (Hobson, 1968; Allen and Robertson, 1994).

Coral reefs are poorly developed at present in the eastern Pacific (Darwin 1842; Durham, 1966; Glynn, 1997), but this condition developed only after final closure of the tropical Atlantic–Pacific connection. There was a greater variety and abundance of reef corals in the eastern Pacific earlier in the Cenozoic, including many with affinities eastward in the Caribbean and beyond (Durham, 1966). The eastern Pacific environment turned against coral reefs late in the Miocene, however, and became increasingly unfavorable to them as uplifting of what is now the Isthmus of Panama progressively closed the Central American Seaway (Stanley, 1989).

Final closure of the tropical Atlantic–Pacific connection coincided with the onset of alternating expansion and contraction of glaciers that characterized the Pleistocene (Stanley, 1989). Seas cooled and dropped to lower levels, as water became ice in each expanding glacier, then warmed and rose to higher levels, as ice became water in each contracting glacier. Although conditions associated with expanding glaciers have been widely destructive to coral reefs, conditions associated with glacier

contraction have provided coral reefs time to recover in many regions. Not so in the eastern Pacific, however, where (as at present) contraction has been a time of frequent and powerful El Niño–Southern Oscillation (ENSO) events that have proved damaging to reef corals (Colgan, 1989; Glynn, 1997).

Although the vast majority of today's tropical eastern Pacific shore fishes have evolutionary ties to the Caribbean and tropical Atlantic, all of the region's current reef-building corals are from the central Pacific. Reef corals present in the eastern Pacific when the tropical Atlantic–Pacific connection finally closed (including the many with links to the Caribbean) were eliminated during Pleistocene glaciation, and subsequent recruitment has been limited to Indo-Pacific migrants from the west (Dana, 1975). But as with Indo-Pacific reef fishes, relatively few Indo-Pacific reef corals have become established in the eastern Pacific. The generally held notion that this has resulted from difficulties in crossing the Eastern Pacific Barrier ignores the findings of many (e.g., Dana, 1975; Colgan, 1989; Glynn, 1997) that the eastern Pacific generally offers poor habitats for coral reefs.

Although the tropical eastern Pacific environment is recognized as “marginal for coral reef development” (Dana, 1975, p. 355), little has been made of the great difference in coral coverage between the offshore islands and the mainland. Reef corals are of relatively few species along both island and mainland shores (Glynn, 1997), but coral coverage is much richer at the islands; Clipperton, the island farthest offshore, is a coral atoll (Glynn, 1996). Conditions are especially poor for reef corals along mainland shores, at least partly because continental runoff into coastal waters typically carries materials damaging to reef corals—notably suspended sediments and algae-nourishing nutrients (Wood, 1999). Localized concentrations of cold water at centers of coastal upwelling also contribute to conditions unfavorable for reef corals near the mainland. (Dana, 1975).

Indo-Pacific reef fishes, too, are more abundant around the islands (Rosenblatt, 1967); a number that are abundant around the islands generally are rare or absent along the adjacent mainland (Rosenblatt et al., 1972, Allen and Robertson, 1994). Furthermore, the few mainland locations noted for unusual abundances of Indo-Pacific fishes—the Cape region of Baja California and the Gulf of Chiriqui in Panama (Walker, 1960; Rosenblatt et al., 1972)—are also noted for unusual abundances of reef corals (Squires, 1959; Dana, 1975). That eastern Pacific distributions of Indo-Pacific fishes and reef corals are so closely matched is consistent with the close ties that have existed between them throughout their histories, as recounted above. Finally, it is telling that though “reef fishes” can be an appropriate term in general reference to fishes around the islands (including those active over sand patches or sediment peripheral to reefs), it is rarely, if ever, appropriate as a general reference to fishes along mainland shores (despite the prominence of reef fishes at some locations). An appropriate term for general reference to fishes along the mainland is “shore fishes”.

It would appear, therefore, that though fishes arriving in the eastern Pacific from the tropical Atlantic and Caribbean often found favorable habitats along western shores of tropical America, fishes from the central Pacific generally have not. The difference may relate to environments encountered as evolutionary lines progressed westward or eastward from origins in the ancestral Indo-Malayan region. With westward distribution progressing along the shores of Tethys, there would have been extensive experience with continents in the evolutionary history of lines that reached the Eastern Pacific from that direction. Certainly this experience would have

weakened, if not eliminated, obligatory ties to coral reefs connected to their early history. (Many of today's eastern Pacific grunts may have such a history, as noted above.) In contrast, as eastward distribution from the Indo-Malayan region progressed from island to island across the Pacific, lines that reached the Eastern Pacific from that direction would lack evolutionary experience with continental shores, and they would also have maintained contact with insular coral reefs throughout their evolution. Lines with this history may well have retained obligatory relations with coral reefs connected to their origins, which could explain why so few migrants from the west have become established in the tropical eastern Pacific.

To Be a California Marine Fish

A review of the geographical affinities of taxa involved is an effective way to begin a consideration of what it has taken to be a successful California marine fish.

SCORPAENIFORMES

The major California scorpaeniforms are among the scorpionfishes (family Scorpaenidae), the sculpins (family Cottidae), the greenlings (family Hexagrammidae), and to a lesser extent, the poachers (family Agonidae). Representatives of these families have affinities that are overwhelmingly temperate. Of the scorpionfishes, species of the genus *Sebastes*—the rockfishes—dominate reef communities across the North Pacific Rim from California to Japan, with 61 species reported from California alone (Eschmeyer et al., 1983; Allen and Smith, 1988). A prominent example is the black rockfish (*Sebastes melanops*, fig. 3-33), a major component of many northern California reef communities. There are no species of *Sebastes* in the tropics, but two other scorpaenids represent the only exceptions to strictly temperate distributions among California scorpaeniforms: the California scorpionfish (*Scorpaena guttata*, fig. 3-34) and the rainbow scorpionfish (*Scorpaenodes xyris*). The former is a warm-temperate representative of a tropical genus that occurs from southern California to the Gulf of California. The latter is widely distributed from southern California to Peru, including the Galapagos Islands (Eschmeyer et al., 1983).

The sculpins (family Cottidae) are widespread in reef communities at higher latitudes, but though more numerous than other families on many reefs, generally they go unnoticed because most are so small and cryptic. An atypically large cottid on many California reefs is the cabezon (*Scorpaenichthys marmoratus*, fig. 3-35), which is the only member of this large family to have commercial importance (Eschmeyer et al., 1983).

The greenlings (family Hexagrammidae) are limited to temperate reefs of the north Pacific (Quast, 1965; Hart, 1973), where they are represented by, in addition to the ling cod introduced above, the kelp greenling (*Hexagrammos decagrammus*, fig. 3-36) and the painted greenling (*Oxylebius pictus*; fig. 3-37)

Most of the poachers (family Agonidae) are fishes of deep-water sediment, but some are numerous, though inconspicuous, on cold-temperate reefs near shore. Examples off central and northern California are the kelp poacher (*Agonomalus mozinoi*) and the rockhead (*Bothragonus swanii*). All are small, cryptic, and sedentary, so generally go unnoticed by casual observation. They are distinctive in being covered by bony plates that meet but do not overlap. Where diets are known,



FIGURE 3-33 Aggregation of black rockfish, *Sebastes melanops*.

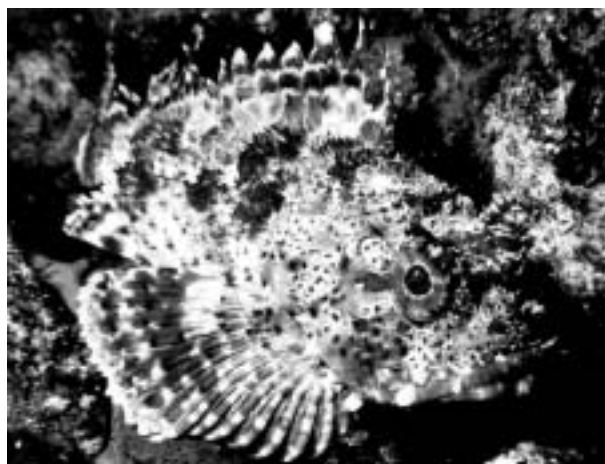


FIGURE 3-34 California scorpionfish, *Scorpaena guttata*.



FIGURE 3-35 Cabezon, *Scorpaenichthys marmoratus*.

their major foods are microcrustacea (Hart, 1973; Eschmeyer et al., 1983).

PLEURONECTIFORMES

Two pleuronectiform families (as defined by Hensley and Ahlstrom, 1984), the Pleuronectidae and the Paralichthyidae, dominate near California shores.

The Pleuronectidae are strictly temperate forms. Of the 20 species that occur in California (Eschmeyer et al., 1983), 17, including the C-O turbot, range only northward to various



FIGURE 3-36 Kelp greenling (male), *Hexagrammos decagrammus*.

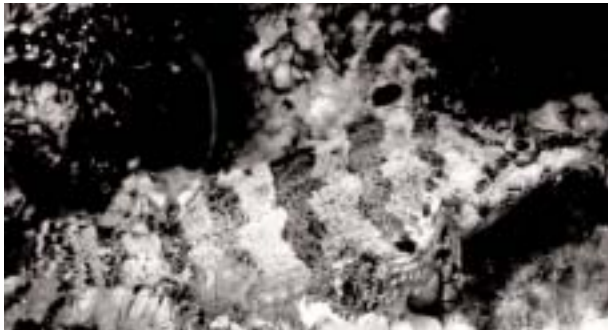


FIGURE 3-37 Painted greenling, *Oxylebius pictus* (from Hobson and Chess 2001, with permission from Springer Science and Business Media).



FIGURE 3-38 Giant kelpfish, *Heterostichus rostratus*.



FIGURE 3-39 Group of kelp perch, *Brachyistius frenatus* next to stipes of giant kelp, *Macrocystis*.

locations across the North Pacific Rim between Alaska and Japan. The other three occur off southern California and Baja California; two also have isolated populations in the northern Gulf of California. There are no pleuronectids in the tropics.

Though most of the Paralichthyidae worldwide are temperate species, the family has many ties to the tropics. Of the seven species that occur off California (Eschmeyer et al., 1983, who considered them bothids), only two, including the speckled sand dab, range north to Alaska. Furthermore, though the California halibut has been reported as far north as Washington, the other four range only southward—three into the Gulf of California, the fourth to Costa Rica. That paralichthyids have many tropical connections is also evident in that they have been considered a subfamily of the Bothidae, a family with many tropical representatives (e.g., Norman, 1934).

PERCIFORMES

Most perciforms on reefs of southern California represent families that occur at least incidentally on tropical reefs. They include the sea basses (family Serranidae), grunts (family Haemulidae), croakers (family Sciaenidae), sea chubs (family Kyphosidae), damselfishes (family Pomacentridae), wrasses (family Labridae), labrisomids (family Labrisomidae), and gobies (family Gobiidae). All but one of these families are prominently represented in coral reef communities throughout the tropics (Hiatt and Strasburg, 1960; Hobson, 1974; Randall, 1967; Sano et al., 1984; Vivien, 1973). Labrisomids, the one exception, are mostly inhabitants of inorganic reefs in the Western Hemisphere tropics (Thomson et al., 1979; Nelson, 1994).

Two perciform families prominent off southern California—the clinids (family Clinidae) and the surfperches (family Embiotocidae)—vary from this pattern. Both are limited to temperate waters (Nelson, 1994), and they are also represented in reef communities throughout California. Among the clinids are the spotted kelpfish (fig. 3-12) and the giant kelpfish (*Heterostichus rostratus*; fig. 3-38); among the ubiquitous surfperches are the kelp perch (*Brachyistius frenatus*, fig. 3-39) and the shiner perch (*Cymatogaster aggregata*, fig. 3-40); nevertheless, although both families are strictly temperate, they have tropical affinities. The clinids are closely related to tropical labrisomids (George and Springer, 1980; Stepien, 1992), and

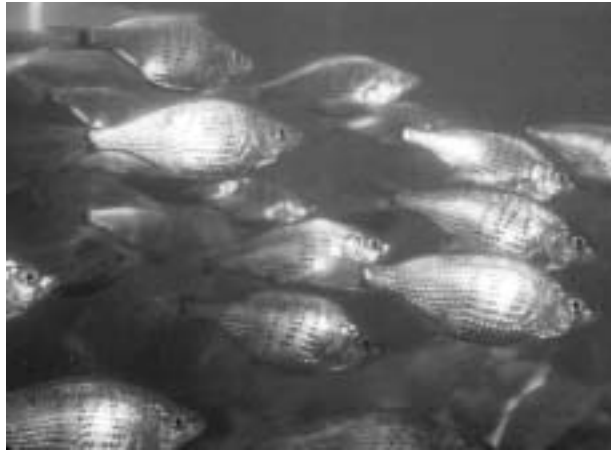


FIGURE 3-40 School of shiner perch, *Cymatogaster aggregata*.

an earlier study that combined the two groups (Hubbs, 1952) concluded that their origin was in the American tropics. Similarly, although the 21 species of surfperches are temperate forms (Eschmeyer et al., 1983), their closest relatives—the cichlids (family Cichlidae) and damselfishes—are tropical, and these three families, along with the tropical wrasses and parrotfishes (Scaridae), constitute the suborder Labroidei, a group with tropical origins (Kaufman and Liem, 1982).

Although the great majority of California perciforms can be linked to tropical origins, there is no evidence of tropical connections for representatives of the perciform suborder Zoarcoidei (as defined by Nelson, 1994). These include the ronquils (family Bathymasteridae), the gunnels (family Pholidae), and the pricklebacks (family Stichaeidae)—all strictly cold-water families that dominate at high latitudes in the northeastern Pacific (Hart, 1973; Allen and Smith, 1988). Examples include the stripedfin ronquil (*Rathbunella hypoplecta*; fig. 3-41) and the kelp gunnel (*Ulvicola sanctaerosae*; fig. 3-42). These two are among the few representatives of this cold-water assemblage to occur southward into southern California.

Products of Other Evolutionary Lines

Earlier in this chapter, it was noted that actinopterygians surviving each episode of global extinctions included evolutionary lines apart from the mainstream. Although lacking mainstream potential to diversify in new environments, these persisted—even dominated—under specific ecological circumstances. Following are examples of some now prominent off California.

LOWER TELEOSTS

Evolutionary lines believed to have developed with the first major teleost radiation were classified by Gosline (1971) as “lower teleosts”, an assessment that would connect their early history with ecosystem resurgence from end-Triassic extinctions. These lines departed the mainstream with primitive features that proved adaptive in Mesozoic habitats and also enabled some to not only survive the end-Jurassic and end-Cretaceous extinctions, but also to persist with prominence into the present. Lower teleosts among modern marine fishes of California include clupeiforms (herrings, sardines, and anchovies), osmeriforms (smelts), and salmoniforms (salmon and anadromous trout).

Clupeiforms are mostly small, silvery fishes that occur in mid-water schools and feed on plankton. Modern representatives



FIGURE 3-41 Stripedfin ronquil, *Rathbunella hypoplecta* (from Hobson 1994, with permission from Springer Science and Business Media).



FIGURE 3-42 Kelp gunnel, *Ulvicola sanctaerosae* (from Hobson 1994, with permission from Springer Science and Business Media).

include two species of the family Clupeidae—the Pacific herring (*Clupea pallasii*) and the California sardine (*Sardinops sagax*). Both occur in coastal waters of California and across the North Pacific Rim from Mexico to Asia. Another is the northern anchovy (*Engraulis mordax*, family Engraulidae), which is a major species from Baja California north to Canada (Eschmeyer et al., 1983).

Osmeriforms have persisted based partly on features adaptive in the deep sea, but some modern species occur in coastal habitats (others in fresh water) at higher latitudes (Nelson, 1994). The order is represented off California by the smelts, family Osmeridae, which, like clupeiforms, are small silvery fishes that occur in schools and feed on zooplankton. Some marine osmerids spawn in shoreline turbulence, others enter rivers or streams to spawn in fresh water. Two of the former, the surf smelt (*Hypomesus pretiosus*) and the night smelt (*Spirinchus starksi*), enter the surf zone from Alaska to California (particularly off northern California) to spawn and lay eggs in coarse sand on an incoming tide. Both may spawn in the same areas, but the surf smelt does so by day, whereas the night smelt, as its name implies, does so at night (Eschmeyer et al., 1983). Among north-coast osmerids that ascend rivers to spawn in fresh water is the longfin smelt (*Spirinchus thaleichthys*; Eschmeyer et al., 1983).

Salmoniforms in California marine habitats—the various salmon and anadromous trout of the family Salmonidae—are like certain osmeriforms in entering freshwater streams to



FIGURE 3-43 Topsmelt, *Atherinops affinis*.

spawn; salmonids have developed this habit far more than osmeriforms or any other group. Salmon of the genus *Oncorhynchus* and trout of the genus *Salmo* are particularly abundant in the northeast Pacific, where many coastal streams lead to appropriate spawning grounds.

INTERMEDIATE TELEOSTS

Evolutionary lines thought to have gained prominence with the resurgence from end-Jurassic extinctions are among those that Gosline (1971) identified as “intermediate teleosts.” Most had attained the acanthopterygian level of teleost development, with mainstream elements represent the series Percomorpha (as defined by Nelson, 1994). The first percomorphs were beryciforms, which, as recounted above, perpetuated the main line and subsequently gave rise to modern forms (the “higher teleosts” of Gosline, 1971). Concurrent with the evolution of percomorphs has been that of another set of acanthopterygian orders, grouped by Nelson (1994) as the series Atherinomorpha. These departed the mainstream based on features adapted to a pelagic setting and, unlike percomorphs, without evidence of reef involvement. Among atherinomorphs that have persisted to the present, atheriniforms (silversides) and beloniforms (needlefishes, halfbeaks, and flyingfishes) are prominently represented in California marine communities, whereas cyprinodontiforms are exceptionally abundant (and diverse) in tropical fresh waters and as aquarium fishes.

California atheriniforms include species of the family Atherinidae: the topsmelt (*Atherinops affinis*), the jacksmelt (*Atherinopsis californica*), and the grunion (*Leuresthes tenuis*). These are elongate, silvery fishes that generally occur in schools and feed on zooplankton in the upper regions of the water column, but though topsmelt often dominate the canopy region of southern California’s kelp forests (fig. 3-43; Hobson et al., 1981), jacksmelt and grunion generally occur away from reefs. Grunion are distinctive in that they spawn by coming up onto beaches during spring and summer with a nocturnal rising tide to deposit eggs in the sand, mainly in southern California (Walker, 1952).

Beloniforms are mostly fishes of warm seas, but several are abundant off southern California. Although a few species of the needlefish family Belonidae are large (a meter or more long) and piscivorous, most are like atherinids in being small and elongate silvery fishes that feed on zooplankton close to the surface. Two of the more common—the California needlefish (*Strongylura exilis*, family Belonidae) and the California halfbeak (*Hyporhamphus rosae*, family Hemiramphidae)—usually are close to shore, often in bays, whereas the California flyingfish

(*Cypselurus californicus*, family Exocoetidae) generally occurs offshore at the surface (Eschmeyer et al., 1983).

BASIS OF THEIR EVOLUTIONARY PERSISTENCE

The continued success of these diverse evolutionary lines can be attributed to some combination of a few highly adaptive features. Foremost are the small size and pelagic habits that have enabled so many to feed on zooplankton, which probably represent the richest source of prey in the sea. In positioning themselves to feed on zooplankton in the water column, they become fully exposed to predators. I suggest that it was largely an adaptive response to this threat that virtually all have evolved as silvery fishes that occur in schools. Schools are to their advantage because predators are likely to have difficulty distinguishing targets from among flashing silver sides of schooling individuals (Hobson 1968, 1978). That these attributes have evolved independently in a variety of lineages is strong evidence that they are highly adaptive. Among lower teleosts, they characterize most clupeiforms and many osmeriforms; among intermediate teleosts, they characterize most atheriniforms and many beloniforms.

Those that have evolved as piscivorous predators may gain another benefit from their silvery sides. According to Denton and Nicol (1962, 1965), light reflected from the sides of silvery fishes can project a mirror-like effect that renders the fish virtually invisible. This effect, however, requires that the fish be rigid and vertical, which questions its effectiveness as a defense for small fishes that occur in large schools—like clupeids and atherinids. The reason is that at any given time various individuals in such schools deviate from the vertical to produce highly visible flashes of reflected light. It is different, however, with large, silvery predators like needlefishes that hover in the water, as these tend to be rigidly vertical when stalking prey. So even though California needlefish may grow to a meter in length and are fully exposed while approaching prey in open water, they may go unseen by their quarry before the attack.

Certain of these lines probably owe their persistence to highly distinctive means of reproduction that allow vulnerable early life-history stages to avoid the marine environment near shore. That grunion leave the sea to deposit eggs under beach sand is a clear indication that eggs are at particularly high risk in coastal waters. Similar though less extreme habits define many of the osmerids; for example, eggs of surf smelt and night smelt are deposited in sand under turbulence of waves breaking on shore. Even more telling are the habits of anadromous salmonids and osmerids that leave the marine environment to spawn in fresh water—presumably finding there more secure settings during vulnerable periods of early life, from eggs through early juveniles. The highly refined behavior that leads salmon and certain trout from the sea to specific streams certainly indicates exceptionally strong selection for means to escape problems with spawning in coastal marine waters.

Problems associated with reproducing near shore in the sea have profoundly influenced behavior, morphology, and distribution among a wide variety of California’s marine fishes, as discussed further in sections that follow.

Determinants of Species Composition in California Marine Communities

Based on the evolutionary history of the mainstream, recounted above, it is evident that virtually all acanthopterygian

lines can be traced to tropical origins; nevertheless, the distribution of California fishes shows that some developed more readily than others at higher latitudes. That generalized carnivores with trophic features widely adaptive in nearshore habitats have more poleward mobility than species with feeding adaptations developed on coral reefs explains the dominance of scorpaeniforms, pleuronectiforms, and zoarcoid perciforms in California's cold-temperate habitats. But what about species composition of communities in warm-temperate habitats south of Point Conception?

It is well known that species in California's warm-temperate communities represent a mix of temperate and tropical lineages (Ebeling and Bray, 1976; Hobson et al., 1981), but less appreciated is the extent that tropical lineages dominate. Of 34 teleost species recorded on transects at Santa Catalina Island during all seasons over three years (9/72–9/75: Hobson and Chess, 1986, 2001), all 24 perciforms and one scorpaeniform (California scorpionfish) are of tropical stock. Clearly their tropical connections did not prevent adapting to warm-temperate conditions; in fact their dominance in communities off southern California might be taken as a contradiction to the notion that advanced perciforms have been limited in poleward distributions by early ties to coral reefs.

That there is greater poleward mobility in evolutionary lines unrestricted by coral reef connections does not mean that coral reef fishes are inherently incapable of acquiring tolerance for temperate conditions or evolving as temperate species; to the contrary, it is clear that many have done so. Although earlier in the chapter it was proposed that evolutionary lines originating with expanding coral reef communities early in the Tertiary were likely to have started with obligate ties to these communities, it was later pointed out that many of these ties were weakened or eliminated by subsequent evolutionary processes—particularly in the highly variable environments off continental shores. Consider the species of tropical lineages now dominant in the warm-temperate habitats of southern California. Presumably many evolved from progenitors of coral reef stock that had previously lost whatever obligatory connections their early ancestors may have had to coral reefs. The grunt family Haemulidae was cited as representing numerous examples, and, two grunts—the sargo (*Anisotremus davidsoni*) and salema (*Xenistius californiensis*)—range northward from the Gulf of California to prominence through southern California. But tropical species of coral reef stock would not have expanded their lines to temperate latitudes without both an incentive and a mechanism.

The incentive could well have been the great store of food resources readily available at higher latitudes. Organisms of types consumed by tropical reef fishes are (and presumably were) more accessible at higher latitudes. Sessile invertebrates are less cryptic and noxious in temperate regions than in the tropics (e.g., Bakus and Green, 1974; Jackson et al., 1971), and zooplankton of types taken by diurnal planktivores are more numerous near kelp forests of southern California than above coral reefs of the tropical Pacific (Hobson and Chess, 1976, 1978). Macrovegetation, too, generally is more abundant and accessible at temperate latitudes than in the tropics. Fishes that feed on such forms in the tropics would gain great trophic benefit by extending their distributions poleward.

The mechanism that enabled certain lines of tropical fishes to become established at temperate latitudes was likely to have involved the latitudinal shifts in isotherms that have periodically extended tropical conditions toward the poles since

Miocene time. It has been suggested that certain families and genera of tropical invertebrates produced temperate representatives this way (Smith, 1919; Durham, 1950), and similar histories can be inferred for certain fishes.

Representatives of the perciform suborder Labroidei have been particularly successful as temperate derivatives of tropical stock. These include the blacksmith and garibaldi (family Pomacentridae); the rock wrasse, senorita, and sheephead (family Labridae); and many of the surfperches (family Embiotocidae), including the kelp perch, shiner perch, black perch, and pile perch (Hobson and Chess, 1976, 1986, 2001). Although relatively few in species compared to tropical labroids, the great numbers of individuals involved is the main reason that tropical derivatives dominate in the warm-temperate communities of southern California.

The great success that labroids have had in warm-temperate habitats is based largely on feeding capabilities inherited from tropical progenitors. Of particular benefit are the relatively small, adaptable mouths and highly evolved pharyngeal dentition that characterize the group. These features, used together, enable feeding on the minute shelled organisms that are so abundant and exposed on California reefs. Among such prey are bryozoans, ascidians, and ophiuroids (Quast, 1968; Bray and Ebeling, 1975; Hobson and Chess, 2001). Although tropical representatives of these invertebrate groups are important prey of labroids on coral reefs (Randall, 1967; Hobson, 1974; Sano et al., 1984), temperate representatives constitute a larger proportion of labroid diets on warm-temperate reefs (e.g., Hobson and Chess, 2001), probably because their defenses are less developed there.

It has been suggested that benthic invertebrates are more cryptic and noxious in the tropics than in temperate regions because threats from predatory fishes increase toward the equator (e.g., Bakus, 1969, 1981; Bakus and Green, 1974; Jackson et al., 1971). This suggestion has been criticized because supporting evidence is perceived as lacking (e.g., by Jones et al., 1991), but I accept it as a valid—and important—generalization based on finding that though many fishes of tropical stock are equipped to feed on these organisms, fishes of temperate stock typically are not.

Despite the great abundance, variety, and ready availability of algae in temperate habitats, there are no herbivores of the more advanced perciform lines there. Two herbivores of tropical stock—the opaleye and halfmoon—are prominent in warm-temperate communities, but both are kyphosids and so considered among the more primitive perciforms (Nelson, 1994); the label “herbivore” is applied to them somewhat loosely because their diets also include invertebrates (Quast, 1968; Hobson and Chess, 2001).

There has been much speculation why there are so few herbivorous fishes at higher latitudes, considering the widespread abundances of benthic algae there (Horn, 1989). Reports have implicated problems with vegetation as food in temperate habitats. One suggested that fishes are ineffective in digesting plant tissues at low water temperatures (Gaines and Lubchenko, 1982), and another that fishes have difficulty processing the coarse tissues of temperate algae (Bakus, 1969). And still another proposed that production rates of turf algae at temperate latitudes are too low to meet the needs of herbivorous fishes (Choat, 1991). These suggestions identify forces of natural selection likely to be at work on temperate herbivores, but the primary reasons that there are so few fishes among them probably transcend factors related specifically to herbivory. This follows from the fact that carnivorous groups closely related to

tropical herbivores are similarly limited in occurrences at higher latitudes (Hobson, 1994; Hobson and Chess, 2001).

Most perciforms of tropical stock that dominate the reef communities of southern California are sharply limited in their distributions farther north. The boundary between warm-temperate and cold-temperate regions of the northeastern Pacific generally is considered at Point Conception (Briggs, 1974; Horn and Allen, 1978), which is essentially the northern limit of perciforms of coral reef stock. Although habitats northward from there to Monterey represent a zone of transition irregularly frequented by southern forms, reef communities north of the Point tend to be dominated by perciforms of temperate heritage, such as the ronquils, pricklebacks, and gunnels.

The obvious question is, why have perciforms with tropical affinities apparently been excluded from north-coast habitats, especially considering their dominance in habitats to the south? If the incentive for labroids to become established in warm-temperate communities was the wealth of foods available to them there, as I have suggested, then why have they not responded similarly to the even greater wealth of the same foods farther north? Consider the labroids that Hobson and Chess (2001) found dominant as benthivorous carnivores in south-coast habitats—the garibaldi, rock wrasse, seniorita, sheephead, pile perch, black perch, and rubberlip perch. Of these, only the last three, which are embiotocids, ordinarily range into northern California. And of the labroids that Hobson and Chess (1976) found highly successful diurnal planktivores—the blacksmith, kelp perch, and shiner perch—only the last two, which are embiotocids, regularly occur along the north coast. In addition, neither of the two warm-temperate herbivores—the opaleye and the halfmoon—normally occurs in north-coast communities.

Clearly the surfperch family Embiotocidae is exceptional. This group originated in California (Tarp, 1952), so it is not surprising that representatives are broadly adapted to conditions throughout the region. Embiotocids inhabiting the north coast are able to use the highly adaptive labroid trophic capabilities to access feeding opportunities generally unavailable to species of temperate stock. The result has been what may be the most trophically diverse family of marine fishes. For example, the kelp perch is a diurnal planktivore, with features similar to certain highly evolved tropical perciforms specialized for this habit, whereas the walleye surfperch schools by day and feeds on the larger crustacea that enter the water column only at night, just like certain basal percoids (Hobson and Chess, 1976, 1986; Ebeling and Bray, 1976). The white seaperch (*Phanerodon furcatus*) and the sharpnose seaperch (*Phanerodon atripes*) are benthivorous carnivores that pluck tiny organisms from a substrate, the latter often taking ectoparasites from the bodies of other fishes (Hobson, 1971; Ebeling and Bray, 1976). The shiner perch has exceptionally broad feeding habits that include both planktivory and benthivory, day and night, at different periods of adult life (Hobson et al. 1981). The black perch and the rubberlip perch have exceptionally broad diets based on their specialized abilities to winnow edible material from mouthfuls of the benthos (Laur and Ebeling, 1983; Hobson and Chess, 1986), and the pile perch has massive (for a surfperch) pharyngeal teeth that are used to crush shells of mollusks and brittlestars (Laur and Ebeling, 1983). The list goes on to include all 18 species of surfperches that occur off California shores, each with features suited to a distinctive diet. It is a radiation that demonstrates the adaptive potential of the group (DeMartini, 1969) and also the



FIGURE 3-44 Wolf eel, *Anarrhichthys ocellatus*. (Photo: Tony Chess, from Hobson 1994, with permission from Springer Science and Business Media.)

availability, in temperate habitats, of feeding opportunities generally unavailable to fishes of temperate stock.

Although fishes of temperate stock generally lack the trophic capabilities needed to feed on sessile invertebrates, zooplankton, and benthic plants so abundantly accessible in north-coast habitats, there are striking exceptions. Among these are a number of zoarcoid and trachinoid perciforms that have acquired trophic capabilities more characteristic of tropical species. For example, the wolf eel (*Anarrhichthys ocellatus*, family Anarrhichadidae, fig. 3-44), a zoarcoid perciform, uses highly specialized teeth to feed on heavily shelled invertebrates (Hart, 1973). The Pacific sand lance (*Ammodytes hexapterus*, family Ammodytidae), a trachinoid perciform, is a highly successful diurnal planktivore (Hart, 1973; Hobson, 1986). Other exceptions include the monkeyface prickleback (*Cebidichthys violaceus*) and the rock prickleback (*Xiphister mucosus*), which are blennioid perciforms (family Stichaeidae) that have acquired abilities to feed on vegetation (Montgomery, 1977; Horn et al., 1982). Although these species have feeding abilities that are highly adaptive in temperate habitats, they are atypical of their families and represent trophic types that generally are poorly developed among fishes of temperate stock.

Fishes of temperate affinities have fewer limitations in southern occurrences. This assessment agrees with Horn and Allen (1978), who concluded, based on an analysis of published range limits, that Point Conception is less of a boundary for northern species than for southern ones. Northern dominants occur more widely in the south than southern dominants do to the north, although the southern occurrences for some northern forms are in deeper water or at points of coastal upwelling (Hubbs, 1948); for example, the dominant embiotocid in the reef communities of northern California—the striped seaperch (*Embiotoca lateralis*)—is sparsely distributed through southern California but abundant in the vicinity of upwelling near Punta Banda in northern Baja California, Mexico. Even more telling are the many species of temperate stock most abundant or even limited to southern habitats. Included are at least two rockfishes (genus *Sebastes*)—the treefish and the kelp rockfish—along with a number of the sculpins, such as the lavender sculpin (*Leiocottus hirundo*, fig. 3-45) and the roughcheek sculpin, *Artedius creaseri* (Eschmeyer et al., 1983). These distributions are exceptions to the general pattern, however. More



FIGURE 3-45 Lavender sculpin, *Leiocottus hirundo* (from Hobson and Chess 2001, with permission from Springer Science and Business Media).



FIGURE 3-46 China rockfish, *Sebastes nebulosus*.

typical of those with temperate affinities is the china rockfish (*Sebastes nebulosus*, fig. 3-46), which ranges southward from Alaska to southern California—but is abundant only through northern California (Love et al., 2002).

So it is evident that fish communities in the region of Point Conception are affected by a northward decline in species of tropical stock and by a southward decline in species of temperate stock. It was to demonstrate resulting effects on these communities that for many years Professor Boyd Walker of UCLA led his students, me among them, to sites near Morro Bay, 90 miles north of the Point. There, collections of the fishes near shore included many ronquils, pricklebacks, gunnels, and poachers—species with northern affinities that were sparsely represented in collections from south of the Point (records of the UCLA Fish Collection now at the Los Angeles County Museum of Natural History). Direct observations of communities north and south of the Point show a sharper faunal break than indicated by published range limits of the species (e.g., Horn and Allen, 1978), which too often represent individuals that have strayed (or were carried) beyond limits of conditions favorable for their species.

The differences in species composition of communities north and south of Point Conception (as well as at other locations along the coast) have been attributed to differences in sea temperatures (e.g., by Horn and Allen), and certainly temperatures are important. That occurrences of various northern species in the south tend to be in deeper water or at centers of upwelling presumably is related to temperature (Hubbs, 1948).

Temperatures alone, however, cannot account for this break in the fauna. Certainly temperatures are important in setting immediate limits to the distribution of species, but evolutionary processes can modify these limits when there are adaptive advantages in doing so. The complex physiological adjustments involved in shifting tolerance limits for temperature have been made many times, as in those tropical lineages that range widely over latitude. An example is the tropical gobiid genus *Coryphopterus*, which has representatives throughout the tropical eastern Pacific (Thomson et al., 1979). One species of this genus that is abundant off southern California, the blackeye goby, has a published poleward limit of northern British Columbia (Eschmeyer et al., 1983), and I have seen it in southeastern Alaska. So although responses to temperature may be the means by which existing species maintain spatial relations with the Point, the advantage of doing so must lie elsewhere. Certainly any such advantage must be great because it would be shared by a diverse assortment of species highly varied in their evolutionary histories.

A likely basis for the faunal break at Point Conception is the prevailing pattern of surface currents (Hobson, 1994). To the north, surface currents associated with coastal upwelling flow seaward during most of the year (Bakun et al., 1974), while to the south, the usual condition is a closed cyclonic eddy (Reid et al., 1958). These two systems are vastly different in ways that must influence the eggs, embryos, and larvae of fishes that expose their early life-history stages to the environment. In developing a case for the importance of hydrographic features to the distribution of these fishes, Cowen (1985) concluded that warm-temperate species are prevented from ranging northward into the cold-temperate region by currents that carry their larvae southward.

Species of tropical stock may be able to exercise their trophic capabilities in warm temperate habitats of southern California only because they experience favorable surface currents in that region. Most release their eggs into the water column (Breder and Rosen, 1966), which is a highly adaptive feature of reproduction under conditions in which their coral reef progenitors developed, as noted above. This mode of egg development is unsuited to coastal waters of the northeast Pacific, however, because offshore currents associated with coastal upwelling would carry them to unfavorable environments. Among families with this limitation are the serranids (e.g., kelp bass), haemulids (salema and sargo), sciaenids (e.g., croakers and queenfish), labrids (senorita, rock wrasse, and sheephead), and kyphosids (halfmoon and opaleye). The eggs and larvae produced by species of these families are pelagic (Breder and Rosen, 1966), and therefore are poorly suited to north-coast conditions.

Some families of tropical derivation produce benthic eggs, and these have had mixed success in extending their distributions northward. The pomacentrids (blacksmith, garibaldi) deposit adhesive eggs in nests on reefs but have failed to populate the north coast, perhaps because their lunar hatching schedule (Johannes, 1978) is inappropriate in a strong upwelling system. Others do well in cold-temperate habitats, however, including certain clinids (e.g., kelpfishes of the genus *Gibbonsia*) and gobiids (e.g., blackeye goby).

The fishes of cold-temperate communities north of Point Conception typically show major adaptations to counter the possibility that their eggs, embryos, and larvae may be carried in surface currents to unfavorable settings. As Parrish et al. (1981) pointed out (p. 175), “The fishes spawning in this region have a wide range of reproductive strategies that reduce

the planktonic phase of early life history." Some species avoid these problems with adaptive behavior as adults. For example, many species with pelagic habits off central and northern California, such as the jack mackerel, *Trachurus symmetricus* (family Carangidae), migrate southward to reproduce off southern California, and certain pleuronectiforms migrate into deeper water beyond reach of surface currents (Parrish et al., 1981). But most species that inhabit California's cold-temperate marine habitats lack the capacity for such migrations and so have acquired modes of reproduction adapted to north-coast conditions.

The pelagic egg represents the point in early life history most vulnerable to unfavorable surface currents, and virtually all north-coast fishes have acquired ways to keep their eggs out of the water column. The scorpaeniform rockfishes have an especially effective mechanism wherein fertilization is internal and the female retains the eggs throughout their development—a practice that probably contributes to the group's extraordinary success in the northeast Pacific. Most of the other reef fishes in this region produce benthic eggs, including such scorpaeniforms as sculpins and greenlings, as well as such perciforms as clinids, gobies, ronquils, gunnels, and pricklebacks (Breder and Rosen, 1966). Moreover, though tropical reef fishes that produce benthic eggs coordinate spawning with lunar phases and therefore tidal currents (Johannes, 1978), fishes that do so in temperate communities of the northeastern Pacific coordinate with seasonal patterns of coastal upwelling (Parrish et al., 1981).

The coastal osmeriforms have other ways of protecting their eggs, as noted above. That the surf smelt and night smelt find it adaptive to enter the north-coast surf zone and deposit their eggs in coarse sand under breaking waves—a highly rigorous setting—represents strong evidence that eggs are at risk in the nearshore water column there.

Such measures effectively protect the eggs, but the eggs of most hatch as planktonic larvae, which are similarly vulnerable to unfavorable transport. To limit this problem, a majority of these species put their larvae into the environment during winter, when shoreward surface transport is most likely. And the larvae of many, including various sculpins, pricklebacks, and gunnels, resist being carried offshore (into the southward flowing California Current) by schooling close to rocks and other benthic structures (Marliave, 1986). At least some that cannot escape unfavorable surface currents descend to more favorable transport in deeper currents (Parrish et al., 1981). These adaptations limiting unfavorable transport of larvae would seem less effective than the adaptations that limit unfavorable transport of eggs, but larvae have less need for them because they have at least some control over their movements.

Probably it is mainly to remove early life stages from problems they would experience near shore in the sea that marine salmonids and some osmerids spawn in fresh water. If so, the complexity of behavior and physiological adjustments that have evolved shows that these problems are profound. Furthermore, it is clear that the problems are particularly acute in the northeast Pacific because that is where the species involved are concentrated.

The most effective means of keeping early life-history stages out of the nearshore water column, however, has developed in the embiotocids. The surfperches avoid unfavorable transport of eggs and larvae by retaining these in the pregnant female throughout their development and delivering the young as small adults (Baltz, 1984). The males of *Micrometrus* spp. are

sexually mature at birth (Hubbs, 1921; Schultz, 1993). Clearly, this has been the key to their widespread success in the coastal waters of the northeast Pacific. It has been largely through their viviparity that members of this family have gained access to exceedingly rich trophic resources largely unavailable to other species of tropical heritage (Hobson, 1994). As a result, Point Conception has been less of a barrier to species of this family than to species of the other major nearshore families—both temperate and tropical.

Perspectives on the California Condition

SPATIAL

Many of the determinants of species composition in California's reef communities have global relevance, but others are limited to the western shore of North America. Differing oceanic conditions account for much of the variation between regions. The coastal upwelling system off California and Oregon, for example, creates conditions intolerable to most fishes of tropical stock poleward of about 35°N, the latitude of Point Conception. Different circumstances, however, exist on the eastern side of the continent. There, a wide variety of tropical fishes routinely occur in high-latitude communities influenced by the Gulf Stream, and tropical derivatives such as the cunner (*Tautoglabrus adspersus*; family Labridae) are established above 45°N (Scott and Scott, 1988).

Other differences are evident in temperate communities of the southwest Pacific, where species of the order Tetraodontiforms are prominent components of coastal marine communities (Ayling and Cox, 1982). This order is now represented in California marine communities only by rare occurrences in the southernmost of puffers (family Tetraodontidae) and porcupine fish (family Diodontidae). At the outset of this chapter, it was noted that the Perciformes, Scorpaeniformes, and Pleuronectiformes—the dominant orders represented among California fishes—are three of the four most recently evolved orders of fishes. In making this assessment, Nelson (1994) identified the fourth as the Tetraodontiformes; he regarded the tetraodontiforms as the most recently evolved of all. Only one tetraodontiform is common in coastal waters off California, however. This is the ocean sunfish (*Mola mola*; family Molidae), which has pelagic habits but often occurs close to shore.

TEMPORAL

The species composition of teleost fishes in California marine communities, therefore, is the product of a continuum of interactions among species and their environment over evolutionary time. There is a natural tendency to consider the current condition as an end point, and certainly it represents a culmination of all that has gone before. But, just as the condition today is forever different from that of yesterday, tomorrow's condition will be forever different from that of today. Constant change is the norm, but it is change constrained within limits set by features of ecosystems that have been stable for tens of millions of years. The history of life on the earth, however, has shown that this stability is finite.

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