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## CHAPTER 8

# Rocky Intertidal Zone

MICHAEL H. HORN AND KAREN L. M. MARTIN

## Introduction

Rocky intertidal habitats are small living spaces occupied by a variety of fishes either year-round as residents or temporarily as visitors. These species live at the very margin of the ocean and thus must contend with the fluctuating conditions of both marine and terrestrial environments. The rocky intertidal zone represents in part a shoreward extension of subtidal rocky reefs, and the intertidal fish fauna comprises those inshore species that to varying degrees have colonized this extreme, partially terrestrial habitat. As a result, some species occur in both subtidal and intertidal habitats although, as is discussed below, intertidal fishes represent largely distinct assemblages.

In this chapter, the main features of rocky shores as habitats for fishes are described followed first by the vertical and horizontal distribution patterns of the associated fauna then by the behavioral, physiological, and reproductive traits of the fishes, with an emphasis on resident species; and, finally, by an account of the structure and dynamics of intertidal fish communities. Californian intertidal fishes are relatively well known in certain ways and are referenced in several other places in this book including chapter 3 (teleost evolution), chapter 4 (ecological classification), chapter 14 (feeding and trophic interactions), and chapter 19 (reproduction).

## Rocky Intertidal Zone as a Fish Habitat

The narrow strip of coastline between the tidemarks on rocky shores represents a unique and demanding habitat for marine fishes (see chapter 4, this volume; Horn et al., 1999). Although often highly productive and rich in seaweed and invertebrate species, the rocky intertidal zone is a wave-swept and turbulent environment with both temporal and spatial variations. On the California coast, the mixed semidiurnal tide regime cuts off the intertidal zone from the open ocean twice a day to varying degrees. The extent of the exposure depends on the time of day and period in the lunar cycle. At low tide, the water that remains in the habitat is confined to isolated pools and under-rock spaces. Thus, any resident fish must be able to withstand some time either completely out of water or at least partly exposed to air although usually in a moist location.

The daily fluctuations in water level combined with time of day can result in rapid and large changes in physical and chemical features of tidepools. During an afternoon low tide on a spring tide series, an isolated pool has ample time, especially under full sun, to increase dramatically in temperature and salinity compared to the conditions that would prevail during a nighttime or an early morning low tide. Intertidal animals and seaweeds are exposed to rapid and sometimes extreme changes in temperature (fig. 8-1), one of the most important factors determining the distribution and physiological performance of these organisms (Helmuth and Hofman, 2001). Oxygen levels also increase during the daytime as photosynthesis proceeds but fall at night when only respiration occurs. Carbon dioxide accumulates, and pH may decline as respiration continues in isolated pools (Davenport and Woolmingon, 1981).

Seasonal changes in climate add another temporal component to the fluctuating conditions within a given rocky intertidal habitat (e.g., Horn et al., 1983; Murray and Horn, 1989; Helmuth and Hofman, 2001). For example, marked differences occur in environmental conditions between winter and summer months on central California shores (fig. 8-2), reflecting the Mediterranean climate that characterizes much of the California coast. The winter months are characterized by short, cool days with long periods of aerial exposure and occasional rainfall frequently accompanied by storms of varying intensity. In contrast, summers days are long and warm with little rainfall and minimum daytime exposure in the intertidal zone. Seasonal differences in water temperature, however, are reduced because of pronounced upwelling during the summer months, which lowers temperatures toward the more uniformly cool sea temperatures of winter. Rainfall and the resulting flow of water into intertidal habitats during the winter reduce salinities that can create osmotic stress for fishes. Not surprisingly, members of intertidal fish communities exhibit mechanisms found in their more completely aquatic predecessors for maintaining internal osmotic, pH, and nitrogen balance even though many physiological questions remain to be answered for fishes in this habitat (Evans et al., 1999).

Spatial variation on several scales adds further complexity to rocky shores as fish habitats. Within a single location,

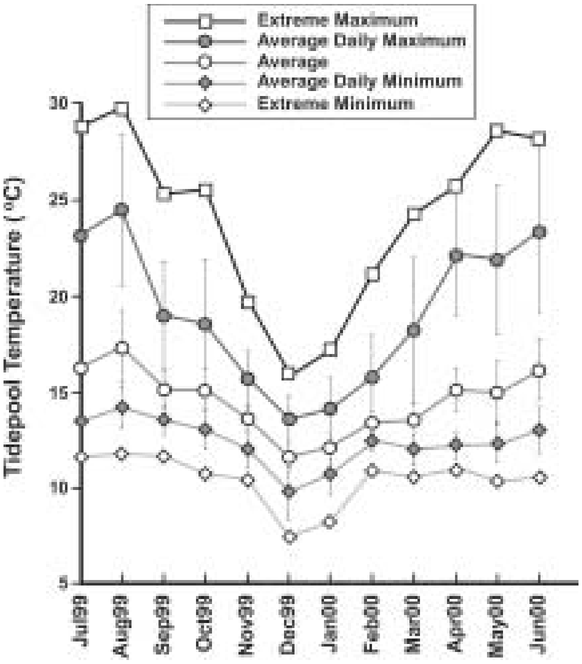

FIGURE 8-1 Monthly temperature variation in a small tidepool on the rocky shore adjacent to Hopkins Marine Station in Pacific Grove on the central California coast (after Helmuth and Hofman, 2001).

habitat heterogeneity is derived from a variety of substratum and microhabitat types. Gravel expanses and boulder fields interspersed with shallow pools are unstable areas and frequently are rearranged by storms and wave action, yet provide many hiding places for small fishes. On the other hand, crevice-type rockpools and fixed rock outcrops often topped with turf or foliose macroalgae exhibit greater permanence, although all microhabitats are subject to the longer term forces of erosion and tectonic activity. Differences in aspect and slope increase the heterogeneity of environmental conditions on rocky shores. For example, Helmuth and Hofman (2001) recorded temperatures consistently higher by several degrees at horizontal microsites than on a north-facing vertical site with intermediate temperatures taken in a nearby tidepool on a rocky shore in Pacific Grove on the central California coast. On a larger spatial scale, rocky intertidal habitats themselves are not continuous but are separated by sandy beaches, steep bluffs, river mouths, or some combination of these coastal features. On a latitudinal scale, temperature and other climatic conditions differ along the expanse of the California coastline and help determine the composition of the intertidal fish fauna at any given location. That two biogeographic provinces are represented in California coastal waters (chapters 1 and 2, this volume) reflects the substantial changes in the environment that occur over the 10° of latitude of the state.

Given the great temporal and spatial variations typical of rocky intertidal habitats, year-round fishes may be expected to show broad tolerance to fluctuating conditions or to possess traits that allow them to survive and even reproduce in the intertidal zone. In contrast, fishes that occur only temporarily in the habitat may be less specialized for intertidal life but are often larger and more mobile and thus better able to avoid or escape the rigors of the intertidal zone as the tide ebbs. The following section of the chapter addresses these expectations and summarizes and evaluates the existing information relevant to them.

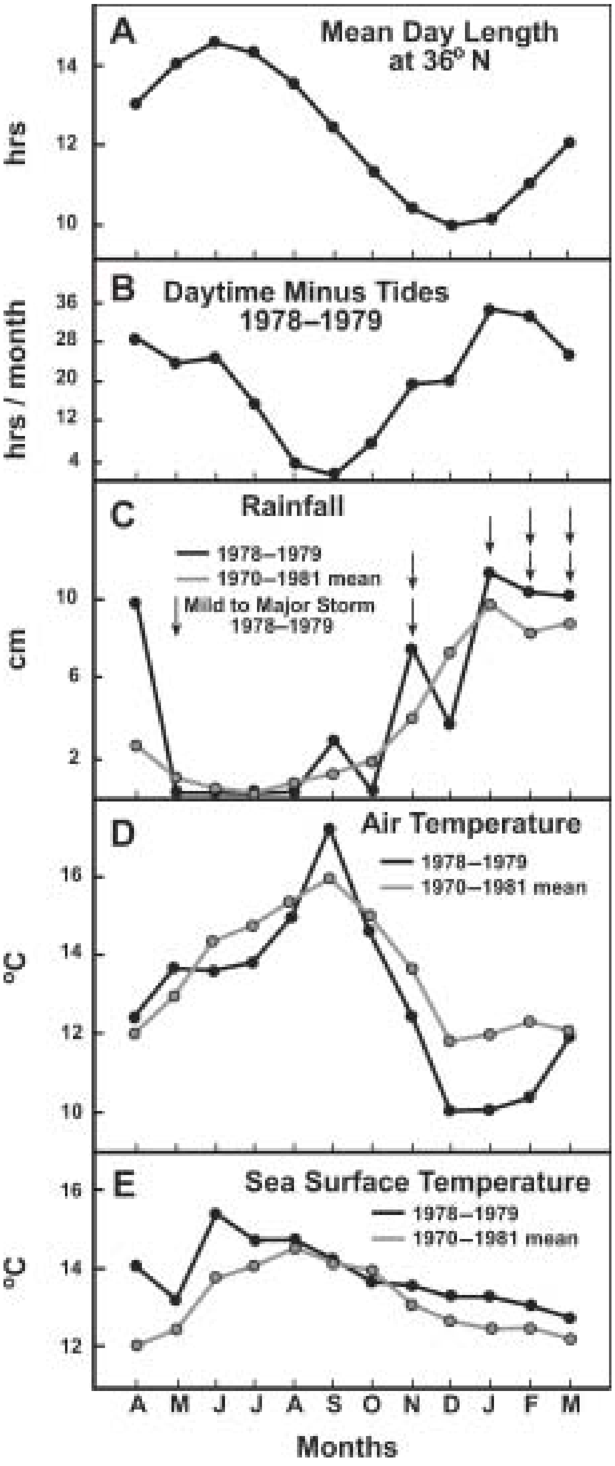

FIGURE 8-2 Seasonal patterns of environmental conditions on the central California coast (after from Horn et al., 1983).

## Distribution Patterns

### Vertical Zonation in Intertidal Fish Assemblages

We are accustomed to thinking of vertical zonation in the rocky intertidal zone as shown by bands of sessile invertebrates and algae (i.e., Stevenson and Stevenson, 1972; Benson, 2002). Intertidal fishes also segregate at different tidal heights as seen among pricklebacks and gunnels on California rocky shores (Horn and Riegle, 1981; Jones, 1981). Physical factors such as tidal height, type of cover, wave exposure, and substratum influence habitat choice in fishes. During low tides, intertidal fishes face potential exposure to aerial or aquatic changes that increase in duration and effect with height on the shore. In addition, habitat use by fish in the intertidal zone is strongly influenced by biotic interactions (Benson, 2002).

For certain fish species, abundance of different size classes varies across the intertidal zone. Larval fish tend to settle on substrata preferred by conspecific adults (Marliave, 1977), but smaller individuals of clingfishes (Stepien, 1990), sculpins, (Nakamura, 1976; Freeman et al., 1985; Wells, 1986), and pricklebacks (Horn and Riegle, 1981) are more abundant higher in the intertidal zone perhaps because larger fish tend to win intraspecific contests (Richkus, 1981). Five species of pricklebacks in the rocky intertidal zone of central California have overlapping, yet distinguishable, vertical distributions (Horn and Riegle, 1981; Barton, 1982). Early juveniles of the rock prickleback *(Xiphister mucosus)* consistently occur higher in the intertidal zone than those of the monkeyface prickleback *(Cebidichthys violaceus)* (Setran and Behrens, 1993). Increased body size results in relatively smaller body surface area and contributes to tolerance of water loss during low tides. Even among amphibious fishes, however, the smaller, more vulnerable juveniles are found higher in the intertidal zone than larger conspecifics (Horn and Riegle, 1981). Juveniles of some shallow subtidal fishes can be found in tidepools (Williams, 1957; Martin, 1993; DeMartini and Sikkel, chapter 19 this volume). Although this occurrence may help juvenile fish avoid large aquatic predators, they face increased exposure to piscivorous birds, which are known to capture fish in the rocky intertidal zone (MHH, pers. obs.).

Some kelpfish in California show sexual differences in vertical distribution. Williams (1954) reported that approximately 90% of spotted kelpfish *(Gibbonsia elegans)* in lower intertidal pools are female but that males and females are present in equal abundance in subtidal habitats. Sex differences in vertical distribution are seen in in other species of tidepool kelpfish; mostly females and juveniles are found intertidally, whereas males are seen only subtidally (Stepien, 1987; Stepien and Rosenblatt, 1991). The explanation is that females migrate to subtidal depths only to mate and lay eggs, whereas the males guard the eggs there until they hatch. Differences in color or morphology among members of the same species collected at different vertical heights may be related to diet.

Limited evidence exists, however, to show that vertical distribution among intertidal fishes may be affected by dietary habits. For example, herbivorous species such as the monkeyface prickleback feed on algae during high tides (Horn et al., 1986; Ralston and Horn, 1986). Some algae-eating fishes show a distinct preference for the upper intertidal zone (Horn, 1989; Horn and Ojeda, 1999), even though in higher pools the fish have less time for foraging, unless they leave the home pool during a low tide. On a larger temporal scale, seaweed abundance is greatest in summer and lowest in winter on the central California coast (Horn et al., 1983) and may influence the vertical abundance of herbivorous fishes.

As described above, many species of sculpins occur in the intertidal zone. This intertidal diversity probably is associated with niche specialization and with differences in vertical distribution. Among the three to six cottid species that coexist in midintertidal pools (Pfister, 1992), the tidepool sculpin *(Oligocottus maculosus)* prefers high tidepools, whereas the fluffy sculpin *(O. snyderi)* is found in lower pools, in both Canada (Green, 1971; Nakamura, 1976) and on the central California coast (Yoshiyama, 1981). Not surprisingly, Nakano and Iwama (2002) found that the tidepool sculpin has a higher temperature tolerance and higher heat shock protein (hsp 70) levels than the fluffy sculpin. The mosshead sculpin *(Clinocottus globiceps)* prefers the lower intertidal zone in Canada (Mgaya, 1992), but it is found in high pools with tidepool sculpins on central California rocky shores. Even within the high zone, the mosshead sculpin is most abundant in pools farther from shore, and the tidepool sculpin occurs in the higher pools where wave exposure is reduced (Yoshiyama, 1981; Yoshiyama et al., 1986).

## Temporal Variations in Vertical Distribution

### DIURNAL CHANGES

The vertical distribution of some intertidal fishes may be subject to diurnal changes, but California species are not well studied in this regard. Changes in fish distribution with tidal level are more often seen in transient species that leave during low tides than in resident intertidal fishes (Gibson, 1999). For example, kelpfishes are typically absent from tidepools during nocturnal low tides, when the danger of hypoxia is great (Congleton, 1980). Tidepools high on the shore may increase in temperature during daytime low tides, resulting in fewer woolly sculpin and opaleye *(Girella nigricans)* in these pools during daytime compared to nighttime lows (Davis, 2001).

### SEASONAL CHANGES

Some species of intertidal fishes show declines in abundance during the winter in California (Burgess, 1978; Chandler and Lindquist, 1981; Davis, 2000b), perhaps because some species, especially the more mobile, transient forms, migrate to deeper waters. Wave turbulence increases during the winter (Horn et al., 1983), and stronger waves generally correlate with fewer intertidal fishes (Grossman, 1982). The tidepool sculpin as well as the monkeyface prickleback and the rock prickleback decline during winter on California shores, probably because of the pounding by heavy waves (Green, 1971; Setran and Behrens, 1993). Intertidal fishes resist being swept away by strong waves in part because they are relatively small and have a reduced or no swimbladder. Some sculpins and clingfishes possess dermal calcifications that help the fish remain attached to the substratum (Zander et al., 1999), and gobies and clingfishes have modified pelvic fins that act at least in some species as ventral suckers to help the fish maintain position during wave wash (Horn and Gibson, 1988).

In summer, increased species richness results from the influx of transient species, both adults and juveniles, as the rocky intertidal zone undergoes its seasonal role as a nursery (Moring, 1986; see below). This greater species richness and increase in the proportion of juveniles usually skew the peak of abundance to pools higher in the intertidal zone. Seasonal temperature fluctuations also may have important effects on vertical zonation. For example, the rockweed gunnel *(Apodichthys fucorum)* occurs higher on the shore in summer than in winter in central California (Burgess, 1978), probably because of temperature changes. Conversely, in a rocky intertidal area of winter upwelling off Baja California, both the number of species and the number of individuals increase during this season (Stepien et al., 1991), perhaps because the cooler waters attract cool-temperate fishes otherwise found at higher latitudes in California. Davis (2000b), however, found relatively stable species distributions for five species of tidepool fishes in southern California, even though temperatures and fish abundances changed seasonally.

## Horizontal Zonation in Intertidal Fishes

### Microhabitats: Aquatic During High Tide

When the rocky shore habitat is inundated at high tide, it takes on important characteristics of the surrounding ocean. These features include relatively uniform temperatures and salinity and oxygen saturation or even supersaturation, a well-buffered pH, and relatively low dissolved carbon dioxide levels (Bridges, 1993). In the rocky intertidal zone, productivity is high (Leigh et al., 1987), and large predators are rare. Oxygen tensions in the ocean are elevated, generally in equilibrium with air, and may even supersaturate with pounding surf or tidepool photosynthesis (Graham et al., 1978). At high tide, wave action mixes and rapidly dispels any short-term changes from weather or biological activities at the transition from subtidal to rocky intertidal habitats. Thus, with the exception that fewer predators may exist in this still relatively small habitat, the intertidal zone when inundated is more or less continuous with and similar to waters beyond the low tidemark.

### Microhabitats: Aquatic During Low Tides—Tidepools

Aside from the fluctuating conditions already described in the introduction, oxygen solubility is an important environmental factor in tidepools. Oxygen solubility is lower in seawater than freshwater (Dejours, 1994) and declines with increasing temperature and salinity, worsening the hypoxia that can occur in pools during low tide. Because transient fish species may become concentrated in these aquatic refuges during low tide, respiration can be a challenge for these active swimmers. At night, in the absence of photosynthesis, hypoxic conditions may become severe (Congleton, 1980; Bridges, 1993).

Carbon dioxide released by respiring animals and seaweeds also affects the tidepool habitat. In the open ocean, respiratory carbon dioxide is buffered by bicarbonates and consumed by algae carrying out photosynthesis. In the small volume of a tidepool, however, and particularly at night in the absence of photosynthesis, bicarbonate buffering may be overwhelmed and the pH may decline by several units during the course of a few hours (Truchot and Duhamel-Jouve, 1980; Bridges, 1993).

### Microhabitats: Aerial Habitats During Low Tide

Vertical zonation is more pronounced in animals and seaweeds on rock substrata exposed to air at low tide than in those species that are confined to tidepools (Metaxas and Scheibling, 1993). On exposed substrata, wind and sun cause desiccation and create temperature fluctuations that are much greater than those in water. Out of water and without its buoyant effects, intertidal fish must adjust to the increased pull of gravity. Although the speed of diffusion of respiratory oxygen increases in air, exposure to air causes desiccation and the collapse of gills (Randall et al., 1981). Dependent upon gills and skin for respiration, most intertidal fishes must remain in moist, sheltered microhabitats under boulders or seaweeds or return frequently to pools to moisten respiratory surfaces (Horn and Riegle, 1981; Martin, 1995). Even though some amphibious species of gobies and blennies in tropical and subtropical regions live above the waterline and are consistently out of water (Graham, 1997), no known temperate-zone fish species, including those in California rocky intertidal habitats, has evolved the specializations necessary for surviving the extreme environment of the supralittoral zone (see below).

## Behavioral and Physiological Traits

### Tolerance to Emersion

All fishes make behavioral choices in their habitats, and intertidal fishes, routinely experiencing ebb tides, may be expected to choose to avoid either a degraded aquatic habitat or accidental stranding in air (Sayer and Davenport, 1991). A number of intertidal fishes on California shores are amphibious to some extent and, under certain stressful conditions, leave the water deliberately (Yoshiyama and Cech, 1994; Martin, 1995; Watters and Cech, 2003). Adults of some species, however, emerge occasionally during low tides as they guard their eggs (Coleman, 1999; DeMartini and Sikkel, chapter 19, this volume). Thus, rocky intertidal fishes may leave the water under stress or as part of the natural life cycle as in parental care.

### Emergence Behaviors

A variety of intertidal fish species occasionally can be found out of water on California rocky shores. Resident intertidal fishes are small, negatively buoyant, and typically lack a swimbladder. The large pectoral fins of sculpins or sinusoidal body of pricklebacks allow them to perch upright on the substratum during terrestrial emergence (Martin, 1991; Horn, 1999). Some degree of desiccation is likely for fish out of water (Horn and Riegle, 1981; Martin, 1996; Luck and Martin, 1999) because the entire body of the fish emerges, including the head and gills, for the duration of the low tide. Some amphibious fish species, even while emerged under boulders, periodically roll to one side into shallow pools (Daxboeck and Heming, 1982; Graham et al., 1985; Brown et al., 1992; pers. obs.), apparently to maintain moisture on the skin surface. This behavior may have the dual effects of resisting desiccation and maintaining the integrity of the skin, and perhaps the gills, as a respiratory surface while the fish is exposed to air.

Three groups of amphibious fishes have been recognized based on the type of emergence behavior they exhibit: (1) skippers, (2) tidepool emergers, and (3) remainers. The latter two types are represented in California (table 8-1). All three types emerge fully from the water and exchange both oxygen and carbon dioxide in air (Martin, 1995). Skippers, known only from tropical latitudes, include the mudskipper gobies (Clayton, 1993) and the rockskipper blennies (Zander, 1972;

TABLE 8-1

California Rocky Intertidal Fishes

| *Family* *Common Name* | *Scientific Name* | *Classification* | *Air Breather* | *Emergence* | *Reference* |
|---|---|---|---|---|---|
| Batrachoididae | | | | | |
| Plainfin midshipman | *Porichthys notatus* | Remainer | Yes | W, LF | Crane, 1981; Martin, 1993 |
| Blenniidae | | | | | |
| Rockpool blenny | *Hypsoblennius gilberti* | Other | Yes | LF | Luck and Martin, 1999 |
| Cottidae | | | | | |
| Smoothhead sculpin | *Artedius lateralis* | Remainer | No | W | Lamb and Edgell, 1986 |
| Rosylip sculpin | *Ascelichthys rhodorus* | Remainer | Yes | W, LV, LF | Cross, 1981; Martin, 1996; Yoshiyama and Cech, 1994; Yoshiyama et al., 1995 |
| Sharpnose sculpin | *Clinocottus acuticeps* | Emerger | No | W | Yoshiyama and Cech, 1994 |
| Woolly sculpin | *Clinocottus analis* | Emerger | Yes | W, LV, LF | Martin, 1991; Watters and Cech, 2003 |
| Mosshead sculpin | *Clinocottus globiceps* | Emerger | Yes | W, LV, LF | Martin, 1993; Yoshiyama and Cech, 1994; Lamb and Edgell, 1986; Yoshiyama et al., 1995; Watters and Cech, 2003 |
| Bald sculpin | *Clinocottus recalvus* | Emerger | Yes | W, LV, LF | Wright and Raymond, 1978; Martin, 1993 |
| Pacific staghorn sculpin | *Leptocottus armatus* | Emerger | Yes | LF | Martin, 1993 |
| Tidepool sculpin | *Oligocottus maculosus* | Emerger | Yes | W, LV, LF | Martin, 1993; Yoshiyama and Cech, 1994; Yoshiyama et al., 1995 |
| Saddleback sculpin | *Oligocottus rimensis* | Emerger | No | W | Yoshiyama and Cech, 1994 |
| Fluffy sculpin | *Oligocottus snyderi* | Emerger | Yes | W, LV, LF | Martin, 1993; Yoshiyama and Cech, 1994; Yoshiyama et al., 1995 |
| Gobiesocidae | | | | | |
| Northern clingfish | *Gobiesox maeandricus* | Remainer | Yes | W, LF | Cross, 1981; Martin, 1993 |
| Kyphosidae (Girellidae) | | | | | |
| Opaleye | *Girella nigricans* | Emerger | Yes | LF | Martin, 1993; R. Orton (pers. comm.) |
| Pholidae | | | | | |
| Penpoint gunnel | *Apodichthys flavidus* | Remainer | No | W | Cross, 1981; Lamb and Edgell, 1986 |
| Crescent gunnel | *Pholis laeta* | Remainer | No | W | Lamb and Edgell, 1986 |
| Rockweed gunnel | *Xererpes fucorum* | Remainer | Yes | W, LF | Horn and Riegle, 1981; Lamb and Edgell, 1986; Martin, 1993 |
| Stichaeidae | | | | | |
| High cockscomb | *Anoplarchus purpurescens* | Remainer | Yes | W, LF | Cross, 1981; Horn and Riegle, 1981; Martin, 1996; Yoshiyama and Cech, 1994; Lamb and Edgell, 1986 |
| Monkeyface prickleback | *Cebidichthys violaceus* | Remainer | Yes | W, LF | Riegle, 1976; Horn and Riegle, 1981; Edwards and Cech, 1990; Martin, 1993 |
| Black prickleback | *Xiphister atropurpureus* | Remainer | Yes | W, LF | Daxboeck and Heming, 1982; Lamb and Edgell, 1986; Martin, 1993 |
| Rock prickleback | *Xiphister mucosus* | Remainer | Yes | W, LF | Horn and Riegle, 1981; Lamb and Edgell, 1986; Martin, 1993 |

NOTE: Classified as either tidepool emergers, remainers, or other, as air breathers (yes) or not (no), and as to whether emergence behavior was observed in the wild (W), forced in the laboratory (LF), or voluntary in the laboratory (LV). "Yes" for air breather means that gas exchange in air has been confirmed by laboratory experiments. All intertidal fishes that are found consistently emerged in the wild probably have the ability to breathe air, but this ability needs to be verified experimentally.

Graham et al., 1985; Martin and Lighton, 1989). These fishes can forage, feed, defend territories, and mate while out of water on tropical shores.

Tidepool emergers move out of the water when aquatic conditions, such as low oxygen tension (hypoxia), become inhospitable. Sculpins have been shown to display this type of emergence behavior in numerous studies (Wright and Raymond, 1978; Davenport and Woolmington, 1981; Martin, 1991; Yoshiyama et al., 1995). Tidepool emergers may use a tail flip or a crawling locomotion involving the pectoral fins to exit from a tidepool. They move about rarely when emerged, but can locomote well enough to escape from predators or move between pools, at least when pursued by scientific investigators (pers. obs.). Tidepool emergers have been seen emerged from pools in caves (Wright and Raymond, 1978) and during the night (Martin, 1993). In addition to conditions of hypoxia, unsuitable levels of temperature, salinity, pH, or carbon dioxide may be important factors, but they have not yet been shown to elicit emergence in marine fishes (Davenport and Woolmington, 1981; Sayer and Davenport, 1991). Tidepool emergers frequently are collected from tidepools but are rarely found emerged under boulders during low tide. Some of these species may opt to breathe at the surface rather than emerging when they perceive the threat of predators (Watters and Cech, 2003).

In contrast to tidepool emergers, which move actively out of pools, remainers emerge passively from water simply by staying in a location that is slowly exposed to air by a low tide (Horn and Riegle, 1981, Martin, 1995). These fishes are found under boulders or in crevices, sometimes in pools only a few millimeters deep. Fishes classified as remainers are not very active on land although they can thrash about, presumably to escape predators (Horn and Gibson, 1988). Species of fish found emerged under these conditions can occur in pools during low tide, but they sometimes are more numerous out of water. Remainers are found among several taxa of California intertidal fishes, including pricklebacks (Horn and Riegle, 1981, Daxboeck and Heming, 1982; Edwards and Cech, 1990), gunnels (Martin, 1993), sculpins (Cross, 1981; Martin, 1996), clingfishes (Eger, 1971; Martin, 1993), and toadfishes (Crane, 1981). Remainers variously can tolerate several hours out of water and considerable desiccation (Horn and Riegle, 1981).

Some intertidal fishes act as remainers in the intertidal zone when they guard eggs. If the nest emerges during low tide, the parental fish remain with the eggs, as in the high cockscomb, *Anoplarchus purpurescens* (Coleman, 1992), and some species of sculpins (Marliave and DeMartini, 1977) in the Pacific Northwest and the plainfin midshipman *(Porichthys notatus)* in California (Crane, 1981; Coleman, 1999). As long as they do not suffer excessive desiccation, egg masses benefit from accelerated development as a result of the increased oxygen levels and higher temperatures afforded by occasional aerial exposure (Strathmann and Hess, 1999; Smyder and Martin, 2002).

A few intertidal fish species, even though they have not been observed out of water in nature and cannot be induced to emerge from hypoxic water in the laboratory, nevertheless, can breathe air when removed from water and can tolerate prolonged emergence of several hours with no apparent ill effects. California species exhibiting these capabilities include juvenile opaleye (Martin, 1993) and adult rockpool blenny, *Hypsoblennius gilberti* (Luck and Martin, 1999). Both of these species can breathe air and survive hours of emergence during a low tide although how frequently these abilities are actually used is unknown.

By contrast, some intertidal fishes and most subtidal species, of course, do not emerge and if taken out of water, will not survive for the duration of a low tide (Davenport and Woolmington, 1981). Tidepool fishes that can neither emerge nor breathe air include kelpfish (Congleton, 1980; Martin, 1996) and, most likely, juvenile rockfishes and surfperches found in tide-pools. Such fishes are not found in tidepools during nocturnal low tides, when hypoxia is most likely to occur; rather, they avoid hypoxia, probably by migrating to subtidal habitats (Congleton, 1980).

## Aerial and Aquatic Respiration

Many of the intertidal fish species in California can breathe air (Riegle, 1976; Martin, 1993, 1995; Yoshiyama and Cech, 1994; Martin and Bridges, 1999), exchanging both oxygen and carbon dioxide at rates similar to their aquatic rates, and at the same rate as they are metabolized (Bridges, 1988; Martin, 1993). Table 1 lists the species of California rocky intertidal fishes that have shown evidence of air-breathing ability. Respiratory gas exchange in these fishes variously can occur across the gills, the skin, and possibly the linings of the opercular and buccal cavities in both water and air. Intertidal fishes often emerge fully from the water when breathing air although occasionally they lift just the head and opercula out of the water, poised at the water's edge, rather than emerging. Some species, such as the pricklebacks, are capable of a wriggling escape behavior and limited locomotion out of water, but mostly they remain calm and move little. Ventilation in air typically includes "gulping," and the rate of ventilation decreases dramatically in air. The gap between the opercula and the body wall may be sealed shut by mucus, changing the gill ventilation from flow-through in water to tidal flow in air.

Oxygen is plentiful in air, and diffusion occurs quickly, so boundary layers are not a problem for respiratory surfaces (Feder and Burggren, 1985). Fish gills, however, typically function in water, and they collapse when fish are out of water, causing a reduction in respiratory surface area. Air-breathing marine fishes cope with this effect in several ways, first by emerging into a moist microhabitat with high humidity. Some amphibious fishes show morphological specializations to strengthen and support the gills for use in air (fig. 8-3; Brown et al., 1992). Also, fish use the skin as an alternative respiratory surface, one that is not subject to collapse (see below). Cutaneous surfaces are in direct contact with the air and need only be kept moist and well supplied with blood to be used in respiration (Feder and Burggren, 1985).

The partitioning of gas exchange between the gills and the skin varies with the taxon (Martin, 1991, 1995; Martin and Bridges, 1999). Long, eel-like fishes tend to rely more heavily on cutaneous respiration than shorter, thicker fishes. Some blennies show increased reddening of certain cutaneous surfaces on emergence (Zander, 1972; Luck and Martin, 1999), suggesting that skin respiration may be more important in air than it is in water.

The gills and other respiratory structures have not been examined in most remainer and tidepool emerger species; however, the black prickleback *(Xiphister atropurpureus)*, a remainer, has cartilaginous rods within its primary gill lamellae (Sanders and Martin unpublished; fig. 8-3) that may stiffen and support the primary lamellae. Some skipper fishes have thickened gill epithelia, reduced surface area of the secondary lamellae, and cartilaginous rods to stiffen and support the

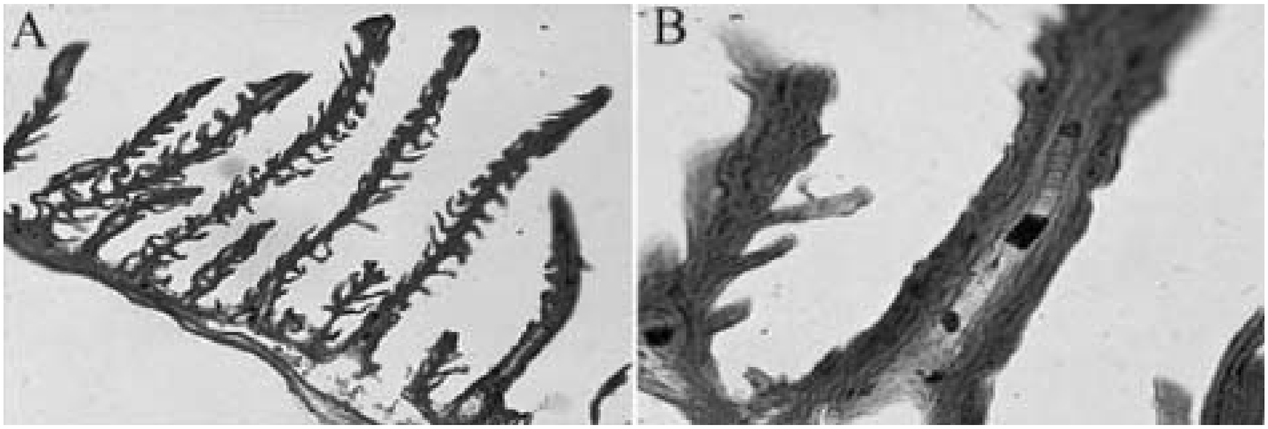

FIGURE 8-3 Photomicrographs of the primary and secondary lamellae of the gills of the black prickleback *(Xiphister atropurpureus):* A. 100x; B. 400x (Sanders and Martin, unpubl.).

primary lamellae (Low et al., 1990; Brown et al., 1992; Graham, 1997). Reduced gill surface area with thicker epithelia, however, could inhibit respiration in water (Graham, 1997), a trade-off that might force fish to emerge during a hypoxic low tide. Specialized air-breathing organs, such as respiratory trees in the pharyngeal region or vascularized stomachs, are rarely present in marine fishes and more typically are found in freshwater fishes that remain aquatic while breathing air at the surface (Graham, 1976). Among the very few marine fishes that remain submerged while breathing air is the longjaw mudsucker *(Gillichthys mirabilis)*. This California estuarine goby uses its highly vascularized buccopharyngeal epithelium as an accessory air-breathing organ (Todd and Ebeling, 1966).

Little evidence exists to demonstrate that rocky intertidal fishes when out of water show a reverse "diving response" although the following observations can be made. Some blennies, including the high intertidal rockpool blenny, have a decreased metabolic rate in air (Luck and Martin, 1999). The monkeyface prickleback does not show bradycardia when placed in air; instead its heart rate increases, then gradually decreases during the time of emergence (Riegle, 1976). A transient drop in heart rate has been observed in California grunion *(Leuresthes tenuis)* on emergence (Garey, 1962), but this fish emerges onto sandy beaches after high tides to spawn (Walker, 1952; Martin and Swiderski, 2001), and it remains emerged only a few minutes, unlike emerging fishes in the rocky intertidal zone. The Mexican goby, *Bathygobius ramosus,* decreases its metabolic rate at high tides and decreased daily temperatures and may also have a diel component in its metabolism (Alcaraz et al., 2002).

No intertidal fish species appears to require anaerobic metabolism while quietly and calmly emerged in air (Riegle, 1976; Martin, 1991, 1995, 1996; Martin and Bridges, 1999). Aquatic oxygen consumption rates are equal before and after long periods of emergence in both the woolly sculpin, *Clinocottus analis* (Martin, 1991) and the rockpool blenny (Luck and Martin, 1999), indicating that no oxygen debt has been incurred. Whole body lactate concentrations did not change in the monkeyface prickleback after four hours of emersion, also indicating no lactate buildup (Riegle, 1976). On the other hand, subtidal sculpins, such as the longfin sculpin *(Jordania zonope),* significantly increase production of lactate when forced to emerge (Martin, 1996).

Few studies have been carried out on marine fishes while they are active out of water partly because most species remain largely inactive when they emerge (Ralston and Horn, 1986; Horn and Gibson, 1988; Martin, 1993). Nevertheless, the relatively inactive black prickleback, a remainer, can double its aerial oxygen consumption over its resting aquatic rate if forced to move about (Daxboeck and Heming, 1982; Martin, 1993). Anaerobiosis also may be involved during some kinds of terrestrial activity (Martin and Lighton, 1989), for example, when remainers thrash about rapidly to escape predators, possibly incurring an oxygen debt. Under asphyxic conditions, the blind goby *(Typhlogobius californiensis)* increases lactate concentrations (Congleton, 1974). Skipper fishes, such as the rockskipper blennies that are highly active out of water on tropical shores, increase aerial oxygen consumption during this activity (Hillman and Withers, 1987; Martin and Lighton, 1989).

For intertidal fishes, carbon dioxide release in air matches their rate of production (Martin, 1993; Martin and Bridges, 1999). In contrast, freshwater air-breathing fishes use lungs and enclosed air-breathing organs that are ventilated tidally and infrequently (Randall et al., 1981; Graham, 1997). Thus, carbon dioxide accumulates within the respiratory organ, causing changes in blood pH. Intertidal fishes use the skin and gills for breathing, where blood capillaries flow in constant, direct contact with the air rather than within an enclosed organ. As a result, carbon dioxide is constantly diffused away, and no carbon dioxide accumulation occurs in the circulatory system of intertidal species (Feder and Burggren, 1985).

Aquatic hypoxia normally causes greater ventilatory responses than hyperoxia in intertidal fishes (Martin and Bridges, 1999), but these responses have not been carefully studied in any California intertidal species. Below a critical aquatic oxygen tension (Pc), intertidal fishes cannot continue to maintain resting metabolic rates, and oxygen consumption falls. The oxygen tension where this happens varies for different species, but the Pc values for intertidal fishes are low compared to those for other teleosts (Hughes et al., 1983). The woolly sculpin, a tidepool emerger, has a lower Pc than that of two remainers, the reef finspot *(Paraclinus integripinnis)* and the spotted kelpfish (Congleton, 1980). The blind goby, with an even lower Pc (Congleton, 1974), can colonize mud burrows of ghost shrimps, and, at what must be very low oxygen tensions, anaerobic metabolism may become important. Further studies are needed on the effects of low oxygen tension on intertidal fishes.

### Osmoregulation and Resistance to Desiccation

Despite the immediate risks of desiccation, no clear evidence exists for physiological or anatomical adaptations to desiccation among California intertidal fishes; instead, they face this challenge with behavioral responses. Some fish emerge only at night (Wright and Raymond, 1978; Congleton, 1980; Martin, 1993), when hypoxic stress is highest but desiccation risk is low in tidepools. During the daytime, when desiccation stresses are greatest, fish may emerge under cover (Cross, 1981; Horn and Riegle, 1981; Martin, 1995, 1996) or remain semisubmerged in very shallow pools (Daxboeck and Heming, 1982).

Some California intertidal fishes can survive emergence for many hours, but mass decreases over time, most likely from evaporative water loss (Horn and Riegle, 1981; Martin, 1991; Luck and Martin, 1999). For five California intertidal species that occur across a vertical tidal gradient but commonly beneath boulders and not in tidepools, Horn and Riegle (1981) found that the monkeyface prickleback, the fish living highest on the shore, had the greatest initial water content and tolerance to desiccation. In contrast, two midintertidal species, the black prickleback and the rockweed gunnel, lost water in air and went on to lose even more water after reimmersion, showing the importance of avoiding desiccation in the first place. On the other hand, five species of sculpins from a vertical tidal gradient in Puget Sound, but more confined to tidepools than the pricklebacks above, showed no difference in the rate of water loss that could not be explained by differences in body size (Martin, 1996).

To recover lost fluids, intertidal fishes drink seawater (Dall and Milward, 1969; Evans et al., 1999). The black prickleback also can osmoregulate in dilute media, maintaining plasma osmolarity when immersed in 20% sea water. Thus, tolerance to alterations in the external medium allows this euryhaline fish to survive ephemeral changes in tidepool salinity, an ability that also may exist in other intertidal pricklebacks.

No California intertidal fishes have been studied with regard to the storage or excretion of nitrogenous waste products in air, although the monkeyface prickleback excretes nitrogen in the form of urea in water (Horn et al., 1995), so this species also may exhibit terrestrial ureotelism. Ip et al. (2002) have identified a number of strategies for amphibious fishes to cope with ammonia production and pH changes while out of water. The physiological mechanisms that allow California intertidal fishes to survive out of water for long periods of time are of particular interest for future studies.

### Movements and Homing

Resident intertidal fishes recognize features of their complex environment well enough to choose specific microhabitats. After swimming out of their home pools, presumably to forage, several species of sculpins excel at finding their way back to these pools (Yoshiyama et al., 1992; Pfister, 1992). The tidepool sculpin can find its home pool from as far way as 100 meters, and woolly sculpins return to the same pools every day (Williams, 1957; Richkus, 1978). Juvenile opaleye normally inhabit low pools during an ebb tide, but they move higher in the intertidal zone during high tides (Williams, 1957).

Some intertidal fishes move between pools but rarely travel more than a few meters, as indicated by mark and recapture studies or telemetry (Stephens et al., 1970; Richkus, 1978), The monkeyface prickleback, one of the larger resident intertidal fishes and a species more abundant in boulder fields than in tidepools (pers. obs.), moves less than 1 $m^2$ per day based on ultrasonic tracking (Ralston and Horn, 1986). When resident fish are removed experimentally from tidepools, member of the same species occupy the vacated habitat (Grossman, 1982). This process, however, may take many weeks (Matson et al., 1986), even in a broad expanse of rocky intertidal habitat with numerous intact pools nearby as sources of newly occupying fish.

Out of water, fish obviously move about differently than when swimming. Sculpins on land generally use their pectoral fins as levers while balanced on the body and tail in a tripod stance. Members of the sculpin family actively emerge from hypoxic water by pushing off the substratum with their tails (Martin, 1991, 1996; Yoshiyama et al., 1995). Elongate intertidal fishes, such as pricklebacks, can slip into crevices between rocks, a behavior probably most often used to avoid predators. Although capable of thrashing and directional sinusoidal locomotion, pricklebacks probably move little during low tides (Ralston and Horn, 1986; Horn and Gibson, 1988). The rockweed gunnel, another elongate remainer, weaves its body between fronds of intertidal seaweeds such as the fucoid brown alga *Sylvetia compressa,* where it emerges, until the tide returns as high as 0.5 m above the substratum if the seaweed is attached atop a large boulder (Burgess, 1978; Martin, 1993).

### Agonistic Behavior, Interference Competition, and Territoriality

Interspecific interactions among fishes of intertidal habitats in temperate latitudes are not well studied. Nevertheless, such interactions ought to be expected especially among resident species, given the numerous co-occurring species and limited space of the habitat. As Gibson and Yoshiyama (1999) point out, major limitations to testing these expectations involve the turbulence of the rocky shore environment and the evasive and cryptic nature of the fishes.

Of the relatively few studies that have been completed on interspecific interactions among intertidal fishes in California or the Pacific Northwest, most were focused on sculpins. Several of these investigations have failed to detect aggressive behavior or territoriality among species (Green, 1971; Nakamura, 1976; Cross, 1981; Grossman, 1986a; Pfister, 1995), and both Cross and Grossman concluded that any competition among the fishes they studied is of the exploitative, not of the interference, type. Nevertheless, various observations and qualitative studies of the woolly sculpin, one of the most abundant resident intertidal species in California, suggest that this species through its aggressive behavior may have a negative influence on the distribution and abundance of other intertidal fishes (see Gibson and Yoshiyama, 1999). Field experiments are needed to test for this possibility. Part of the reason for the seeming lack of interspecific aggression among intertidal fishes may lie in their limited contact with each other, based on studies by Davis (2000b) in southern California on a guild of five co-occurring species—woolly sculpin, opaleye, rockpool blenny, California clingfish *(Gobiesox rhessodon),* and spotted kelpfish. She found that these species partitioned tidepool habitats spatially and seasonally and reasoned therefore that contact was limited and that interference and exploitative competition were reduced, at least during low tide.

Even though the four species of pricklebacks that commonly co-occur in rocky intertidal habitats on the central California coast often shelter beneath the same individual boulder at low tide (pers. obs.), laboratory experiments carried out by Jones (1981) suggest that aggressive interactions and competitive exclusion occur among them. Jones first established that the high cockscomb is found associated significantly more often with sandy substrata in the habitat at low tide than the monkeyface prickleback, black prickleback, or rock prickleback, all three of which are associated more frequently with rocky substrata. In isolation in the laboratory, the high cockscomb preferred rocky substrata. Jones then set up one-on-one species experiments with one high cockscomb and one individual of one of the three other prickleback species and with substratum type (sandy or rocky) as the treatment to test the hypotheses that a sandy substratum is suboptimal for all four species and that the high cockscomb is relegated to this substratum type by interference competition from each of the three other species. The findings supported his hypotheses: all four species preferred rocky substrata, and the high cockcomb occurred more frequently on sandy substrata in the presence of individuals, especially larger ones, of any of the three other species. The experiments, however, were conducted under simulated high tide conditions and were designed to represent what is rarely seen in the intertidal zone, that is, the behavior of fishes during high tide.

### Sensory Systems

When intertidal fishes are out of the water, they encounter light rays with a different refractive index in air than in water, sound waves that travel slower in air than in water, and a lateral line system that cannot function in air. Fishes have eyes with round lenses, not elliptical lenses as do terrestrial vertebrates, and accommodate for near vision by moving the lens (Graham, 1971). Mudskippers, however, which are among the most terrestrial of fishes, have a flattened lens adapted to aerial vision (Graham, 1971), and rockskippers, another highly amphibious group, have a flattened cornea (Graham and Rosenblatt, 1970). The eyes of California intertidal fishes, including remainer or tidepool emerger species that generally emerge only during low tides, have not been studied. These species, however, clearly respond when on land to visual stimuli by evasion (pers. obs.), perhaps as a survival mechanism to avoid potential predators.

Sound is probably not used for communication by most intertidal fishes because of the consistent background noise from the surf and their lack of a swimbladder that could serve as a resonating organ. One exception is the plainfin midshipman, which has a swimbladder modified for sound production. Male midshipman congregate in the intertidal zone during the spawning season and form mating choruses that are loud enough to be heard by nearby humans (Brantley and Bass, 1994; pers. obs.).

Lateral lines sense near-body movement and water displacement with hair cells that can function only under water. All aquatic vertebrates, including larval amphibians, possess lateral lines, but no terrestrial animals do, including most adult amphibians. Some highly amphibious skippers have a greatly reduced lateral line system (Zander, 1972). On the other hand, a comparison of 12 species of Mediterranean blennies shows no clear correlation of vertical zonation with lateral-line development, but a trend toward shortened lateral lines and fewer pores occurs among intertidal species (Zander, 1972). Anatomical features of the lateral line have not been studied in California intertidal fishes.

Chemosensory structures also are unstudied among California shore fishes, but, given the known homing abilities of a number of the species, such structures may be important in a variety of taxa.

## Reproduction

### Spawning and Parental Care

Resident intertidal fishes live and reproduce in the rocky shore habitat and exhibit different ways of protecting their offspring (Coleman, 1999; DeMartini and Sikkel, chapter 19, this volume). Typically, resident species lay demersal rather than planktonic eggs. The eggs are sometimes attached to a rocky substratum, to seaweeds or seagrasses, or only to one another. Pricklebacks, a group that contains resident intertidal species, have external fertilization and lay eggs that adhere to one another but not to the substratum. In these fishes, a parent guards the egg mass and keeps the eggs from being washed away or consumed by predators, remaining with them even when low tides expose them to air (Marliave and DeMartini, 1977). As an indication of the importance of turbulence to fishes that spawn in the intertidal zone, the black prickleback spawns in protected locations on rocky shores during the storms of late winter but in more exposed locations during the calmer conditions of spring (Marliave and DeMartini, 1977). The plainfin midshipman exhibits another variation on parental care of eggs in the intertidal zone. Territorial males establish under-boulder nest sites and mate with multiple females (Crane, 1981). These males then guard the eggs that are attached as a single layer on the underside of a boulder until the well-formed young fish break free and swim on their own. In this case, the eggs adhere to the substratum, not to each other as in the coherent, but unattached mass formed by pricklebacks. At least two live-bearers, reef perch *(Micrometrus aurora)* and dwarf perch *(M. minimus),* are associated with rocky intertidal habitats as transient species and occasionally may bear their young there (Hubbs, 1921; Warner and Harlan, 1982).

Not surprisingly, sculpins, the most species-rich group of fishes in the California rocky intertidal zone, show highly diverse forms of reproduction, including the rocky shore habitat. Resident species such as the fluffy sculpin and bald sculpin spawn demersal eggs in tidepools (Morris, 1952, 1956). The cabezon *(Scorpaenichthys marmoratus)* migrates to the intertidal zone to spawn, and its conspicuous eggs are highly toxic to vertebrates (DeMartini and Sikkel, chapter 19, this volume). The buffalo sculpin *(Enophrys bison)* spawns in the low intertidal zone, and the male guards the eggs and fans them with his pectoral fins (DeMartini, 1978). Sharpnose sculpin *(Clinocottus acuticeps)* spawn beneath fucoid brown algae (*Fucus* sp. or *Sylvetia* sp.) in the high intertidal zone to prevent desiccation while increasing the exposure of eggs to oxygen (Marliave, 1981). Males of scalyhead sculpin *(Artedius harringtoni)* guard eggs in the intertidal zone (Ragland and Ficher, 1987). To add to the diversity of reproductive behavior in cottoid fishes, the female grunt sculpin *(Rhamphocottus richardsonii)* have been observed in aquaria to chase the male into caverns and to trap him there until she lays her eggs (Eschmeyer et al., 1983).

Eggs laid in the intertidal zone may be exposed to air for extended periods during extreme low tides. These exposed eggs may accrue certain advantages as long as desiccation is prevented (Strathmann and Hess, 1999). For example, increased oxygen availability and higher temperatures may speed development and thus reduce the chances of egg mortality from hypoxia or from aquatic predation. Eggs of Pacific herring *(Clupea pallasi),* which are spawned on seagrasses in the low intertidal zone, survive better than eggs laid in subtidal habitats, presumably because of reduced predation in the intertidal zone (Jones, 1972; Blaxter and Hunter, 1982).

### Recruitment

The larvae of most intertidal fishes that have been examined spend about 1 to 2 months in the plankton (Stephens et al., 1970; Marliave, 1986; Stepien et al., 1991), a range of times influenced by temperature fluctuations, spawning dates, and current patterns. Despite a period of planktonic existence, the larvae of rocky intertidal fishes dipserse only short distances and tend to stay within the area in which they were hatched (Marliave, 1986). These results were corroborated by Setran and Behrens (1993) who found that larvae of black prickleback, rock prickleback, and monkeyface prickleback declined in density offshore and somehow avoided offshore and perhaps longshore drift. For sculpins, kelpfishes, and other tidepool-oriented fishes, the larvae are likely to settle on the same substratum as the adult fish prefer although higher on the shore (Marliave, 1977; Pfister, 1995). High intertidal pools may act as refuges for small intertidal fishes because lower pools hold larger individuals (see above). Pfister (1995) found little evidence for competitive interactions in recruitment of three species of intertidal sculpins to tidepools and no effect of the presence of an adult on the distribution of species among recruits to a particular pool. In addition, the number of recruits do not necessarily correlate well with the number of adult females or with the number of adults in subsequent years (Pfister, 1999).

For pricklebacks, which associate more closely with the gravel and cobble of boulder fields, the preferred substratum does change as the fish grow in size after settlement. This statement is based on the work of Setran and Behrens (1993), who found in laboratory experiments that, soon after settlement (17–22 mm total length, TL), both rock prickleback and monkeyface prickleback prefer gravel and cobble; then at 30–36 mm TL they preferred cobble over gravel, apparently because the latter provided insufficient interstitial space for larger juveniles. These experiments corroborated the field collections made by Setran and Behrens and supported the view that the physical characteristics of the substratum are important for microhabitat selection by the two prickleback species. Substratum preference and microhabitat selection by the different types of rocky intertidal fishes are complex but important subjects that deserve further study and probably will require long-term data sets to unravel.

### Community Structure and Function

The concept of community faces special scrutiny when applied to intertidal fish assemblages. Given the dynamic nature and relatively small size of the rocky intertidal zone, questions arise as to whether such a habitat supports groups of populations that are predictable in space and time or whether the species at a particular locality are merely stranded there at low tide and thus participate minimally in the intertidal ecosystem. The results of numerous studies show that the former is the case and that intertidal fish faunas clearly offer examples of the community, if it is defined as a group of populations living in the same place (Fauth et al., 1996; Ricklefs and Miller, 2000). This definition works particularly well for rocky intertidal fish communities in the sense that they are demarcated sharply by the land on one side and separated abruptly along the shore by stretches of sandy beach or muddy river mouths. The distinction, however, is blurred to the seaward at the intertidal/subtidal boundary, as revealed in the ecological classification described in chapter 4 (this volume). In full, the intertidal fish community consists of both resident species that live year-round in the habitat and transient species that enter the intertidal zone from adjacent waters only at high tide. This mixed composition demonstrates the complex and dynamic nature of intertidal fish communities and, again, challenges the concept of community. As observed by Gibson and Yoshiyama (1999), resident species have received greater attention because they are more interesting to study as a result of their presumed adaptations to an extreme habitat and are easier to study because they can be sampled at low tide. Despite the changing species composition of intertidal fishes on a diel basis and the unbalanced treatment of resident versus transient species, this section of the chapter attempts to describe the intertidal fish community as a whole. Focus is placed on certain interrelated components of community structure and function (Ricklefs and Miller, 2000), species diversity and relative abundance, age composition, trophic relationships, and resilience to perturbation. The overall goal of the section is to identify the members of the community and the interactions that tie them together into an intricate web.

### Taxonomic Composition

Intertidal fish communities on California and northern Baja California shores are dominated by advanced acanthopterygian (spiny-rayed) fishes, primarily in two orders—Scorpaeniformes and Perciformes, as would be expected from Hobson's analysis of reef fish evolution in the northeastern Pacific (chapter 3, this volume). This dominance is seen in the family and species compilations for three geographic regions of California as well as northern Baja California (table 8-2; fig. 8-4). Among the scorpaeniforms, the Cottidae (sculpins) are represented in all regional rocky intertidal habitats, and the Scorpaenidae (rockfishes), Hexagrammidae (greenlings), and Liparidae (snailfishes) are frequently represented by one or more species. Among the perciforms, the families Stichaeidae (pricklebacks), Pholidae (gunnels), and Clinidae (kelpfishes) are relatively diverse and common, and one or another species of clingfish (Gobiesocidae) is consistently present in these habitats (fig. 8-5A). In the regional compilations shown in Table 2 and fig. 4, greenlings occurred only at northern California localities; graveldivers (Scytalinidae) only in central California habitats; and blennies (Blenniidae), nibblers (Girellidae), and labrisomids (Labrisomidae) only in southern California or northern Baja California. Pricklebacks were absent from both of these latter sites, and gunnels were not recorded in the rocky intertidal zone in southern California.

TABLE 8-2

Most Common Fishes Collected from the Rocky Intertidal Zone

| | | *% of Total* | | | |
|---|---|---|---|---|---|
| *Common Name* | *Scientific Name* | *Northern California* | *Central California* | *Southern California* | *Northern Baja California* |
| Black rockfish | *Sebastes melanops* | 6% | — | — | — |
| Grass rockfish | *Sebastes rastrelliger* | 4% | — | — | — |
| Black-and-yellow rockfish | *Sebastes chrysomelas* | — | 1% | — | — |
| Blue rockfish | *Sebastes mystinus* | — | 1% | — | — |
| Kelp greenling | *Hexagrammos decagrammus* | 2% | — | — | — |
| Fluffy sculpin | *Oligocottus snyderi* | 28% | 2% | — | 3% |
| Tidepool sculpin | *Oligocottus maculosus* | 7% | — | — | — |
| Mosshead sculpin | *Clinocottus globiceps* | 2% | — | — | — |
| Woolly sculpin | *Clinocottus analis* | 1% | 2% | 50% | 20% |
| Bald sculpin | *Clinocottus recalvus* | 1% | — | 1% | — |
| Smoothhead sculpin | *Artedius lateralis* | — | 3% | — | 4% |
| Saddleback sculpin | *Oligocottus rimensis* | — | 2% | — | — |
| Cabezon | *Scorpaenichthys marmoratus* | 6% | 1% | — | — |
| Rosy sculpin | *Oligocottus rubellio* | — | — | — | 10% |
| Tidepool snailfish | *Liparis florae* | 2% | — | — | 1% |
| Opaleye | *Girella nigricans* | — | — | 24% | 8% |
| Reef perch | *Micrometrus aurora* | — | — | — | 2% |
| High cockscomb | *Anoplarchus purpurescens* | 2% | 2% | — | — |
| Monkeyface prickleback | *Cebidichthys violaceus* | — | 4% | — | — |
| Black prickleback | *Xiphister atropurpureus* | 11% | 25% | — | — |
| Rock prickleback | *Xiphister mucosus* | 8% | 12% | — | — |
| Penpoint gunnel | *Apodichthys flavidus* | 7% | 1% | — | — |
| Rockweed gunnel | *Xererpes fucorum* | 2% | 18% | — | 4% |
| Graveldiver | *Scytalina cerdale* | — | 1% | — | — |
| Reef finspot | *Paraclinus integripinnis* | — | — | 5% | — |
| Striped kelpfish | *Gibbonsia metzi* | 2% | 2% | — | 8% |
| Crevice kelpfish | *Gibbonsia montereyensis* | — | 5% | — | 12% |
| Spotted kelpfish | *Gibbonsia elegans* | — | — | 7% | 22% |
| Rockpool blenny | *Hypsoblennius gilberti* | — | — | 4% | — |
| Northern clingfish | *Gobiesox maeandricus* | 2% | 11% | — | — |
| California clingfish | *Gobiesox rhessodon* | — | — | 7% | 1% |

NOTE: Includes species >1% identified by cluster analysis (see Chapter 4) for four latitudinal regions of California and northern Baja California. Occurrences and abundances derived from all sources used in the analysis. See Fig. 4 for a pictorial representation of most species in the four regions.

With few exceptions, the intertidal fish communities of California and northern Baja California comprise species of cold-water affinities (chapter 1, this volume). Both the sculpins and the rockfishes of the genus *Sebastes* occur only in the Northern Hemisphere as do the other scorpaeniforms represented (greenlings and snailfishes). Pricklebacks, gunnels, kelpfishes, and the graveldiver among the perciforms also have cold-temperate distributions. In contrast, nibblers, labrisomids, and blennies occur primarily in warm-temperate or tropical waters. Surfperches (Embiotocidae) are distributed broadly in warm- and cold-temperate latitudes of the northeastern Pacific, and clingfishes are represented worldwide in temperate and tropical habitats.

## Species Richness and Relative Abundance

Taxonomic compilations for four California and northern Baja California localities show that fish species richness is highest in Northern and central California (table 8-2, fig. 8-4). Eighteen species are listed for northern California, 17 for central California, 12 for northern Baja California, and only seven for southern California. At the family level, the Cottidae are represented by the most species in all four regions. Although differences in sampling effort must be taken into account, the regional differences in species richness may reflect the prevalence of cold-temperate fishes, especially sculpins, in the northeastern Pacific and their increased presence at higher latitudes and in areas of strong upwelling as in northern Baja California.

A similar picture of dominance prevails in the numbers of individuals apportioned among families and species. Summaries of relative abundance based on the compilations from all sources (table 8-2) show that sculpins account for the largest proportion of individuals in northern California (46%) and southern California (51%) and the second largest proportion in northern Baja California (37%). Particularly abundant sculpins are the fluffy sculpin in northern California and the woolly sculpin in southern California and northern Baja California. The general abundance of these two sculpins at several northern and central California collection sites is illustrated in fig. 8-5b. In central California, sculpins are

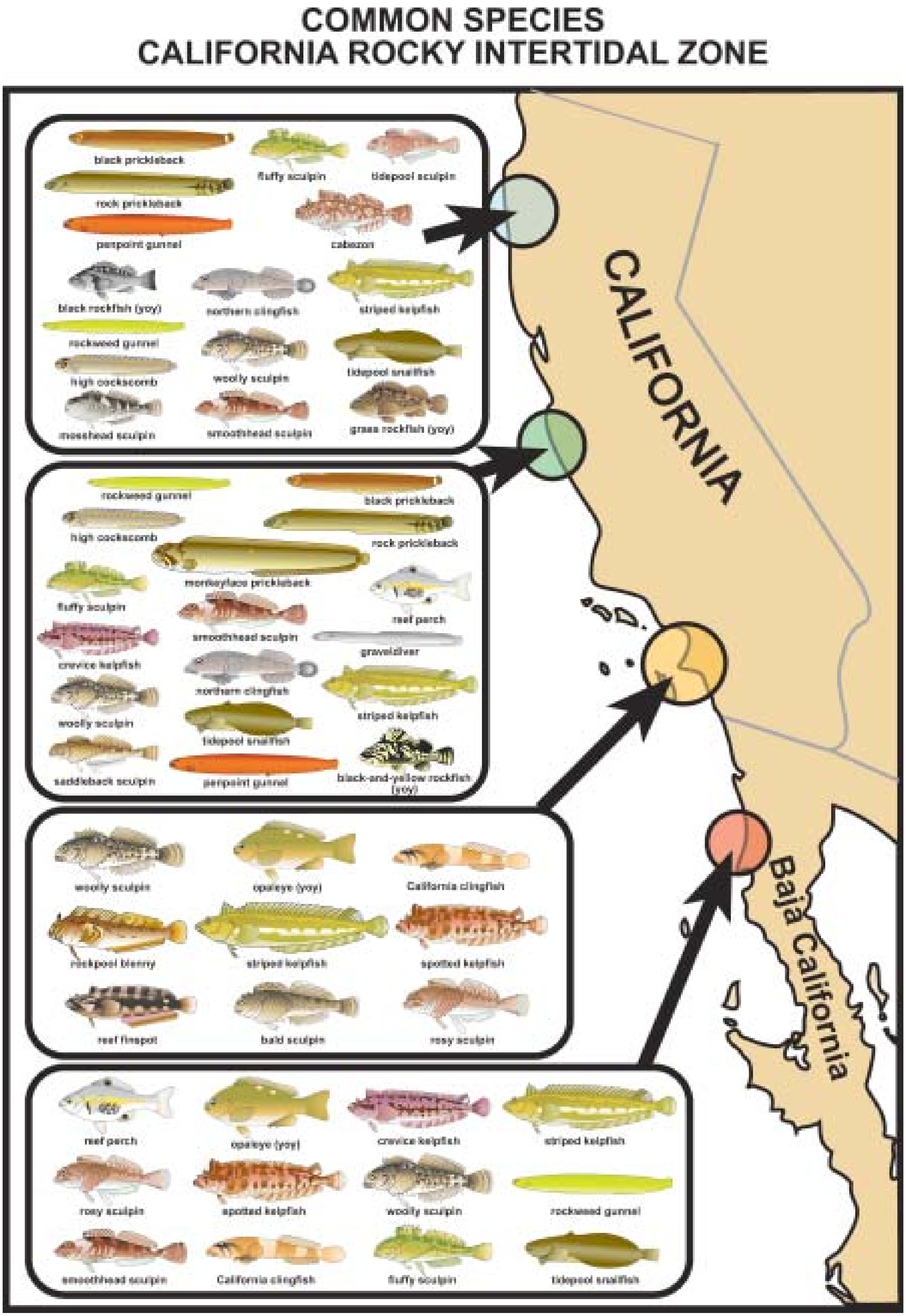

FIGURE 8-4 Pictorial representations of common fish species from rocky intertidal habitats in northern California, central California, southern California, and northern Baja California.

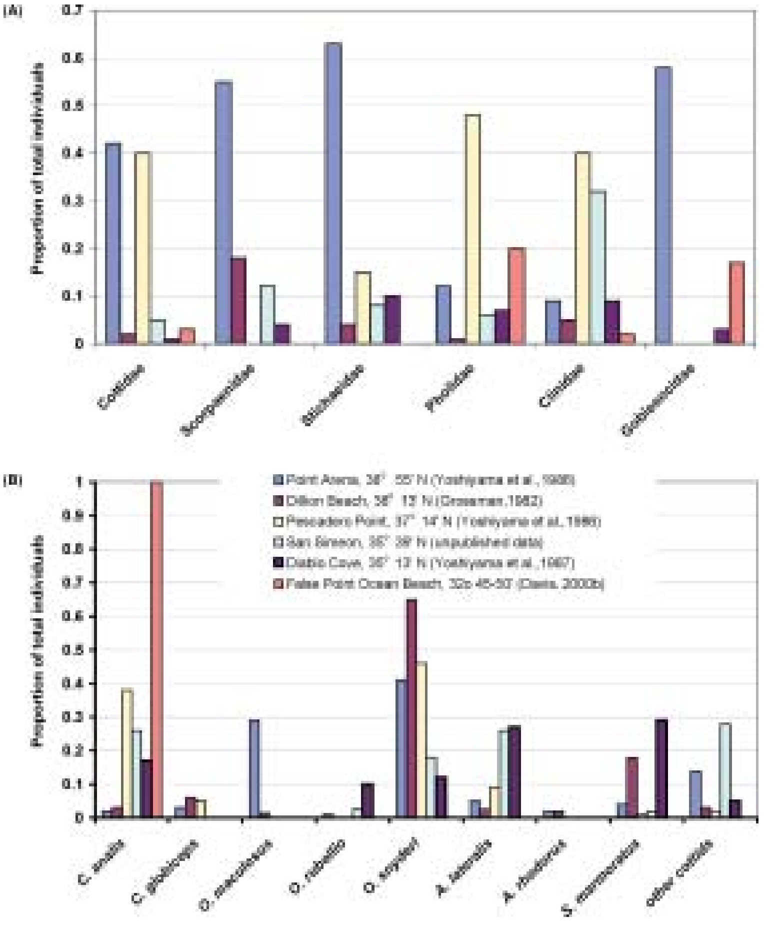

FIGURE 8-5 Proportional abundances of rocky intertidal fish families (A) and species of Cottidae (B) at six localities on the California coast. The names, latitudes, and references for each locality are given between the graphs. In (B) the genera represented by the major species are *Clinocottus, Oligocottus, Artedius* (*A. lateralis*), *Ascelichthys* (*A. rhodorus*), and *Scorpaenichthys*. Common names are *C. analis* (woolly sculpin), *C. globiceps* (mosshead sculpin), *O. maculates* (tidepool sculpin), *O. rubellio* (saddleback sculpin), *O. snyderi* (fluffy sculpin), *A. rhodorus* (rosylip sculpin), and *S. marmoratus* (cabezon) (after fig. 8-2 in Gibson and Yoshiyama, 1999).

replaced as the most abundant intertidal species. Here, collection summaries reveal that members of the Stichaeidae (43%) and Pholidae (19%) are the predominant species, in particular, black prickleback and rockweed gunnel. In northern Baja California, the Clinidae (42%) are the best represented family, especially by spotted kelpfish.

### Residents and Visitors

Part of the complexity and dynamics of intertidal fish communities results from the differing periods of time that various species spend in the rocky shore habitat. As already mentioned, some species spend virtually their entire lives between the tidemarks, whereas others visit only briefly at high tide. A continuum of types exists between these extremes and has led to several attempts to classify intertidal fish faunas accordingly. Gibson and Yoshiyama (1999) point out, however, that all such attempts reach the same basic distinction that the community consists of residents, species that live permanently in the intertidal zone, and transients, which are species that visit the habitat for differing lengths of time during their lives. Nevertheless, these variations in occupancy of the habitat lead to some further, potentially useful distinctions along the continuum of intertidal species (Gibson and Yoshiyama, 1999). Primary residents are those small, cryptic species that are the typical (Breder, 1948) inhabitants, and to show various specializations for intertidal life. They settle out of the plankton as larvae and transform into juveniles, then grow to adults, reproduce, and live out their lives in the intertidal zone. In contrast, secondary residents (Thomson and Lehner, 1976) are mainly larger, subtidal species that reside as juveniles in the intertidal zone for varying lengths of time and then as adults enter the habitat for breeding or foraging at high tide, daily or seasonally. Still other species occur as casual visitors that feed over the intertidal zone at high tide then occasionally become trapped in pools at low tide. Unlike both resident and transient species, casual visitors probably play only minor roles in the ecology of rocky intertidal communities.

On California shores, the proportions of primary and secondary residents and transient species vary widely in both species and individual fish (table 8-3). For a series of northern and central California rocky intertidal sites, the proportions of primary residents range from less than a third to more than 80% of the total species, whereas secondary residents comprise less than half and transients a third or less of the species, depending on the location. In proportions of individuals, primary residents rise to greater prominence and account for more than 90% of the total fish at most of the sites sampled. These high proportions of year-round species are not surprising, given that the collections were made at low tide when the smaller, bottom-associated fishes commonly thought of as residents would be captured with greater likelihood than the more mobile and often pelagic secondary residents or transients.

Comparisons between widely separated geographic regions in the world are difficult because equivalent categories are seldom used. Despite this difficulty, a broad range of proportions

TABLE 8-3

Proportions of Primary Residents, Secondary Residents, and Transients in Rocky Intertidal Assemblages at Five Northern and Central California Localities

| | *Primary Residents* | | *Secondary Residents* | | *Transients* | | *Totals Numbers* | | |
|---|---|---|---|---|---|---|---|---|---|
| *Locality (N Latitude)* | *Sp* | *Ind* | *Sp* | *Ind* | *Sp* | *Ind* | *Sp* | *Ind* | *Reference* |
| Trinidad Bay (41° 31′) | 42% | ? | 45% | ? | 13% | ? | 31 | 1599+ | Moring, 1986 |
| Dillon Beach (38° 15′) | 31% | 77% | 35% | 19% | 35% | 3% | 29 | 2857 | Grossman, 1982 |
| Dillon Beach (38° 15′) | 83% | 94% | 17% | 6% | — | — | 12 | 62 | Boyle, 2004 |
| Pescadero Point (37° 14′) | 73% | 92% | 27% | 8% | — | — | 11 | 64 | Boyle, 2004 |
| Pescadero Point, Bean Hollow, and Pigeon Point (37° 14′) | 54% | 90% | 33% | 9% | 13% | 1% | 24 | 3703 | Yoshiyama, 1981 |
| San Simeon (35° 39′) | 40% | 91% | 33% | 8% | 27% | 1% | 30 | 3265 | Boyle, 2004 |

NOTE: Sp = % of species; Ind = individuals. After Table 1 in Gibson and Yoshiyama, 1999.

of residents and transients is seen in intertidal fish communities around the world (Gibson and Yoshiyama, 1999; Table 1). The extremes of proportions are illustrated in Gibson's and Yoshiyama's tabulation because the range extends from the absence of transients on certain South African shores (Prochazka, 1996) to the lack of residents in Maine tidepools where fish are absent in winter (Moring, 1990). These variations emphasize the fact that both resident and transient species play important roles in the structure of intertidal fish communities, but the degree depends greatly on season and geographic location.

## Age Composition

Most resident species of rocky intertidal fishes are relatively short-lived, mostly ≤ 5–6 years (Gibson, 1969; Stepien, 1990; Gibson and Yoshiyama, 1999), perhaps reflecting the small body size attained by most of these fishes. For example, the four species in the cottid genus *Oligocottus* occur commonly in tidepools in California and farther north and attain maximum sizes of only about 60–100 mm TL (Eschmeyer et al., 1983). Populations of *O. maculosus* in northern California are made up mostly of 0- and 1-year age classes and a smaller proportion of somewhat older fish (Moring, 1979). Another member of the genus, *O. snyderi,* can be represented in tidepools by as many as five age groups beyond the young of the year (Chadwick, 1976), but still within the small size reached by the species. Longer lived exceptions include some species of stichaeids, in particular, the monkeyface prickleback, estimated to reach 18 years of age (Marshall and Echeverria, 1992) and cabezon, reported to attain 13+ years (O'Connell, 1953; Grebel, 2003). The monkeyface prickleback also is an exception in size as it is one of the largest resident intertidal fish, attaining a length of 760 mm SL (Marshall and Echeverria, 1992). In fact, however, the larger monkeyface pricklebacks live lower on the shore or, like the cabezon, which reaches nearly 1 m in length (Eschmeyer et al., 1983), become associated with subtidal reefs (pers. obs.; chapter 9, this volume). These examples of increasing depth of occurrence with age indicate spatial differences in age structure within fish species that occur mainly during the early part of their lives in the intertidal zone.

Information showing that some marine fish species are represented mainly by young fish in the intertidal zone leads to the supposition that rocky intertidal habitats are nursery areas for subtidal species. The examples above involving cabezon and monkeyface prickleback lend support to this suggestion, but too few studies of intertidal fish communities in California have provided detailed age structure data on community members to make a strong case for a nursery function of the habitat. Nevertheless, our compilation of the proportion of juveniles for 12 species of fishes collected in 18 quarterly samplings from a tidepool near Piedras Blancas on the central California coast shows that, with one exception, the majority or all individuals collected were juveniles (table 8-4). Although other species were captured in the tidepool, the list of species here is limited to those for which age at maturity information is available. The data in Table 4 provide evidence for a nursery role for this central California intertidal habitat, but further studies and support are required to establish unequivocally that rocky intertidal habitats serve a nursery function. This challenge is heightened with the proposal (Beck et al., 2001) that to qualify as a nursery ground, an inshore habitat must contribute to a greater production per unit area of individuals that recruit to adult populations than that of other habitats in which juveniles occur (see chapter 5, this volume). Clearly, further research is needed in this area of intertidal fish ecology.

## Trophic Interactions

The majority of intertidal fish species are either carnivores or omnivores (table 8-5). Most fishes that feed in rocky intertidal habitats in California and other temperate regions consume benthic invertebrates, especially copepod, amphipod, and decapod crustaceans; other invertebrates, such as mollusks and polychaetes, are less important dietary items as are larger crustaceans, fishes, and algae (fig. 8-6; Grossman, 1986a; Gibson and Yoshiyama, 1999; Horn and Ojeda, 1999; Norton and Cook, 1999). The rarity of herbivores parallels that found in other temperate-zone marine habitats and continues to inspire speculation as to cause (e.g., Gaines and Lubchenco, 1982; Horn, 1989; Horn and Ojeda, 1999). The two California intertidal fishes that rely most heavily on macroalgae as an energy source are the monkeyface prickleback and the rock prickleback. Feeding and digestion in these two species have been the subject of several studies in recent decades (e.g., Montgomery, 1977; Barton, 1982; Horn et al. 1982, 1986, 1995; Fris and

TABLE 8-4

Proportions of Juveniles in 18 Samples Collected from a Tidepool on the Central California Coast Near San Simeon from 1979 to 1983

| *Common Name* | *Family* | *Total No. Collected* | *% Juveniles* |
|---|---|---|---|
| Plainfin midshipman | Batrachoididae | 20 | 0 |
| Gopher rockfish | Scorpaenidae | 17 | 94 |
| Black-and-yellow rockfish | Scorpaenidae | 3 | 67 |
| Grass rockfish | Scorpaenidae | 3 | 100 |
| Black rockfish | Scorpaenidae | 1 | 100 |
| Olive rockfish | Scorpaenidae | 1 | 100 |
| Cabezon | Cottidae | 5 | 100 |
| High cockscomb | Stichaeidae | 70 | 93 |
| Monkeyface prickleback | Stichaeidae | 135 | 98 |
| Black prickleback | Stichaeidae | 673 | 64 |
| Rock prickleback | Stichaeidae | 144 | 85 |

TABLE 8-5

Relative Abundance of Species 4 by Trophic Category in Four Rocky Intertidal Fish Assemblages on the California Coast

| *Locality (N Latitude)* | *Carnivore* | *Omnivore* | *Herbivore* | *Total No. Species in Sample* | *Basis of Assessment* | *Reference* |
|---|---|---|---|---|---|---|
| Dillon Beach (38° 15′) | 86% | 7% | 7% | 15 | % food mass | Grossman, 1986a |
| Dillon Beach (38° 15′) | 40% | 40% | 20% | 10 | Average % food mass | Boyle, 2004 |
| Pescadero Point (37° 14′) | 56% | 33% | 11% | 9 | Average % food mass | Boyle, 2004 |
| San Simeon (35° 39′) | 50% | 36% | 14% | 14 | Average % food mass | Boyle, 2004 |

NOTE: Carnivores arbitrarily classified as species with <5% plant material in diet, omnivores as those with 5–69%, and herbivores as those with diets of ≥70% plant material. After Table 2 in Gibson and Yoshiyama, 1999.

Horn, 1993, Chan et al., 2004; German et al., 2004). Omnivorous fishes, which consume a mixture of seaweed and animal material (table 8-5), are more common than strict herbivores in California intertidal habitats and include woolly sculpin, mosshead sculpin, and reef perch (fig. 8-4; Grossman, 1986a). Perhaps the availability of a diverse and abundant standing crop of algae on California rocky shores has led to its use as part of the diet in some species, as intertidal fish communities have evolved under a scenario of food resource partitioning proposed by Grossman (1986a). The food webs involving intertidal fishes and the fish assemblages in other California marine habitats are analyzed in chapter 14 (this volume).

Ontogenetic shifts in diet appear to be a common feature in the life history of intertidal fishes. As pointed out by Norton and Cook (1999), intertidal fishes commonly increase twofold to fourfold, but as much as 15-fold, in length from metamorphosis to adulthood. With this growth, they change their diets, either qualitatively by adding or dropping items from the diet or quantitatively by changing the relative importance of prey types or the size of given prey items. One of the most dramatic qualitative shifts among California intertidal fishes is that documented for the monkeyface prickleback and the rock prickleback. Both species begin to shift from carnivory to herbivory at about 45 mm standard length (SL) (Horn et al., 1982; Setran and Behrens, 1993), a size of only 6–8% of the maximum size recorded for these two species. Recent feeding experiments and digestive enzyme studies support the hypothesis that the shift is genetically fixed, because as these two fishes increase in size the relative activities of their proteases and carbohydrases change even when the fishes are fed a high-protein diet (German et al., 2004). These two pricklebacks also exhibit quantitative shifts once they become herbivores because certain algae that are too tough for small fish to bite become increasingly important foods for larger fish (e.g., Miller and Marshall, 1987). Another qualitative ontogenetic shift in diet is seen in the woolly sculpin in which harpacticoid copepods and gammarid amphipods were commonly found in the diets of the smallest fish (<34 mm SL) studied but dropped out of the diets of larger fish (>40 mm SL) to be replaced by crabs, limpets, chitons, and algae (Norton and Cook, 1999). These changes in diet observed in the woolly sculpin as it grows larger are typical of a common pattern in intertidal fishes: harpacticoid copepods and gammarid amphipods dominate the diets of the smallest fish to be replaced in ontogeny most often by crabs, fishes, and algae (see Norton and Cook, 1999; Table 2).

Mouth size and biting strength increase with size in fishes and, therefore, allow fish to expand their diets and to consume variously larger, more abundant, or mobile prey (Norton and Cook, 1999). In simplest terms, small fish are limited to items that fit within their gape (mouth) because they cannot generate enough force to bite pieces from larger prey. Adding to the complexity of the ontogenetic change in diet is the fact that fish may change their attack strategy with an increase in body size. For example, the woolly sculpin appears to use ram feeding when young (Cook, 1996) and suction feeding as an adult

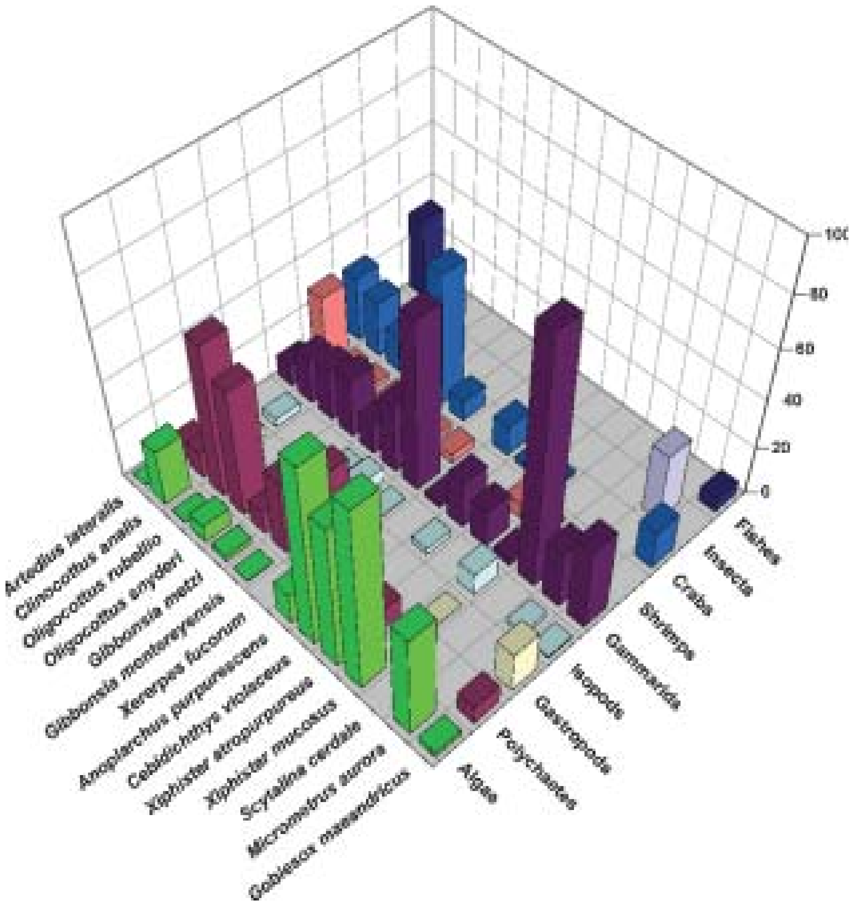

FIGURE 8-6 Diet spectrum of 14 fish species (n = 7–25) collected from three central California rocky intertidal habitats based on the average contribution of each prey type to the total food biomass for each fish (from unpubl. data in Boyle, 2004)

(Norton, 1991). Dietary shifts that involve different combinations of ram, suction, and biting attacks are likely to occur as well and deserve further study in California intertidal fishes.

A prevailing notion is that herbivory and predation in the broader sense by fishes have little effect on the structure of temperate intertidal communities (e.g., Gibson, 1982; Horn, 1989; Raffaelli and Hawkins, 1996). Nevertheless, the question still seems open because too few studies have been conducted to test the impact hypothesis adequately. Norton and Cook (1999) list three kinds of information that can be used to assess the impacts of fish feeding on intertidal communities: (1) elaborate antipredator traits of potential prey organisms, (2) fish consumption estimates compared to prey production estimates, and (3) experimental manipulations of fish consumers and potential intertidal prey species. The evidence that Norton and Cook assemble on these three sources of evidence is drawn from a wide array of inshore habitats but is sparse for temperate, rocky intertidal communities.

Three intriguing examples of potential impacts of fishes on intertidal organisms in California can be mentioned in the context of the Norton–Cook framework. The first example is of an antipredator trait. The chemical defenses found in the foot of the limpet, *Collisella limatula,* is effective against intertidal fishes and crabs but not against sea stars, octopi, or gulls (Pawlik et al., 1986). The implication is that the evolution of this trait was driven at least in part by fish predation. A second case is that of grazing by the high cockscomb on the distasteful polychaete worm, *Cirriformia luxuriosa,* interpreted by Yoshiyama and Darling (1982) as an example of circumventing an antipredator mechanism possibly in a coevolved relationship. Apparently, the high cockscomb is the only intertidal fish that feeds on this worm and thus may gain access to an otherwise little-used food resource. A third example is that of the selective feeding by the mosshead sculpin on sea anemones, as shown in dietary studies by Grossman (1986a) and confirmed in laboratory experiments by Yoshiyama et al. (1996a,b). Grossman proposed that sustained feeding by the fish on sea anemones could have a significant impact on biomass production and relative abundance of anemones in rocky intertidal habitats. In all three of the foregoing examples, manipulative experiments are needed to provide further insights into the relationships described.

A marked example of a grazing impact on algae by an intertidal fish has been documented in experimental field manipulations not in California but in Chile showing that an herbivorous blenniid fish *(Scartichthys viridis)* exerts a strong effect on macroalgal abundance and diversity in the intertidal zone of the central Chilean coast (Ojeda and Muñoz, 1999). We are not aware of a similar type of experimental study on fish–algae grazing relationships in the intertidal zone of California. Assessing the potential impacts of fishes on rocky intertidal communities in California is clearly open for investigation.

## Stability, Resilience, and Persistence

One of the enduring questions about communities is whether their structure, basically species composition and relative abundance, changes over time or whether the structure persists for years and decades. Long-term studies obviously are required to test for community persistence and, therefore, are likely to be few in number for most systems. The increased interest in environmental monitoring and assessment, however, promises to lead to increasing numbers of long-term studies that will allow more tests of community persistence. According to Gibson and Yoshiyama (1999), the most comprehensive studies on the persistence of intertidal fish communities have been conducted on the west coast of North America.

A tidepool on the central California coast near Piedras Blancas, defaunated quarterly over a 5-year period (1979–1983) followed by another year of quarterly fish removals about 20 years later (2000–2001), revealed a high degree of persistence in the assemblage (Horn, Allen, and Boyle, unpubl. data). For example, two species, black prickleback and northern clingfish *(Gobiesox maeandricus),* ranked first or second in all 23 sampling periods; the former species ranked first 19 times and second four times. Together, these species accounted for 35–70% of the total individuals collected in each sampling period. Of the total list of 30 species captured during the entire study period, five species made up 67–78% of the individuals collected. In addition to the two species mentioned before, the top five species usually included the rock prickleback, monkeyface prickleback, and penpoint gunnel *(Apodichthys flavidus)*.

Other studies conducted in California rocky intertidal habitats also have shown some degree of persistence. An intertidal fish community sampled at Dillon Beach on the north-central coast during a 42-month period was interpreted as deterministically structured based on the persistence of relative abundances of species (Grossman, 1982, 1986b). Although the top three species fluctuated from year to year and the relative abundances of species changed somewhat, the overall structure remained unchanged statistically. At Pescadero Point, another central California site, the intertidal fish community exhibited some degree of constancy, but the fluffy sculpin, one of the primary resident species, had declined noticeably in abundance after 7 years (Yoshiyama, 1981; Yoshiyama et al., 1986). As Gibson and Yoshiyama (1999) observe, species abundances are bound to change somewhat from year to year as a result of variations in spawning and recruitment under differing environmental conditions.

Repeated defaunations of tidepools during varying time periods have been conducted in California affording a test of whether intertidal fish communities are stable and resilient, two other temporal measures of community structure related to persistence. These two features refer to the ability of a community to maintain its structure in the face of environmental perturbations and to recover from intermittent disruptions of that structure. Grossman (1982) showed that a resident fish assemblage at Dillon Beach subjected to repeated defaunation over a 29-month period recovered and therefore showed resilience to this type of disturbance. Polivka and Chotkowski (1998) removed the fishes from tidepools near Piedras Blancas during a 90-day period and found that after one or two removals the recolonization involved the same dominant species but that the less common species in the assemblage were more variable in composition and abundance. Species diversity was restored after 60–90 days, but some species were depleted in the area during this period.

These results suggest that the rarer or patchily distributed species may not recover from external disturbances as well as the more common and uniformly distributed species. In addition, the restricted movements of many intertidal fishes (Moring, 1976; Gibson, 1999) may limit their capacity to recover from local depletion of their populations. The rate and amount of recovery appears to depend on the severity of the disturbance and the magnitude of repeated removals. For example, Alaskan intertidal fishes required two or more years to recover from the *Exxon Valdez* oil spill (Barber et al., 1995), and intertidal organisms including fishes may require years to recover from continuous, heavy collecting (Moring, 1983).

### Influence of Climate Change

As evidence has mounted in recent decades for accelerated global climate change, especially warming on different temporal scales (e.g., Pittock, 2002), increased attention has been focused on the potential impacts of this change on marine organisms (e.g., Fields et al., 1993; Scavia et al., 2002). In the northeastern Pacific, the increase in sea surface temperature that has already been documented (Smith, 1995; Sagarin et al., 1999; Bograd and Lynn, 2003) may be expected to cause a northward shift in the ranges of at least some species as it did during warming after the Pleistocene glaciations (Hubbs, 1948). Of course, not all species will shift their ranges in response. If their rate of northward migration is too slow to keep pace with the changes, they will either adapt genetically, live under suboptimal conditions, or perhaps go locally extinct. If climate change is not too extreme, some species may adjust phenotypically and thus tolerate climate change in place (Fields et al., 1993). Intertidal organisms might be expected to exhibit broad tolerances given the temporally dynamic environment in which they live (see Tomanek and Somero, 1999).

Some northward shifts in abundance in response to climate change have already has been documented for intertidal organisms in California. Barry et al. (1995) and Sagarin et al. (1999) provided data to show that during a 60-year period (1931–1933 to 1993–1996) at Hopkins Marine Station on the central California coast, macroinvertebrates changed in abundance as related to geographic ranges of species. Ten of 11 southern species increased in abundance, five of seven northern species decreased, and widespread species showed no clear pattern with 12 increasing and 16 decreasing. Shoreline temperatures for the 60-year period increased by 0.79°C, whereas average summer temperatures increased by 1.94°C. This climatic warming explained the changes in abundance better than the alternative hypotheses of habitat changes, anthropogenic effects, indirect biological interactions, ENSO events, or upwelling episodes. In another study, focused on mussel *(Mytilus californianus)* populations, Helmuth et al. (2002) showed that climatic warming and timing of low tides in the northeastern Pacific produce more thermally stressful conditions at northern sites compared to southern sites and proposed that "hot spots" of extinction rather than poleward shifts of intertidal organisms may occur at northern sites.

Intertidal fishes exhibit limited powers of dispersal (Marliave, 1986), and rocky intertidal habitats are separated by stretches of sandy or muddy shores (Horn and Ojeda, 1999), so that northward migration in response to ocean warming may not be an option for some species. Little attention has been focused on the responses of intertidal fishes to climate change although the removal study near Piedras Blancas, described above, that spanned the 1982–1983 El Niño and a 20-year period overall, showed little response by the fish assemblage to the El Niño or to the two-decade time frame

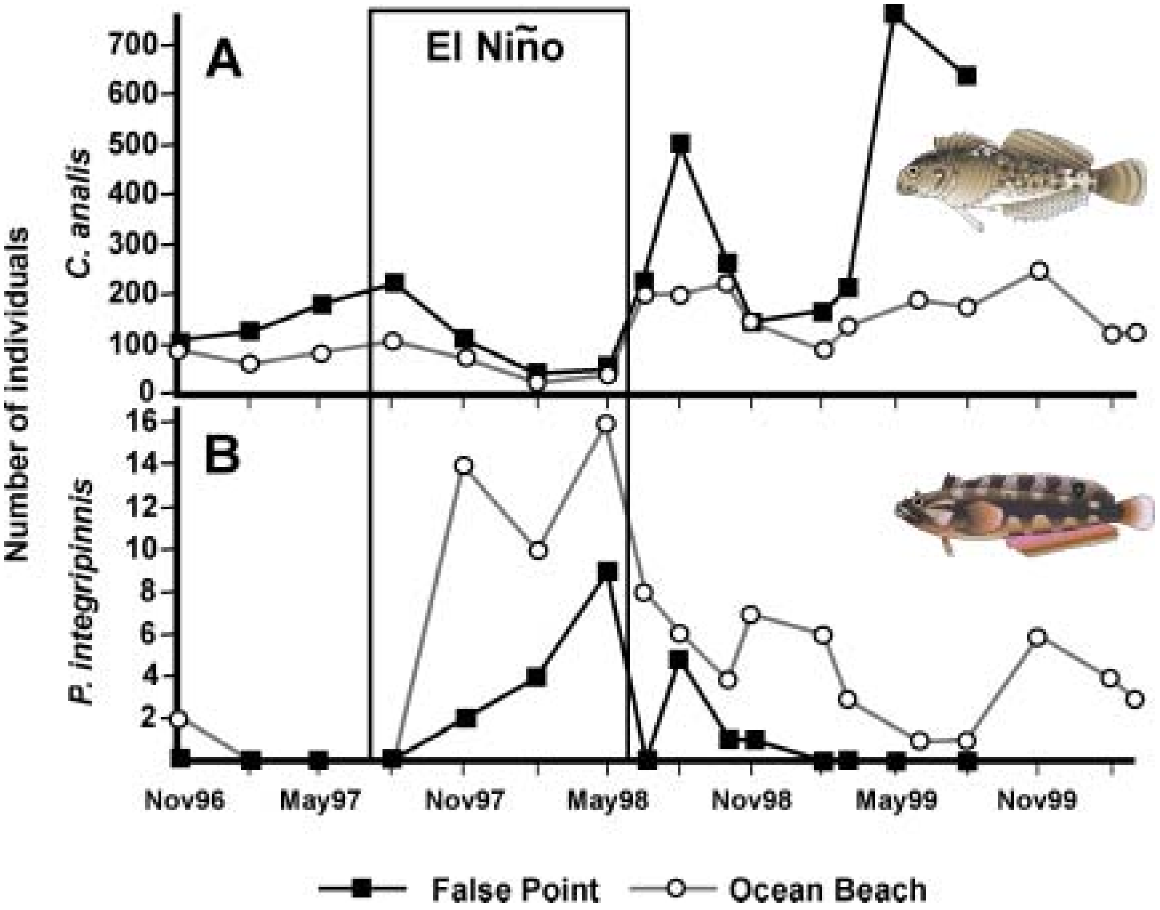

FIGURE 8-7 Abundance of (A) *Clinocottus analis* (woolly sculpin), a member of the cool-temperate family Cottidae and (B) *Paraclinus integripinnis* (reef finspot), a member of the tropical/warm temperate family Labrisomidae, in tidepools at two sites near San Diego, California, before, during, and after the 1997–1998 El Niño (after Davis, 2000a).

(Horn, Allen, and Boyle, unpubl. data). In a shorter term study, Davis (2000a) monitored the changes in assemblage structure and habitat use of a guild of intertidal fishes in response to ENSO conditions at two sites near San Diego, California, during the 1996–2000 time period. Although habitat use of the fishes was only slightly affected by the El Niño, two of the six species responded measurably to the fluctuating climate (fig. 8-7). The woolly sculpin, a member of the cool-temperate family Cottidae, decreased in abundance during the El Niño because of lack of recruitment but increased during the La Niña that immediately followed. In contrast, reef finspot, a member of the tropical/warm temperate family Labrisomidae, was more abundant during the El Niño. As climate change continues, further studies are warranted to document and predict changes in rocky intertidal fish assemblages in California.

## Recommendations for Future Studies

Several types of investigations are needed if we are to deepen our understanding of the way intertidal fishes, especially the resident species, survive and flourish in rocky intertidal habitats in California, and by extension, elsewhere. Comparative studies of intertidal fishes and their subtidal relatives seem particularly important to appreciate how resident species have been shaped, presumably through some combination of adaptive traits and phenotypic plasticity. Of critical interest is to advance our knowledge so we can protect and manage fishes that live in such small, vulnerable, and widely separated habitats at the interface of the land and sea. Here are some of the types of studies that seem worthy of attention in future research:

1. Compare air-breathing abilities in rocky intertidal fishes and their subtidal relatives from a phylogenetic perspective. Air breathing associated with emergence is complex and variable, occurring in numerous taxa and correlated to some extent with the vertical distribution of these species on the shore. The families Cottidae and Stichaeidae are well suited for comparative analysis. These two families are species-rich in both rocky intertidal and subtidal habitats in California.
2. Determine the contributions of the gills, skin, and other organs to respiratory gas exchange when the fish is in water and out of water. Histological examination, microsphere perfusion, and enzymatic assays for carbonic anhydrase will aid the elucidation of these structures and their functions. Biochemical assays of the hemoglobins in fish blood could illuminate the affinities to oxygen, the sensitivity to acid–base disturbances, and possibly the ontogenetic changes in the expression of different forms of hemoglobin, particularly for species in which the juveniles inhabit tidepools and the adults occur in deeper waters.
3. Compare the contributions of aerobic and anaerobic metabolism to the activity of intertidal fishes during aquatic and terrestrial locomotion. Especially intriguing would be to examine the possibility that metabolic acidosis caused by anaerobic terrestrial activity could be reversed by respiratory release of carbon dioxide

from the gills. The potential accumulation of lactate under hypoxic aquatic conditions needs to be investigated as do the excretion of nitrogenous wastes and the excretory acid–base balance. These physiological studies need to be coupled with detailed field observations of the natural history and ecology of air-breathing fishes on California rocky shores.

4. Compare sensory structures, especially the eyes, lateral line, and chemosensory organs in rocky intertidal fishes with their subtidal relatives from a phylogenetic perspective. These organs are little studied among species in the rich California fauna, especially with research designed to test for adaptations to intertidal life. Again, the families Cottidae and Stichaeidae offer excellent opportunities for comparative analysis.
5. Investigate substratum preferences and microhabitat selection in larval fishes as they settle out of the plankton into the rocky intertidal habitat. Following how these preferences and selection processes change with age in tidepool versus boulder field species could be rewarding and might help explain patchy distributions on different spatial scales and even the limits of geographic ranges. The work by Setran and Behrens (1993) offers a good model for further studies.
6. Test the nursery-role hypothesis of Beck et al. (2001) for rocky intertidal and adjacent habitats in California. This role is often assumed for rocky intertidal habitats, but data are lacking. If tested as proposed, this demanding hypothesis could increase the appreciation of rocky intertidal habitats as nurseries and enhance the effectiveness of conserving and managing these habitats and their fish assemblages.
7. Design and implement field experiments to test for interspecific aggression among co-occurring fishes in the rocky intertidal zone of California. Most studies to date have failed to detect aggressive behavior or territoriality, but more research needs to be conducted during high tide or simulated high tide rather than only at low tide. The works by Jones (1981) and Pfister (1995) provide useful models for further investigation.
8. Design and implement field experiments to test for the impacts of herbivory and predation by fishes on the structure of rocky intertidal communities. The kinds of information that Norton and Cook (1999) recommend to assess the impacts of fish feeding on these communities are still sparse, especially in temperate waters including California.
9. Assess and predict the impacts of climate change from long-term monitoring of fish assemblages in rocky intertidal habitats of California. Climate change is likely to accelerate the effects of pollution or other stresses on rocky shore fishes through higher water temperatures and alterations in salinity, precipitation, and sea level. Marine reserves designed to protect intertidal communities should be planned with recognition of long-term changes anticipated as a result of climate change.

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