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L.G. Allen, D.J. Pondella, and M. H. Horn (eds.). University of California Press, Berkeley, 670 pp.

CHAPTER 9

Rocky Reefs and Kelp Beds

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Introduction

California's kelp bed and rock-reef habitats are among the most spectacular marine habitats in the world, due in part to the assemblage of fishes that occupy these areas. In Chapter 3, two shallow subtidal reef assemblages associated with kelp beds and rocky reefs were discussed. These assemblages are discussed together in this chapter for several reasons. Kelp beds are largely restricted to rocky reefs because they depend on hard substrate for the attachment of holdfasts. The composition of fishes within these two habitat groups overlaps almost entirely because there are very few obligate kelp species. Kelp may be limited in its abundance and distribution by various factors, but most of the fishes associated with it are not susceptible to the same limitations. In fact, the abundance and distribution of kelp along California's coastline fluctuates appreciably because of seasonal and annual variability and episodic events. Although the variability in the abundance and distribution of reef fishes responds to the presence and absence of kelp, it is only one of many factors that affect the distribution of these species. Thus, all of these nearshore reef fishes are treated together.

Due to their accessibility, their ecological and commercial importance, the high diversity and abundance of fishes, and their sheer beauty, rocky reefs and kelp beds have been studied intensively for more than five decades. The diversity and abundance of the fish assemblage is higher than those in most other California marine habitats. Recent estimates suggest that this habitat supports between 6 and 15 times the density of fishes compared to a similar area of soft substrate (Bond et al., 1999). Rocky reefs and kelp beds are an important resource for the neritic fishes of California and are economically important (chapter 22). These, plus the aesthetic appeal of conducting research in such picturesque settings, are some of the major reasons that such a large body of research has been conducted on these fishes. In addition, much of what we know about the community organization (Unit III), behavioral ecology (Unit IV), and spatial and temporal changes (Unit V) of California marine fishes has been based on studies of rocky reef fishes. The major goals of this chapter are to describe that body of work, provide readers a feeling of where the field is today, and discuss avenues for research in the future.

Historical Review

Initial surveys in the nineteenth century, which were based largely on fishery landings, provided the first taxonomic descriptions and data on distributions for California fishes. By the late nineteenth century and early twentieth century, several guides to identification and distribution had appeared (e.g., Jordan and Gilbert 1881; Starks and Morris, 1907; Barnhart, 1936). Investigation of the biology of some groups (such as viviparity in embiotocids; see the review in Tarp, 1952) began in the nineteenth century and continued into the early twentieth century. By the postwar years, natural history information on a range of species was part of the fisheries lore (e.g., Cannon, 1953; Schenck, 1955), although not all of this was information was available in the scientific literature. Concern over increased levels of sport fishing after World War II, plus the general expansion of marine research, led to more focused studies of life history in a number of exploited species (e.g., O'Connell, 1953; Young, 1963). The advent of the scientific use of scuba, however, allowed the greatest expansion of research on fishes of rock reefs and kelp forests. Concern over the effects of kelp harvesting on sportfish abundance led to a long-term research program on kelp-forest ecology that was carried out largely with scuba. This produced Limbaugh's (1955) pioneering descriptions of distribution and habitat preferences of kelp-forest fishes and Quast's quantitative studies of the distribution, abundance, habitat utilization, and diet of kelp-forest fishes (North and Hubbs, 1968). Pequegnat (1964) published one of the first scuba-based descriptions of subtidal faunas. Department of Fish and Game biologists provided additional information on the habits and habitats of reef and kelp-forest fishes (Carlisle et al., 1964; Turner et al. 1968, 1969). The observations of Conrad Limbaugh and Charles Turner were published posthumously in Feder et al. (1974). These works are all important contributions to the body of knowledge on fishes of rocky reefs and kelp forests off California. Papers by Clarke (1970), Stephens et al. (1970), and Hobson (1971) were among the first observational/experimental studies on kelp-forest fishes that evaluated broader themes in ecology and led the way for many of the works discussed in this volume.

Overview of Reef Structure

The distribution of nearshore reefs varies throughout California. Along the mainland coast of the Southern California Bight and Baja California, rocky reefs are distributed patchily, separated by long stretches of sandy beaches, although this has varied over the glacial–interglacial cycles (Graham et al., 2003). Approximately 10–15% of the mainland of the southern California coast is rock, and this rock is primarily associated with headlands. The Southern California islands consist largely of rocky shorelines and constitute a substantial fraction of the rocky reef and kelp habitat off southern California. Because of these islands, there is as much coastline in the Southern California Bight as in the rest of the state of California. Rocky shorelines are predominant from Point Conception to the north, interrupted mainly by embayments such as Morro Bay, Monterey Bay, and San Francisco Bay, and by river mouths in the north. However, though it is possible to characterize the shoreline in many areas, the relief and extent of rocky bottom has not been determined for many portions of the California coast, making it nearly impossible to assess the extent of habitat for nearshore reef and kelp fishes and to assess their overall abundances.

Shallow coastal reefs share their geological composition with the adjacent terrestrial shoreline. Both emergent and submergent shorelines occur in California, the result of eustatic changes from intrusions and crustal deformation as well as sea level changes from glacial modifications. The resultant rock formations can then be subject to burial by sedimentation (Graham et al., 2003). Rocky substrates can consist of boulders, sedimentary formations (sandstone, mudstone, shale), igneous formations (basalts, andesites), or metamorphic formations (schists, gneisses, and quartzites). Emery (1960) suggested that the latter three types of rock occur in a ratio of 90:7:3 in southern California, but this varies geographically. For example, the substrate between San Francisco and Monterey Bay is largely shale, whereas the substrate around the Monterey Peninsula and south past Pt. Lobos is composed largely of granite.

The composition of rock reefs can affect reef ecology in at least three ways: the hardness of the reef matrix, the pattern of bottom relief, and the clarity of water over the reefs. Very hard rock resists modification by boring and scraping organisms and on a scale of centimeters, presents a smooth and uncomplicated surface. Softer rock allows burrowing by mollusks, such as piddocks and date mussels, and erosion by gastropods, echinoderms, etc., which provides small-scale habitat complexity and sites of protection for small benthic fishes. The composition of rock reefs may also affect habitat on a scale of meters. Sedimentary rocks often form relatively flat surfaces but do provide vertical relief and areas of broken rock (with attendant cavities used by fish and their prey) when tilted strata emerge and break off. Depending on the circumstances, igneous and metamorphic rock may form more continuous areas of boulders and rubble and higher vertical relief. The type of rock (along with many other factors) can also affect water clarity. Most sedimentary rocks produce finer particles when eroded than igneous or metamorphic rocks, and these particles reduce water clarity when suspended.

In addition to rock reefs, extensive biogenic reefs are present in some areas. The colonial sand tubeworm, *Phragmatopoma californica,* can create extensive reef habitat that is used by fishes and as an attachment substrate for giant kelp.

Overview of Kelps and Their Characteristics

The two major canopy-forming kelps off California are *Macrocystis pyrifera* and *Nereocystis luetkeana* (Abbott and Hollenberg, 1976; Foster and Schiel, 1985). *Macrocystis pyrifera*, or giant kelp, occurs along the Pacific coast from central Baja California to approximately Año Nuevo Island, between Santa Cruz and San Francisco. Occurring between depths of about 5 and 20 m (Foster and Schiel, 1985), *M. pyrifera* forms the bulk of the offshore kelp forests off southern California and much of central California. Young plants begin with a single stipe, but produce additional stipes as they mature (Tegner et al., 1996), and these stipe bundles may act as points of orientation or as shelter for fish in the midwater region (Quast, 1968b; Larson and DeMartini, 1984; Nelson, 2001). At the surface, stipes and fronds spread to form a canopy, which also serves as a point of orientation for fish and as shelter for some fish and invertebrates. *Macrocystis* is a perennial, although beds are thinned by wave action during the winter, especially in central California. *Nereocystis luetkeana*, or bull kelp, occurs primarily north of Pt. Conception and is common in wave-exposed sites (Foster and Schiel, 1985). It may occur intermixed with giant kelp, or it may occur in monospecific stands. It is the only offshore canopy-forming kelp north of Año Nuevo. It grows as a single stipe with one float, from which large fronds hang. As a result, bull kelp may serve as a point of orientation in the water column for fishes, but it does not provide the same complexity of cover as giant kelp. In addition, bull kelp is an annual. Inshore of *Macrocystis pyrifera* and *Nereocystis* kelp beds, *Macrocystis integrifolia* and *Egregia menziesii* may occur in dense stands that also form canopies. *Macrocystis integrifolia* occurs primarily north of Point Conception. Together with surf grass, *Phyllospadix* sp., these organisms provide cover for fish and invertebrates in the shallow nearshore region. Offshore of giant kelp beds in southern California, *Pelagophycus porra* (elk kelp) extends into the water column and occasionally to the surface. It is not common, but it can form extensive beds. *Cystoseira osmundacea* sometimes co-occurs with *M. pyrifera* and forms dense masses of reproductive tissues in the summer that can serve as shelter for juvenile fishes. Likewise, *Sargassum* sp. can form canopies in winter–spring in southern California, especially in shallow water, and attracts some fishes normally associated with *Macrocystis*, such as kelp perch, *Brachyistius frenatus*. Several species of brown algae (*Pterygophora californica*, *Laminaria farlowii* and *L. setchellii*, *Eisenia arborea*, and *Desmarestia ligulata*) form understory canopies in some areas.

Assessing Reef Fish Abundance

Various techniques have been used to study the abundance of reef fishes. Some types of mobile fisheries gear (such as trawls and seines) are ineffective in kelp forests and rock reefs because the gear cannot be deployed. Stationary fishing gear (gill nets, traps, hook and line) can be deployed successfully in kelp forests, providing at least estimates of relative density. However, in the three-dimensional structure of a kelp forest, scuba gear has proved the most widespread method for assessing the abundance of kelp-forest fishes. Scuba-based techniques can provide estimates of relative density, or of absolute density, if the area sampled can be estimated. Increasingly quantitative methods for sampling have been applied to kelp forests, and quantitative habitat assessment techniques that are currently under development will prove valuable in assessing abundance.

The distribution and abundance of rock-reef and kelp-forest fishes have been assessed with differing degrees of quantification and precision, and these different techniques have often been used to different ends. Range limits, or the presence/absence of species in different regions, can be useful in the analysis of biogeography and evolution (Quast, 1968b; Horn and Allen, 1978; Hobson, 1994; chapters 1 and 2), and in the effect of climate change on distribution (Lea and Rosenblatt, 2000; Richards and Engle, 2001). Nonquantitative observations have been very useful in formulating the initial descriptions of habitat use and behavior in kelp-forest fishes (Limbaugh, 1955; Feder et al., 1974) and are always useful in formulating questions and hypotheses. Because they are not based on replicable measurements, however, the results of such studies cannot be evaluated or repeated. For example, without any indication of the effort expended in observation, it is difficult to evaluate comparisons of presence and absence, and nonquantitative notes on observations can be biased in a number of ways. Semiquantitative indices of distribution and abundance can provide greater information and can be replicated if the criteria for sampling and scoring are clear. For example, Engle (1993) used a consensus of observers to develop ordinal scores for abundance of fishes, which he then used to evaluate the geographical distribution of fishes on the southern California islands (see figure 9-10). Pequegnat (1964) included a somewhat greater degree of quantitative replicability in his assessments of 22 species of reef fish by basing counts on the total number of fishes counted by two observers throughout a dive (twin 2500 psi tanks). His index is a rough measure of catch per unit effort (CPUE), based on fish counted per unit of time. Systematic sampling surveys based on consistent levels of sampling effort can produce estimates of relative abundance (or CPUE) when the sampling area is unknown, estimates of density when the sampling area is known, and estimates of total abundance when the estimates of density can be extrapolated to the area of habitat that is to be represented. A number of techniques are available for assessing abundance; each has its own biases, advantages, and disadvantages.

Traps, hook and line, spears, and gill nets can provide estimates of relative abundance (CPUE) of reef fishes. These techniques also provide the ability to obtain precise measurements of fish length, biomass, and maturity stage. They are also the techniques preferred by commercial and recreational fisheries (see chapter 23), allowing data to be obtained in cooperative endeavors. Fish traps are presently used extensively to capture rockfishes and sheephead for the live finfish fishery (Stephens, 1992; Love et al., 2002). Gill nets had been used for commercial fisheries in southern California kelp beds; they were outlawed within state waters in southern California (within 3 miles of the mainland and 1 mile of the islands) in 1992. They have been used in scientific monitoring programs (Pondella and Allen, 2000). Data from both gill nets and traps can be standardized as CPUE by dividing the catch by each net or trap set by soak time. In these studies, each fish is identified by species, measured, and weighed, allowing precise biomass and taxonomic information. Specimens can also be vouchered for museum collections. One drawback of these techniques is that they are invasive, potentially damage the substrate, and remove fishes from the environment when they cannot be returned alive. These techniques can also be biased toward more mobile fishes, those attracted to the bait used in traps, and those sizes of fish best captured or retained by the sampling device.

Hook and line has been used extensively to capture individuals for life-history and tagging studies (Young, 1963; Love et al., 1987). In these studies, relatively shallow water fishes, kelp bass and California scorpionfish, were caught, tagged, and released. Hook and line data can be standardized as CPUE. On a small scale, this technique is extremely variable because of the complex behavior of fishes. However, on a large scale, this data can be extremely valuable in describing regional and temporal trends (Love et al., 1998).

These CPUE techniques afford the opportunity for tagging fishes prior to release. Recapture data has been used extensively to estimate stock size in other habitats and other parts of the world (Ricker, 1975). Mark and recapture/resighting techniques can provide direct estimates of abundance, and, unlike visual census techniques, are not biased against cryptic species and do not depend on accurate estimates of the amount of area sampled. However, they usually require marking a substantial portion of the population and that marked individuals mix randomly with the remainder of the population (Krebs, 1998). Martell et al. (2000) used mark and resighting techniques based on diver-applied dart tags and diver surveys to estimate the abundance of lingcod at sites in British Columbia. They used a Bayesian estimation technique to analyze the results of the mark/recapture survey, which allowed marking a smaller proportion of the population. In California, Davis and Anderson (1989) conducted a modified Schnabel (Ricker, 1975) mark and resighting experiment by capturing kelp-bed fishes with a subtidal electroshocker, tagging, releasing, and resighting them. In this study, they compared the estimates of fish abundance in belt transects, video transects, and baited stations to the density estimates from the modified Schnabel density estimates. Although they acknowledged the limitations of the mark and resighting technique, they concluded that all three techniques underestimated the density of kelp-bed fishes. They found that visual band transects gave the most accurate and precise density estimates.

Electroshocking and the tag and resighting technique were noted to be labor-intensive and obviously dangerous. In a similar comparative approach, the rapid visual technique (RVT), which has been used in coral reef systems, was evaluated for this temperate system and found inaccurate (DeMartini and Roberts, 1982). Certainly, more comparative studies would be pertinent to this science.

Probably the most daring attempt to quantify a reef fish assemblage was conducted by Quast and colleagues in the late 1950s when they used a wall net (similar to a purse seine) and rotenone to poison all fishes within a set area of a reef (Quast, 1968c). If practical, this technique would be the best for obtaining one-time estimates of absolute density and biomass. This technique was tried only three times, and Quast switched to "belt" transects (also referred to as band transects), originally developed by Brock (1954), which have become the standard technique used today.

Belt transects and their variants are the most commonly applied sampling technique for kelp-forest fishes. In belt transects, divers swim a predetermined distance, usually along a measuring tape, and record on a handheld slate the number of all fishes seen within a certain distance of the tape. The slate may also contain a thermometer, depth meter, and a compass. If conducted consistently, belt transects can provide comparable estimates of relative abundance, and if the volume or area covered can be estimated accurately, belt transects can provide estimates of density. Belt transects were originally carried out near the bottom but have also been employed in the water

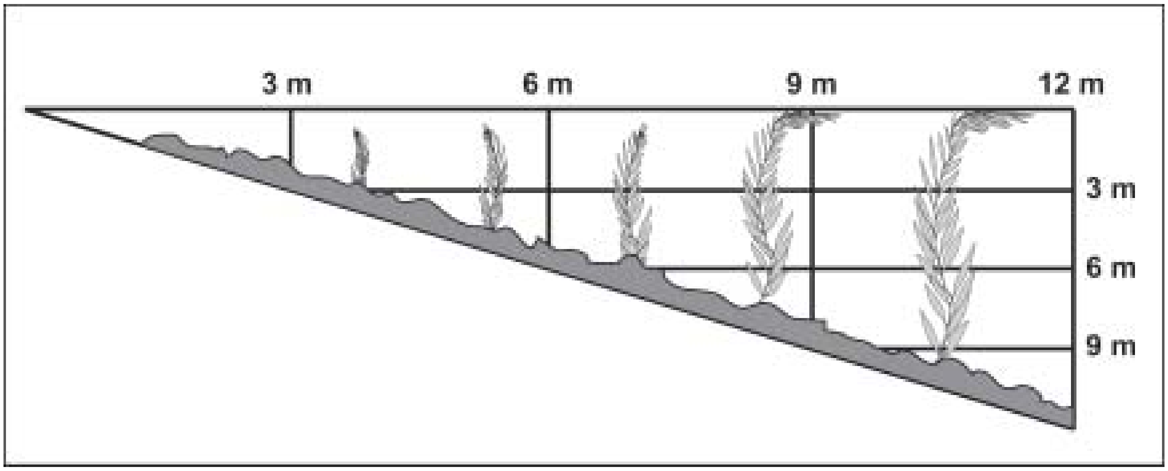

FIGURE 9-1 Orientation of diver transects in kelp beds.

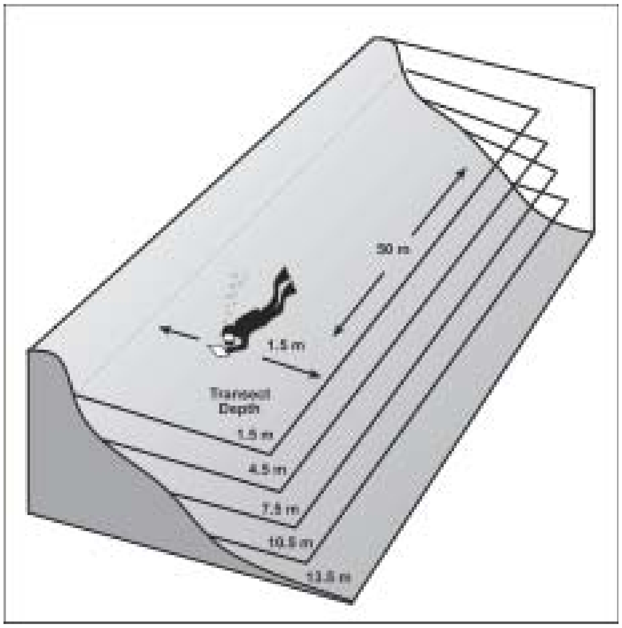

FIGURE 9-2 Orientation of diver transects on breakwaters.

column and kelp canopy (fig. 9-1; Ebeling et al., 1980a,b; Stephens et al., 1984; Larson and DeMartini, 1984). If the belt-transect sampling program is stratified over water-column position and on-offshore gradients, estimates of total abundance or water-column density can be obtained (Stephens et al., 1984; Larson and DeMartini, 1984). However, the accuracy of density estimates obtained from belt transects depends on the how accurately the volume or area sampled has been estimated. Variation in the volume or area sampled can also influence the degree to which estimates of relative abundance can be compared.

A number of variations on the basic belt-transect method have been employed in California. First, the basic method of obtaining counts has been refined. Terry and Stephens (1976) and the Channel Islands National Park (Davis et al., 1999) used replicate counts from a pair of divers swimming along the transect line. Terry and Stephens (1976) used the highest counts for small schools and individuals and an average of estimates for large schools. This technique takes into account that single observers inevitably miss fish on transects, such as when they look at their slates, and in general provides the obvious advantage of replicated observation and averaging of potential observer biases. It has also been used as a training tool by the Channel Islands National Park (Davis et al., 1999). Logistically, this method may be easiest to implement on permanent transects or when a transect course is clearly determined. Another variation has been the use of film or videotape to record fishes ("cinetransects" of Ebeling et al., 1980a, b; Larson and DeMartini, 1984; DeMartini and Roberts, 1990). In the method of Ebeling et al., the camera is essentially used as the slate for recording fishes. Divers search for fishes along the course of the transect as if they were conducting a visual transect, but pan the camera over fishes as they are encountered instead of recording them manually. This method provides a permanent record, does not require the diver to divert attention to the slate while recording, and may allow counting large schools of fish frame by frame. However, the resolution of both film and videotape is less acute than the human eye, making some fish identifications difficult. In addition, this method requires considerable time in the laboratory for counting fish (a 5:1 ratio of laboratory observation to transect time according to Ebeling, 1982).

Another variation in the conduct of belt transects is the means for determining their lengths. Permanent transect lines can be established for long-term monitoring (Davis et al., 1999), automatically fixing the length of a transect. Playing out a measuring tape or reel of line can also fix the length of a transect, but usually requires time to rewind before beginning another transect. However, Ugoretz et al. (1997) developed the use of retractable dog leashes for measuring the distance of underwater transects, avoiding the problem of rewinding the transect tape. Transect length has also been standardized by time. Timed transects, when swum at a constant rate, can allow time for a greater number of transects because the measuring tape need not be retrieved. The ability to conduct more replicates per dive allows greater precision per effort and is especially useful for deeper dives. In addition, deployment of a measuring tape can be difficult in the water column, over very rugose substrates, and on vertical walls. Terry and Stephens (1976) employed timed transects at King Harbor; these are swum along isobaths at fixed sections of the breakwater (fig. 9-2). The National Marine Fisheries Service used timed transects for juvenile rockfish off Northern

California (Ralston and Howard, 1995; Adams and Howard, 1996), and the cinetransects of Ebeling et al. (1980a,b) were essentially timed (by the duration of a film cassette). If timed transects consistently cover the same distance, they can provide comparable estimates of relative abundance, and if the distance covered in timed transects can be determined, the transects can provide estimates of density (Ebeling et al., 1980b; Stephens et al., 1984; Larson and DeMartini, 1984). Larson and DeMartini (1984) found a standard deviation of about 5.2 m in the length of 12 simulated cinetransects in the kelp canopy, which was 6.9% of the average length of 75.6 m.

The width of belt transects has also been determined in different ways. Quast (1968c) used the limits of visibility for his density estimates. However, later researchers have often used a fixed distance, usually 1–2 meters, for their density estimates. This reduces the variance in counts associated with changes in visibility and increases the accuracy of counts because the likelihood of fish detection decreases at greater distances. Using devices to fix the distance from the transect line is not practical because of the rugosity and unevenness of the rocky reefs and the presence of kelp, and because of the loss of survey time. As a result, even in belt transects that are supposed to be of fixed width, the width is still estimated. Larson and DeMartini (1984) found an asymptotic relationship between the distance at which fish could be distinguished on film and the limits of underwater visibility as determined by eye. This set an upper limit to the width of cinetransects. They also developed a method for estimating the volume of a cinetransect, given the relationship between camera range and horizontal visibility and assumptions about the cross-sectional shape of a cinetransect. We feel that though it is possible to estimate fish density from both visual belt transects and cinetransects, additional cross-referencing evaluations of these estimates should be undertaken.

Another variation in the use of belt transects is the incorporation of information on fish size and age classes. Terry and Stephens (1976) distinguished age classes of fish (adults, subadults, and juveniles) at King Harbor. The age classes are based on size classes for a particular species. For instance, many species of surfperch can be categorized into three size classes: adults (>150 mm SL), subadults (100–150 mm SL), and juveniles (<100 mm SL) (Ebeling and Laur, 1985). Depending on the experimental design, more size classes can be used. However, the accurate estimation of fish sizes can be difficult for various reasons. Underwater objects are magnified and it takes extensive training for divers to adjust for this visually. One technique that is commonly used to overcome this problem is the use of parallel lasers that are a fixed distance apart with video (Gingras et al., 1998). The video is reviewed and fish length is estimated as a ratio of the distance between the lasers and the total length of the fish. This technique is labor-intensive and can have other significant problems. The fish need to be perpendicular to the field of view to be accurately measured, and there can be considerable error in these estimates if not done correctly (Yoshihara, 1997; Gingras et al., 1998).

Some other important issues in the use of belt transects still need to addressed. We have already discussed the difficulties in determining the length and width of belt transects. In addition, whether filming or counting fishes, scuba divers repel and attract certain species of fish. It is not uncommon for schools of various species of fish to follow divers along transects. For example, wrasses (California sheephead and señorita) are notorious for being attracted to divers. Thus, it is critical for accurate density estimates that divers not count fish that pass them from behind. The divers must be aware of this when starting a transect because the attracted fish will generally be circling the divers at this time. Scuba divers may also repel many fishes. For instance, white sea bass typically avoid divers, and many elasmobranchs that frequent kelp beds are also rarely observed by divers (Pondella and Allen, 2000). Larger individuals of species that are hunted in certain areas will tend to be wary of divers (California sheephead and kelp bass). An excellent summary of the utility of diver observations can be found in Ebeling (1982).

Finally, divers must be trained adequately to conduct visual belt transects. Observers must be physically fit and experienced and comfortable with scuba, so that they devote attention to the technical aspects of data collection. Even fit and experienced divers typically have steep learning curves. Identifying fishes underwater is difficult because of variable lighting and visibility constraints. The loss of colors with depth also adds to the difficulty. Typically problematic taxonomic groups are the rockfishes and the surfperches. Most temperate conspicuous reef fishes (fig. 9-3) are mobile, requiring that they be identified at all angles and at various speeds. Taxonomic identifications must be made instantly while the counts are being taken, often at the same moment size class estimations are being made. Many programs train divers in pools with models to learn to estimate sizes. Repeated dives with an experienced fish counter and continued discussion of the techniques and results are essential. Generally a complete season of diving is necessary to train a diver in this technique because the amount of training required can vary substantially among individuals. However, after this training period, data can be collected efficiently and effectively. At this point, belt transects are very cost-effective and reliable and allow relatively precise density estimates. This is a major reason that belt transects are used today.

Cryptic species (fig. 9-3) are not surveyed adequately by visual techniques. Cryptic species are four times as dense as conspicuous fishes and may double the ichthyofaunal diversity on a reef, although their biomass may not be large (Allen et al., 1992). From an ecological standpoint, the influence of these taxa must be significant, but this subset of the reef community has been included in studies only a few times (Stephens and Zerba, 1981; Stephens et al., 1984, 1986; Allen et al., 1992). Surveys of cryptic reef fishes are often conducted with an ichthyocide (usually quinaldine or rotenone) in a standardized fashion. A typical quadrat is 1 meter square, and all of the fishes within the quadrat are either anesthetized or poisoned. Rotenone is more difficult to use subtidally because it clouds the water and works best when constrained within a particular area. Thus, the best method for working with rotenone is to tarp off the meter-square (Allen et al., 1992). Quinaldine mixed with isopropyl alcohol (1:9 ratio) and administered directly to the reef with a standard laboratory squeeze bottle is cloudy upon release, enabling the divers to see the release point, but it becomes clear within a few seconds. Because it does not cloud the reef, fishes can easily be captured when they lose consciousness and float off the reef. Divers can capture fish in small 333-μm mesh bags (commercial paint bags work well) or use an airlift on complex reefs or reefs with high densities of cryptic fishes (Stephens et al., 1984). The airlift was modified from Roach et al. (1964) in which a standard inflater hose was fitted to a rigid intake pipe attached to 1.5-m flexible hose (~5 cm in diameter) with a 333-μm mesh bag attached to the other

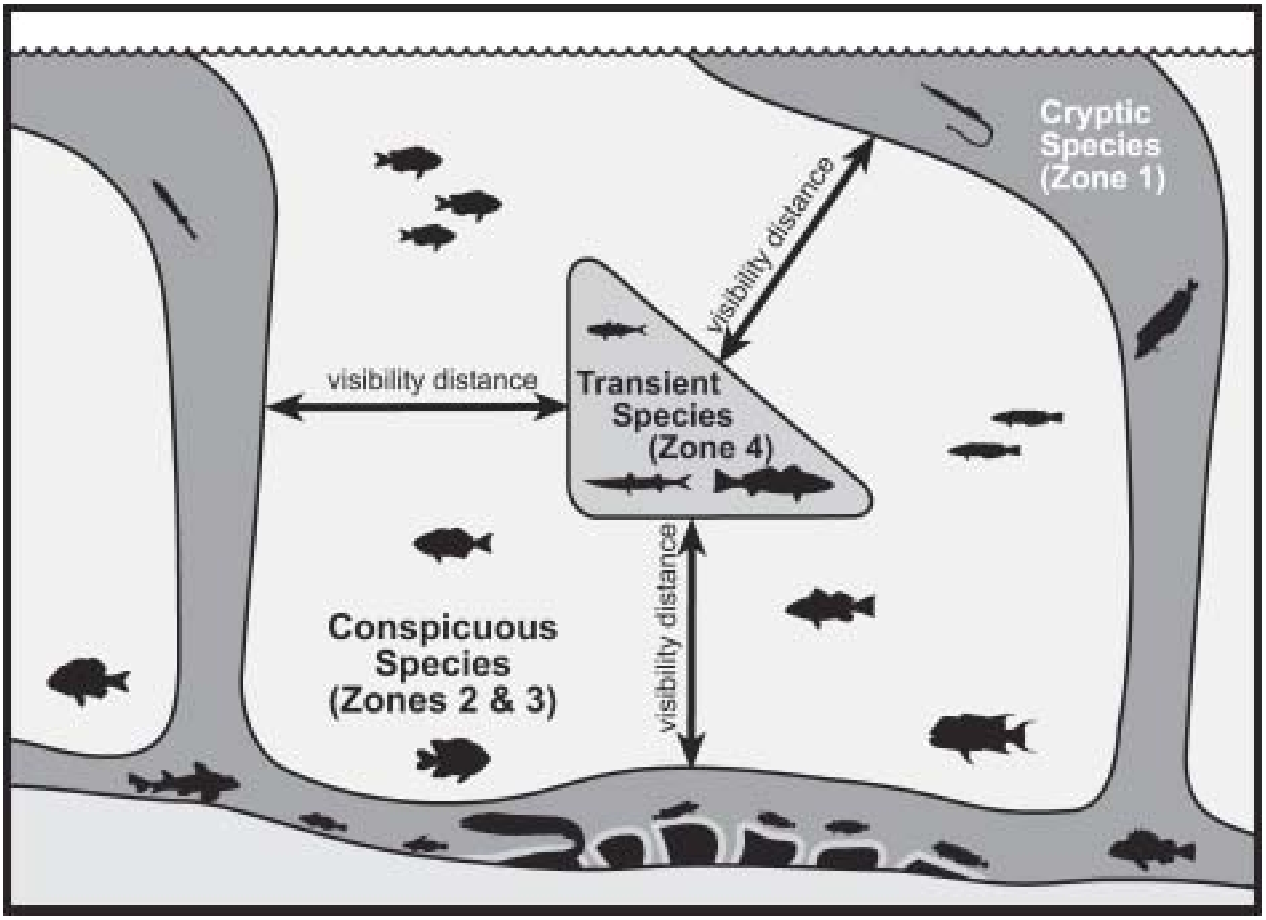

FIGURE 9-3 Comparison of life zones (Zones 1,2,3, and 4) defined by Quast (1968b) and the categories of conspicuous, cryptic, and transient (associated) species referred to in this chapter.

side. As the air flows up the hose, it creates a vacuum that delivers fish into a mesh bag. Using quinaldine, fish are anesthetized and not necessarily sacrificed, so fish can be returned to the reef if desired. Meter-square quadrats have been typically made of PVC, but they can be cumbersome. Lead line works better and can be easily transported by divers. The airlift and anesthetic captures close to 100% of the small cryptic fishes, but larger camouflaged species (rockfishes, scorpionfishes, black croaker, moray eels) are not as susceptible to the anesthetic in open environments, and their presence needs to be noted by divers. Predatory fishes are also a problem in cryptic collections and need to be deterred from entering the study area. There are other anesthetics and poisons on the market, but their use subtidally has not been widely studied in California. Cyanide poisoning is the most commonly used collection technique for aquarium fishes in the tropics; however, its use is not recommended. In addition, larger but hidden fishes can be counted in belt transects using techniques that are specifically designed for maximizing detection of these fishes. For example, Larson (1980) counted black-and-yellow rockfish along fixed transects by peering to the extent possible into crevices and into cavities using a dive light.

Settlement and recruitment of larval fishes to reefs was and continues to be of interest to reef ecologists (chapter 15). Assessment of this critical life-history stage has been conducted using both diver surveys and ichthyoplankton tows (chapters 11 and 15).

Major Taxa of Reef and Kelp Fish

The fishes found in and near rock reefs and kelp forests represent a variety of taxa (table 9-1). The more than 150 species listed in Table 1 show differing degrees of association with rock reefs and kelp forests per se, but they do interact with the reef and kelp community. Taxa contributing the greatest biomass, numerical abundance, or species richness to the rock-reef and kelp-forest community are Acanthopterygians (Hobson, 1994), including Serranidae, Pomacentridae, Labridae, Kyphosidae, Embiotocidae, Scorpaenidae (especially *Sebastes*), Hexagrammidae, Gobiidae, and Cottidae. Transient, pelagic species from the Clupeidae, Engraulidae, Scombridae, Carangidae, and Sciaenidae may play a significant role in the energetics of reef and kelp communities. The taxonomic composition of both conspicuous and cryptic fishes in kelp-rock habitats varies considerably with latitude (figs. 9-4 and 9-5) and with a number of features of the habitat (see next section).

Factors Affecting Species Composition and Abundance of Fishes

There is no such thing as a unitary assemblage of fishes inhabiting reef and kelp habitats off California, even within biogeographic regions. Although areas of reef and kelp habitat within a biogeographic region may harbor a familiar assemblage of species, most of these species appear to respond differently to

TABLE 9-1

Californian Rocky-Reef Fishes by Range, Position, Habitat, and Behavioral Characteristics

Scientific Name	*Common Name*	*Range*	*Position*	*Habitat and Behavioral*
Hexanchiformes				
Hexanchidae	Cow sharks			
Notorynchus cepedianus (Peron, 1807)	Sevengill shark	W		
Squatinaformes				
Squatinidae-angel sharks				
Squatina californica (Ayres, 1859)	Angel shark	C	Bt	
Heterodontiformes				
Heterodontidae-bullhead sharks				
Heterodontus francisci (Girard, 1855)	Horn shark	S	Bt	n
Lamniformes				
Alopiidae-thresher sharks				
Alopias vulpinus (Bonnaterre, 1788)	Thresher shark	W	WC	p
Carcharhiniformes				
Scyliorhinidae-cat sharks				
Cephaloscylium ventriosum (Garman, 1880)	Swell shark	S	Bt	n
Triakidae-hound sharks				
Mustelus californicus (Gill, 1864)	Gray smoothhound	S	Bt	ab,n
Mustelus henlei (Gill, 1863)	Brown smoothhound	N,S (C?)	Bt	ab,n
Galeorhinus galeus (Linnaeus, 1758)	Soupfin	W	WC	ab
Triakis semifasciata (Girard, 1855)	Leopard shark	C	Bt	ab
Torpediniformes				
Torpedinidae-torpedo electric rays				
Torpedo californica (Ayres, 1855)	California electric ray	C	Bt	n
Rajiformes				
Rhinobatidae-guitarfishes				
Rhinobatis productus (Ayres, 1854)	Shovelnose guitarfish	S,B	Bt	
Zapteryx exasperata (Jordan & Gilbert 1880)	Banded guitarfish	S,B	Bt	
Platyrhynidae-thornbacks				
Platyrhinoides triseriata (Jordan & Gilbert, 1880)	Thornback	S	Bt	
Myliobatiformes				
Urolophidae-round stingrays				
Urobatis halleri (Cooper, 1863)	Round stingray	C	Bt	
Myliobatidae-eagle rays				
Myliobatis californica (Gill, 1865)	Bat ray	C	Bt	
Anguilliformes				
Muraenidae-morays				
Gymnothorax mordax (Ayres, 1859)	California moray	S	Bt	h
Clupeiformes				
Engraulidae-anchovies				
Engraulis mordax (Girard, 1854)	Northern anchovy	C	WC	p,sc
Clupeidae-herrings				
Sardinops sagax (Jenyns, 1842)	Pacific sardine	C	WC	p,sc
Salmoniformes				
Salmonidae-trouts and salmons				
Onchorynchus keta (Walbaum, 1792)	Chum salmon			
Onchorynchus kisutch (Walbaum, 1792)	Coho (silver) salmon			
Onchorynchus tshawytscha (Walbaum, 1792)	Chinook (king) salmon			
Ophidiiformes				
Bythitidae-viviparous brotulas				
Brosmophycis marginata (Ayres, 1854)	Red brotula	N	Bt	
Batrachoidiformes				
Batrachoididae-toadfishes				
Porichthys myriaster (Hubbs & Schultz, 1939)	Specklefin midshipman	S	Bt/WC	
Porichthys notatus (Girard, 1854)	Plainfin midshipman	C,N	Bt/WC	
Atheriniformes				
Atherinopsidae-New World silversides				
Atherinops affinis (Ayres, 1860)	Topsmelt	C	WC	p,sc
Atherinopsis californiensis (Girard, 1854)	Jacksmelt	C	WC	p,sc
Leuresthes tenuis (Ayres, 1860)	Grunion	S	WC	p,sc
Gasterosteiformes				
Aulorhynchidae-tubesnouts				
Aulorhynchus flavidus (Gill, 1861)	Tubesnout	C	WC/Bt	c,sc

TABLE 9-1 (continued)

Scientific Name	*Common Name*	*Range*	*Position*	*Habitat and Behavioral*
Syngnathidae-pipefishes				
Cosmocampus arctus (Jenkins & Evermann, 1889)	Snubnose pipefish			
Syngnathus californiensis (Storer, 1845)	Kelp pipefish	S	WC	c/st
Scorpaeniformes				
Scorpaenidae-scorpionfishes				
Scorpaena guttata (Girard, 1854)	California scorpionfish	S	Bt	
Scorpaena histrio (Jenyns 1840)	Player scorpionfish	B		
Scorpaenodes xyris (Jordan & Gilbert, 1882)	Rainbow scorpionfish	B,S		
Sebastes atrovirens (Jordan & Gilbert, 1880)	Kelp rockfish	S, N	WC/Bt	st,h,sc
Sebastes auriculatus (Girard, 1854)	Brown rockfish	C	Bt	
Sebastes carnatus (Jordan & Gilbert, 1880)	Gopher rockfish	C	Bt	h
Sebastes caurinus (Richardson, 1844)	Copper rockfish	C	Bt	ab,sr
Sebastes chrysomelas (Jordan & Gilbert, 1881)	Black-and-yellow rockfish	C	Bt	h
Sebastes constellatus (Jordan & Gilbert, 1880)	Starry rockfish	S		
Sebastes dallii (Eigenmann & Beeson, 1894)	Calico rockfish	S	Bt	ab,sr
Sebastes flavidus (Ayres, 1862)	Yellowtail rockfish	N		
Sebastes hopkinsi (Cramer, 1895)	Squarespot rockfish	S	WC/Bt	st,ab
Sebastes melanops (Girard, 1856)	Black rockfish	N	WC	ab
Sebastes miniatus (Jordan & Gilbert, 1880)	Vermilion rockfish	C	Bt	ab
Sebastes mystinus (Jordan & Gilbert, 1881)	Blue rockfish	C	WC	st,sc,n
Sebastes nebulosus (Ayres, 1854)	China rockfish	N	Bt	h
Sebastes paucispinis (Ayres, 1854)	Bocaccio	C	Bt	ab,sc
Sebastes rastrelliger (Jordan & Gilbert, 1880)	Grass rockfish	C	Bt	h
Sebastes serranoides (Eigenmann & Eigenmann, 1890)	Olive rockfish	C	WC/Bt	st,ab
Sebastes serriceps (Jordan & Gilbert, 1880)	Treefish	S	Bt	h
Hexagrammidae-greenlings				
Hexagrammos decagrammus (Pallas, 1810)	Kelp greenling	N	Bt	
Hexagrammos lagocephalus (Pallas, 1810)	Rock greenling	N	Bt	
Ophiodon elongatus (Girard, 1854)	Lingcod	C	Bt	
Oxylebius pictus (Gill, 1862)	Painted greenling	C	Bt	cr
Cottidae-sculpins				
Artedius corallinus (Hubbs, 1926)	Coralline sculpin	C	Bt	al
Artedius harringtoni (Starks, 1896)	Scalyhead sculpin	C	Bt	
Enophrys bison (Girard, 1854)	Buffalo sculpin	N	Bt	
Hemilepidotus spinosus (Ayres, 1854)	Brown irish lord	N	Bt	
Jordania zonope (Starks, 1895)	Longfin sculpin			
Leiocottus hirundo (Girard, 1856)	Lavender sculpin	S	Bt	rs
Oligocottus rubellio (Greeley, 1899)	Rosy sculpin			
Orthonopias triacis (Starks & Mann, 1911)	Snubnose sculpin	S	Bt	al
Ruscarius creaseri (Hubbs, 1926)	Roughcheek sculpin	S	Bt	al
Scorpaenichthys marmoratus (Ayres, 1854)	Cabezon	C	Bt	
Hemitripteridae-sea sravens				
Nautichthys oculofasciatus (Girard, 1858)	Sailfin sculpin			
Perciformes				
Polyprionidae-wreckfishes				
Stereolepis gigas (Ayres, 1859)	Giant sea bass	S,B	Bt	ab
Serranidae-sea basses and groupers				
Epinephelus analogus (Gill, 1865)	Spotted cabrilla	B	Bt	
Epinephelus labriformis (Jenyns, 1840)	Flag cabrilla	B	Bt	
Mycteroperca jordani (Jenkins & Evermann, 1889)	Gulf grouper	B	Bt	
Mycteroperca xenarcha (Jordan, 1888)	Broomtail grouper	S,B	Bt	
Paralabrax auroguttatus (Walford, 1936)	Golden spotted rock bass	B	Bt	
Paralabrax clathratus (Girard, 1854)	Kelp bass	S	WC/Bt	st
Paralabrax nebulifer (Girard, 1854)	Barred sand bass	S	Bt	fs,rs
Paranthias colonus (Valenciennes, 1846)	Pacific creolefish	B	WC/Bt	
Serranus psittacinus (Valenciennes, 1846)	Banded serrano	B	Bt	
Apogonidae-cardinalfishes				
Apogon guadalupensis (Osborn & Nichols, 1916)	Guadalupe cardinalfish	B	Bt	
Apogon pacificus (Herre, 1935)	Pink cardinalfish	B	Bt	
Malacanthidae-tilefishes				
Caulolatilus princeps (Jenyns, 1840)	Ocean whitefish	C	Bt	ab,p
Carangidae-jacks				
Seriola lalandi (Valenciennes, 1833)	Yellowtail	C	WC	p,sc

TABLE 9-1 (continued)

Scientific Name	*Common Name*	*Range*	*Position*	*Habitat and Behavioral*
Trachurus symmetricus (Ayres, 1855)	Jack mackerel	C	WC	p,sc
Haemulidae-grunts				
Anisotremus davidsonii (Steindachner, 1876)	Sargo	S	WC/Bt	st,sc
Anisotremus interruptus (Gill, 1862)	Burrito grunt	B		
Xenistius californiensis (Steindachner, 1876)	Salema	S	WQ	c,n,sc
Sparidae-porgies				
Calamus brachysomus (Lockington, 1880)	Pacific porgy	B	Bt	
Scieanidae-croakers				
Atractoscion nobilis (Ayers, 1860)	White sea bass	C	WC	st,o,sc
Cheilotrema saturnum (Girard, 1858)	Black croaker	S	Bt	ab,h,n
Parques viola (Gilbert, 1898)	Rock croaker	B	Bt	
Seriphus politus (Ayres, 1860)	Queenfish	C	WC	st,p,n,sc
Mullidae-goatfishes				
Mulloidichthys dentatus (Gill, 1862)	Mexican goatfish	B	Bt	
Chaetodontidae-butteryflyfishes				
Chaetodon humeralis (Gunther, 1860)	Threebanded butterflyfish	B	Bt	
Johnrandallia nigrirostris (Gill, 1862)	Barberfish	B	Bt	
Prognathodes falcifer (Hubbs & Rechnitzer, 1958)	Scythe butterflyfish	B	Bt	
Pomacanthidae-angelfishes				
Pomacanthus zonipectus (Gill, 1862)	Cortez angelfish	B	Bt	
Kyphosidae-sea chubs				
Girella nigricans (Ayres, 1860)	Opaleye	S	WC	st/c,sc
Hermosilla azurae (Jenkins & Evermann, 1889)	Zebraperch	S	WC	st/c,sc
Medialuna californiensis (Steindachner, 1876)	Halfmoon	S	WC	st/c.sc
Embiotocidae-surfperches				
Brachyistius frenatus (Gill, 1862)	Kelp perch	C	WC	c/st
Cymatogaster aggregata (Gibbons, 1854)	Shiner perch	C	WC	st,sc
Embiotoca jacksoni (Agassiz, 1853)	Black perch	S	Bt	ab,sl
Embiotoca lateralis (Agassiz, 1854)	Striped seaperch	C	Bt	ab,ca
Hyperprosopon argenteum Gibbons, 1854	Walleye surfperch	C	WC	st,i,n,sc
Hyperprosopon ellipticum (Gibbons, 1854)	Silver surfperch	C	WC	st,i,n,sc
Hypsurus caryi (Agassiz, 1853)	Rainbow seaperch	C	Bt	ab,sr,sc
Micrometrus aurora (Jordan & Gilbert, 1880)	Reef perch	N	Bt	ab,i
Micrometrus minimus (Gibbons, 1854)	Dwarf perch	S	Bt	ab,i
Phanerodon atripes (Jordan & Gilbert, 1880)	Sharpnose seaperch	C	WC	c
Phanerodon furcatus (Girard, 1854)	White seaperch	C	B/WC	c,ab,sc
Rhacochilus toxotes (Agassiz, 1854)	Rubberlip seaperch	C	WC/Bt	st,ab
Rhacochilus vacca (Girard, 1855)	Pile perch	C	Bt	ab,sr
Pomacentridae-damselfishes				
Abudefduf troschelli (Gill, 1862)	Panamic sergeant major	B	Bt	
Azurina hirundo (Jordan & McGregor, 1898)	Swallowtail damsel	B		
Chromis alta (Greenfield & Woods, 1980)	Silverstripe chromis	B	Bt	
Chromis atrilobata (Gill, 1862)	Scissortail chromis	B	WC/Bt	
Chromis punctipinnis (Cooper, 1863)	Blacksmith	S	WC/Bt	h,ab,u,sc
Hypsypops rubicundus (Girard, 1854)	Garibaldi	S	Bt	cr,ab
Stegastes rectifraenum (Gill, 1862)	Cortez damselfish	B	Bt	
Labridae-wrasses				
Bodianus diplotaenia (Gill, 1862)	Mexican hogfish	B	Bt	
Halichoeres dispilus (Gunther, 1864)	Chameleon wrasse	B	Bt	
Halichoeres melanotis (Gilbert, 1890)	Golden wrasse	B	Bt	
Halichoeres semicinctus (Ayres, 1859)	Rock wrasse	S	Bt	ab,sc
Oxyjulis californica (Gunther, 1861)	Senorita	C	WC/Bt	st.sc
Semicossyphus pulcher (Ayres, 1854)	California sheephead	S	Bt	ab
Thalassoma lucasunum (Gill, 1862)	Cortez rainbow wrasse	B	Bt	
Scaridae-parrotfishes				
Nicholsina denticulata (Evermann & Radcliffe, 1917)	Loosetooth parrotfish	B	Bt	
Bathymasteridae-ronquils				
Rathbunella alleni (Gilbert, 1904)	Stripedfin ronquil	C	Bt	h
Rathbunella jordani (Gilbert, 1889)	Northern ronquil	N	Bt	h
Stichaeidae-pricklebacks				
Anoplarchus insignis (Gilbert & Burke 1912)	Slender cockscomb			

TABLE 9-1 (continued)

Scientific Name	*Common Name*	*Range*	*Position*	*Habitat and Behavioral*
Cebidichthys violaceus (Girard, 1854)	Monkeyface prickleback	N	Bt	h
Chirolophis decoratus (Jordan & Snyder, 1902)	Decorated warbonnet			
Chirolophis nugator (Jordan & Williams, 1895)	Mosshead warbonnet	N	Bt	h
Plagiogrammus hopkinsii Bean, 1894	Crisscross prickleback			
Xiphister mucosus (Girard, 1858)	Rock prickleback	N	Bt	h
Pholidae-gunnels				
Ulvicola sanctaerosae (Gilbert & Starks, 1897)	Kelp gunnel	S	WC	c
Anarhichadidae-wolffishes				
Anarrhichthys ocellatus (Ayres, 1855)	Wolf-eel	N	Bt	h
Tripterygiidae-triplefins				
Enneanectes reticulatus (Allen & Robertson, 1991)	Flag triplefin	B	Bt	
Labrisomidae-labrsomid blennies				
Alloclinus holderi (Lauderbach, 1907)	Island kelpfish	S	Bt	cr
Labrisomus xanti (Gill, 1860)	Largemouth blenny	B	Bt	
Paraclinus integripinnis (Smith, 1880)	Reef finspot	S	Bt	h,al
Clinidae-clinids				
Gibbonsia elegans (Cooper, 1864)	Spotted kelpfish	S	Bt	al
Gibbonsia metzi (Hubbs, 1927)	Striped kelpfish	C	Bt	al
Gibbonsia montereyensis (Hubbs, 1927)	Crevice kelpfish	N	Bt	al
Heterostichus rostratus (Girard, 1854)	Giant kelpfish	C	WC/Bt	st
Chaenopsidae-pikeblennies				
Neoclinus stephensae (Hubbs, 1953)	Yellowfin fringehead	S	Bt	h
Blenniidae-combtooth blennies				
Hypsoblennius gentilis (Girard, 1854)	Bay blenny	S	Bt	
Hypsoblennius gilberti (Jordan, 1882)	Rockpool blenny	S	Bt	
Hypsoblennius jenkinsi (Jordan & Evermann, 1896)	Mussel blenny	S	Bt	h
Ophioblennius steindachneri (Jordan & Evermann, 1898)	Panamic fanged blenny	B	Bt	
Plagiotremus azaleus (Jordan & Bollman, 1890)	Sabertooth blenny	B	Bt	
Gobiesocidae-clingfishes				
Gobiesox meandricus (Girard, 1858)	Northern clingfish	C	WC/Bt	c.al
Rimicola muscarum (Meek & Pierson, 1895)	Kelp clingfish	C	WC	c
Rimicola eigenmanni (Gilbert, 1890)	Slender clingfish			
Gobiidae-gobies				
Lythrypnus dalli (Gilbert, 1890)	Bluebanded goby	S	Bt	sl
Lythrypnus zebra (Gilbert, 1890)	Zebra goby	S	Bt	h
Rhinogobiops nicholsii (Bean, 1882)	Blackeye goby	C	Bt	fs,sr,h
Sphyraenidae-barracudas				
Sphyraena argentea (Girard, 1854)	Pacific barracuda	S	WC	p,s
Sphyraena ensis (Jordan & Gilbert, 1882)	Mexican barracuda	B	WC	
Scombridae-mackerels				
Sarda chiliensis (Cuvier, 1832)	Pacific bonito	C	WC	p,sc
Scomber japonicus (Houttuyn, 1782)	Pacific chub mackerel	W	WC	p,o,sc
Pleuronectiformes				
Paralichthyidae-sand flounders				
Citharichthys stigmaeus (Jordan & Gilbert, 1882)	Speckled sanddab	C	Bt	fs
Hippoglossina stomata (Eigenmann & Eigenmann, 1890)	Bigmouth sole	S	Bt	fs
Paralichthys californicus (Ayres, 1859)	California halibut	C	Bt	fs
Pleuronectidae-righteye flounders				
Pleuronichthys coenosus (Girard, 1854)	C-O sole	C	Bt	rs,fs
Tetraodontiformes				
Balistidae-leatherjackets				
Balistes polylepis (Steindachner, 1876)	Finescale triggerfish	S,B	Bt	
Suflamen verres (Gilbert & Starks, 1904)	Orange-side triggerfish	B	Bt	
Tetraodontidae-puffers				
Sphoeroides annulatus (Jenyns, 1842)	Bullseye puffer	B	Bt	
Diodontidae-porcupinefishes				
Diodon hystrix (Linnaeus, 1758)	Porcupinefish	B	Bt	

NOTE: S = southern; N = northern; C = through out coastal California, generally temperate north Pacific; B = southern Baja California, W = worldwide. Bt = bottom; WC = water column; C = water column-canopy; st = stipes; O = outer kelp margin; I = inner kelp margin; U = upcurrent margin; P = pelagic; FS = bottom-fringing sand; SR = sand/rock interface; SL = slope; CR = crest; H = in substrate; AL = algae; AB = above substrate; SC = often in schools; N = primarily nocturnally active.

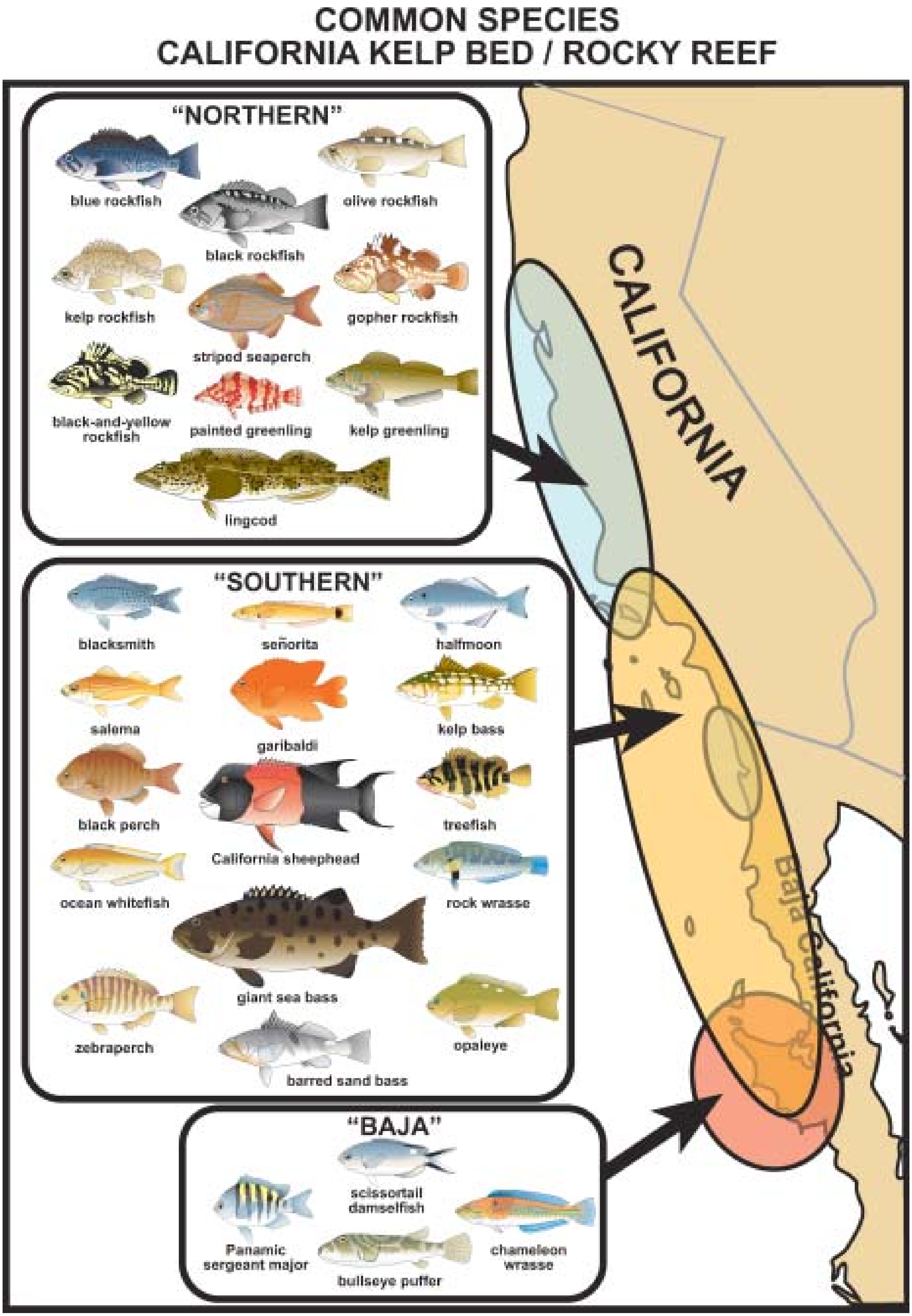

FIGURE 9-4 North, south, and Baja latitudinal distribution of conspicuous reef fishes.

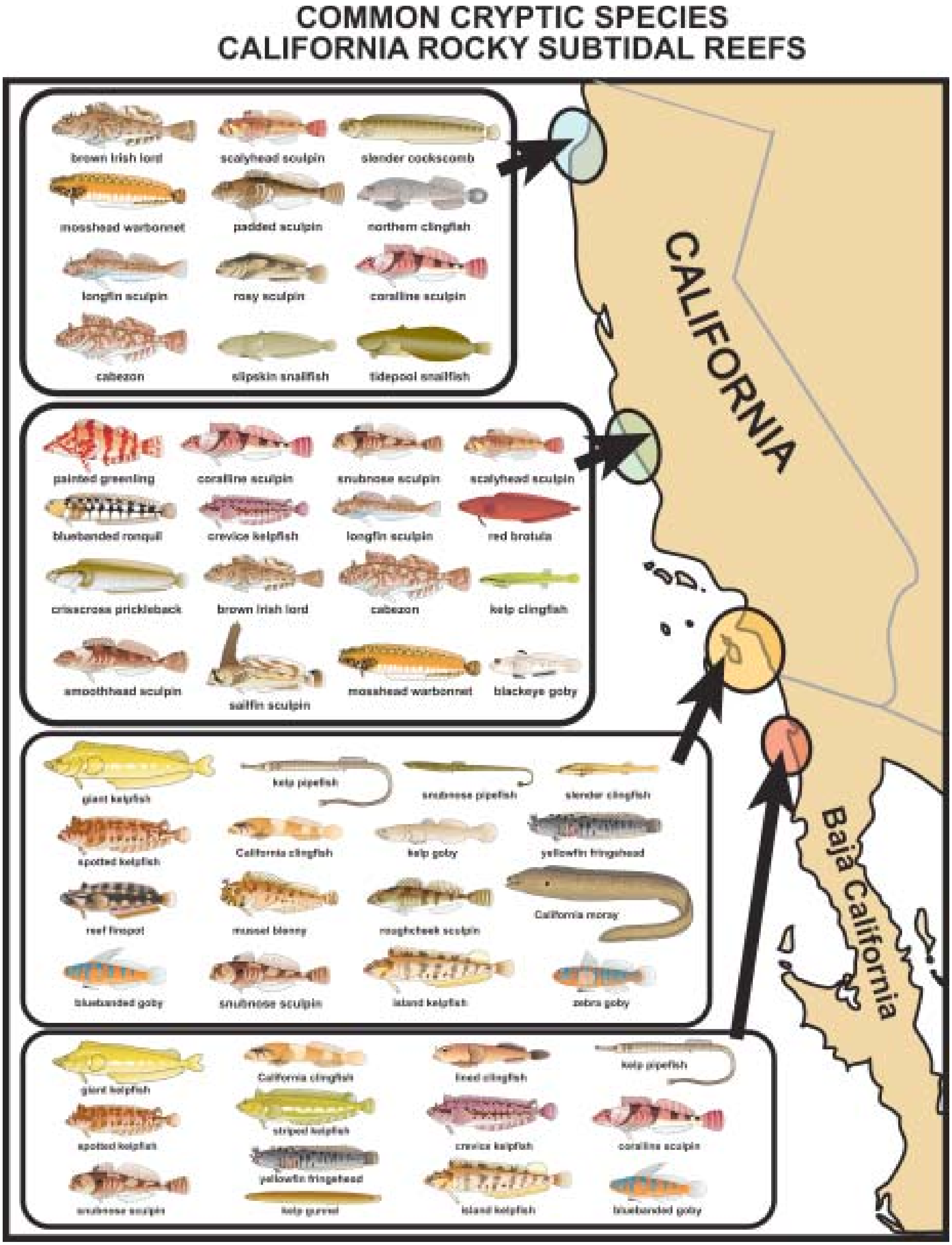

FIGURE 9-5 North and south latitudinal distribution of representative cryptic reef fishes (list compiled from Quast, 1968c; Yoshiyama et al., 1987; Stephens et al., 1986; and Allen et al., 1992).

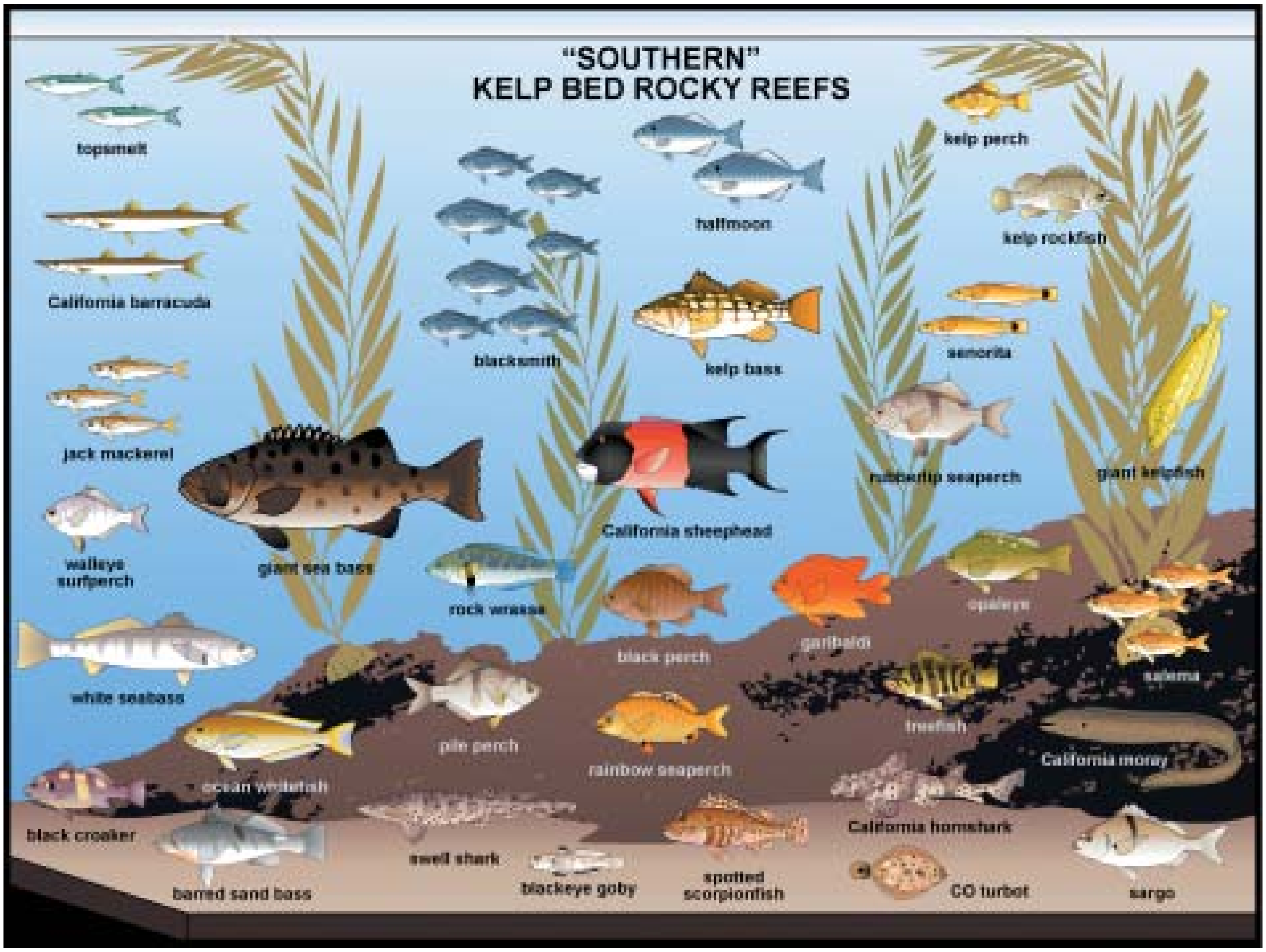

FIGURE 9-6 A representative southern reef fish scene.

variation in environmental factors. Some of the more important environmental factors are latitude (or exposure to different oceanographic conditions), bottom depth, bottom composition (presence or absence of rock or other hard substrates and the relief and rugosity of reefs), and vegetation (the presence, species composition, and density of kelp and other forms of vegetation, including drift). One of the major issues in the ecology of reef and kelp fishes off California has been the role of kelp in determining the species composition and abundance of fishes.

Latitude

The species composition of fishes changes rapidly at some major biogeographic boundaries off California, such as Point Conception and Punta Eugenia (Garth, 1955; Hubbs, 1960; Quast, 1968b; Horn and Allen, 1978; chapter 1). These changes in species composition have a profound influence on the nature of the assemblages. Three faunal provinces are found off the coast of the Californias: Oregonian, San Diegan, and Cortez. In the San Diegan Province, the reef fish assemblage includes three faunal elements. One element consists of species from families that are distributed primarily in the tropics and subtropics, including chubs (Kyphosidae), grunts (Haemulidae), croakers (Sciaenidae), damselfishes (Pomacentridae), wrasses (Labridae), gobies (Gobiidae), blennies (Blenniidae), and basses (Serranidae) (fig. 9-6). The warm-temperate California representatives of these families exhibit historically derived tropical characteristics (chapter 2), and they are relatively unimportant elements in the Oregonian Province north of Pt. Conception. A second element consists of Oregonian species that dominate north of Pt. Conception, particularly members of the rockfishes *(Sebastes)*, surfperches (Embiotocidae), greenlings (Hexagrammidae), and sculpins (Cottidae), which may occur at least in some areas in Southern California. A final element consists of species that can be called San Diegan, which are generally derived from cool-temperate taxa, but whose distributions are centered in the San Diegan Province. Examples of such fishes are kelp rockfish and black perch. In addition to these primary faunal elements, more tropical members of some families expand into the Southern California Bight during warming periods, as has been observed during the last 25 years (Mearns, 1988; Pondella and Allen, 2001). The Southern California Bight is a transitional zone between the San Diegan and Oregonian faunas and may be dominated by either fauna, depending on oceanographic conditions (Horn and Allen, 1978; Holbrook et al., 1997).

In central California, the Oregonian fauna (fig. 9-7) dominates with incursions from the south during warming events. northern California is overwhelmingly Oregonian and is dominated by taxa such as rockfish, greenlings, and cottids. Fish assemblages in rock reef and kelp habitats off southern Baja California (fig. 9-8) are generally similar to those from

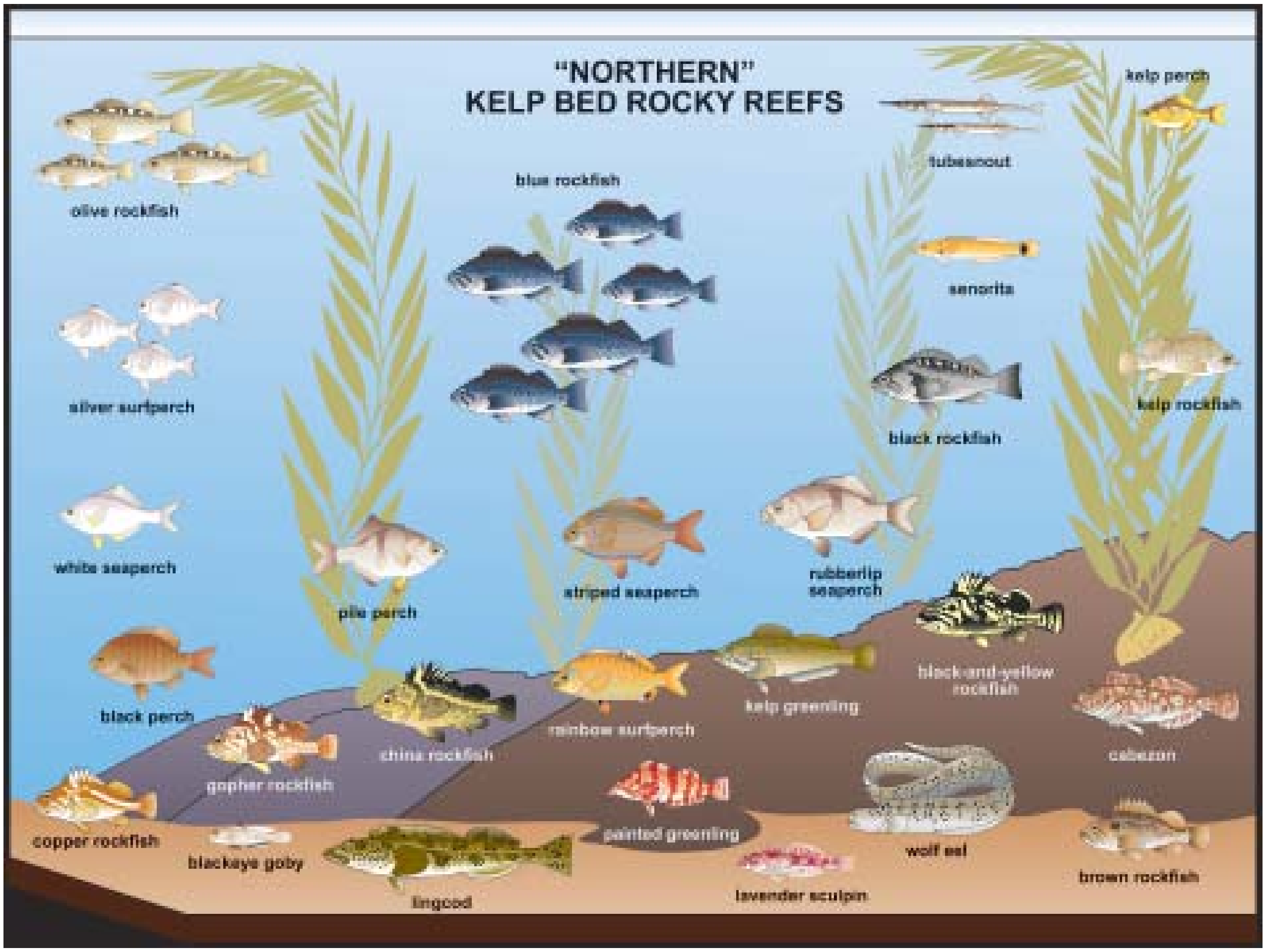

FIGURE 9-7 A representative northern reef fish scene.

southern California but differ primarily by the occurrence of four tropical species (sergeant major, chameleon wrasse, bullseye puffer, and scissortail chromis). All of these species have been reported in southern California in recent years. The coastline from just north of Punta Eugenia to around the international border complicates the fish fauna off Baja California. This section of coastline is primarily Oregonian (figs. 9-4 and 9-9) due to continual coastal upwelling (Hubbs, 1948; Horn and Allen, 1978). Finally, Cortez Province, which lies below the San Diegan, is basically unstudied.

Although the species composition of reef and kelp fishes does vary geographically and changes most strongly at some important places, not all species are affected in the same fashion by biogeographic boundaries. Even within a biogeographic region, there may be incremental changes in species composition that are related to biogeographical factors. For example, though some species of fish reach their geographical limits at or near Pt. Conception, other species that are characteristic of one geographic region occur beyond this typical range. Garibaldi and California scorpionfish are now extremely rare north of Pt. Conception, but several other species of fish from tropical families occur north of Pt. Conception (such as señorita, blacksmith, opaleye, kelp bass, California sheephead, and halfmoon). Furthermore, even within this group, some species seem better adapted to conditions in central California. The señorita appears to have recruited nearly every year in Monterey during the 1990s, whereas blacksmith and California sheephead recruited only during El Niño years and blue-banded gobies recruited only during the El Niño of 1983 (Lenarz et al., 1995; Walters, 2002). Señoritas are an example of a wrasse that is clearly not a subtropical species. Furthermore, although some species that are characteristic of central and northern California are very uncommon south of Pt. Conception (such as kelp greenling and China rockfish), others have been common in the southern California Bight (such as black-and-yellow, blue, and olive rockfish), at least before 1977. The distribution and abundance of central California expatriates off southern California also indicate an incremental response to biogeographical factors. For example, the kelp rockfish seem to have been common throughout the southern California Bight, but the olive rockfish, black-and-yellow rockfish, and blue rockfish have been progressively less common (Limbaugh, 1955; Quast, 1968b,c; Hobson and Chess, 1976). Fish surveys on the California Channel Islands (fig. 9-10) further illustrate this phenomenon. The biogeographical differences among the islands are clear, but different species appear to respond differently to the biogeographical gradient (fig. 9-10). Patton et al. (1985) demonstrated that the abundance of a number of reef and kelp fishes changed along the mainland coast of southern California. Their analyses indicated that geographic position within the Southern California Bight influenced the species composition of fishes on rock bottoms as much as bottom relief and kelp density. In addition, some northern species may be able to survive off southern California by submergence (Hubbs, 1948, 1952), as they seek cooler, isothermal conditions beneath the warmer surface waters.

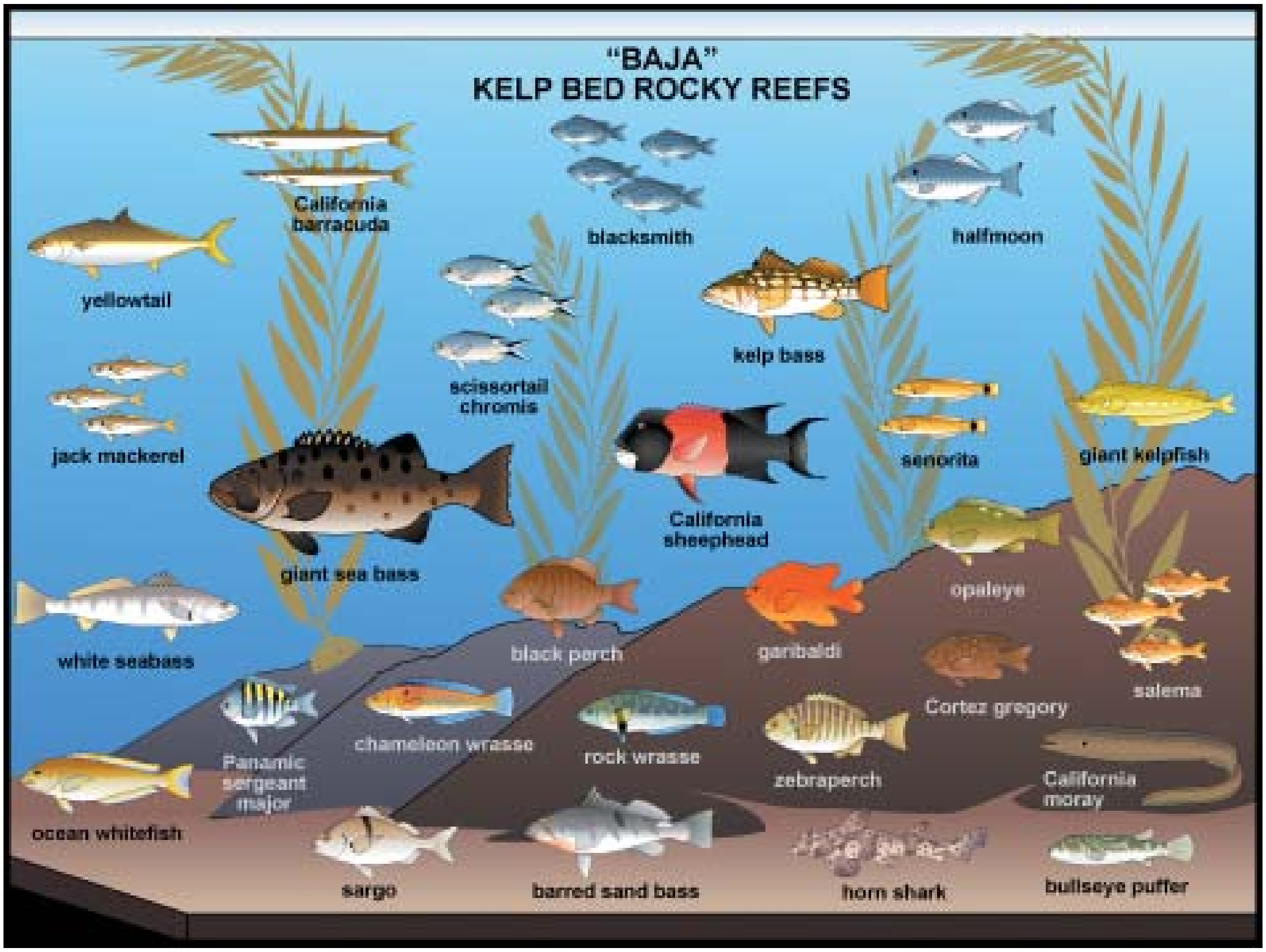

FIGURE 9-8 A representative Baja reef fish scene.

Incremental differences in latitudinal distribution also seem to be correlated with differences in recruitment. For example, recruitment of olive rockfish in the Southern California Bight, as indicated by entrainment in power plants, seems to have persisted since 1977, whereas recruitment of blue rockfish ceased during the period covered in the study (Stephens et al., 1994; Love et al., 1998). Cowen and Bodkin (1993) found that some southerly species occurred at San Nicolas Island from 1981 to 1986 and documented the irregular recruitment of some species (such as California sheephead, rock wrasse, and garibaldi) but regular recruitment of others (such as blacksmith and señorita). Finally, distributions of nearshore fishes have changed in response to changes in ocean climate (Hubbs, 1948; Stephens et al., 1994). These observations show that, though major biogeographic features do strongly influence the species composition of nearshore fishes, the species composition of fishes in kelp and rock assemblages still exhibit incremental variation within regions.

Bottom Depth

The composition of fish assemblages in rock and kelp habitats also changes with bottom depth. Some of this change seems to be related to depth or depth-related abiotic factors per se, but some of this change may be related to habitat and vegetation. Temperature is the abiotic factor with the greatest direct effect on fishes. Even though the reefs with which we are concerned are relatively shallow (<30m), water temperature gradients can be seasonally stable and persistent, and reef fishes often distribute themselves with regard to these gradients (Terry and Stephens, 1976). Stephens and Zerba (1981) showed that species composition changed with depth-related changes in water temperature at King Harbor and suggested that the overall diversity of fishes at this site was enhanced by the heterogeneity of temperature conditions produced by the conjunction of entrained upwelling from a nearby submarine canyon and the discharge of power plant thermal effluent. Temperature-related depth distributions of mobile fish should change with daily, seasonal, or annual changes in these gradients. For less mobile species, temperature changes are sometimes reflected in changes in activity (Ebeling and Hixon, 1991).

The depth distributions in several species of fish appear to be related to the occurrence of vegetation. Ebeling et al. (1980a) and DeMartini (1981) found that shallow habitats with surf grass (and sometimes *Egregia* and other brown algae) supported some species that are also found on deeper reefs in *Macrocystis* forests (such as subadults and adults of black perch, rainbow seaperch, opaleye, señorita, garibaldi, and kelp bass) and others that are limited to those habitats, at least during the daytime (dwarf perch, walleye surfperch). Related to bottom depth, but not dependent on bottom depth per se, is the relationship between fish abundance and the margins of the kelp forest. Both in southern California (Ebeling et al., 1980a; Bray, 1981; Larson and DeMartini, 1984) and in central California (Stallings, 2002), several species of fish (especially plankton feeders such as blacksmith and blue rockfish,

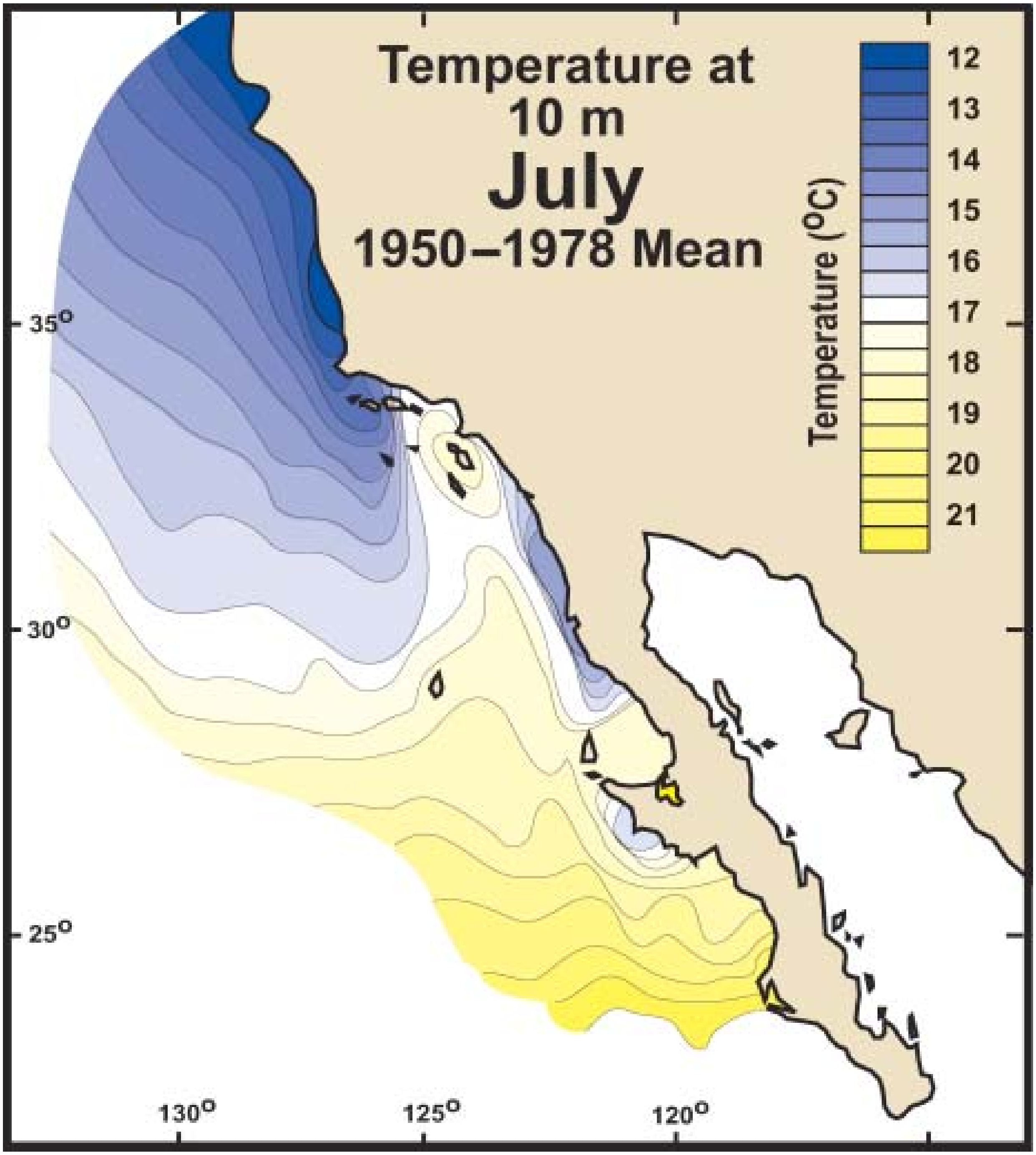

FIGURE 9-9 Mean July isotherms (°C at 10 m depth) off California and Baja California recorded during CalCOFI cruises from 1950 to 1978.

but also other species such as olive rockfish) tend to concentrate at the upcurrent and outer margin of the kelp forest. Here, kelp provides a point of visual orientation. It is not clear what the effects of lack of kelp might be on the overall abundance of these species. Blacksmith appeared to form water-column aggregations closer to shore off Santa Cruz Island in 1996, when kelp was less abundant than in the 1970s (Larson, personal observation), and orient to pinnacle reefs lacking kelp as well as to seamounts without kelp (Pondella, personal observation). Blue rockfish orient toward rock outcrops when kelp is absent. The tendency for many species to concentrate along the kelp-bed margins results in an unequal distribution of densities across a bed.

Within the depth range of kelp forests, a number of species show limited depth distributions (such as grass rockfish, black-and-yellow and gopher rockfish and striped and black perch). Several species that occur in kelp forests also occur much more deeply (such as California sheephead, many species of rockfish, and blackeye goby) or may migrate seasonally between deeper and shallower waters (such as lingcod). Some of the information on deeper dwelling fishes is available from fisheries, but the preponderance of research on fishes from rock and kelp habitats has been based on observations by scuba divers and may therefore underrepresent the significance of those portions of populations living below typical scuba depths. The use of surveys by submersibles (chapter 9) will

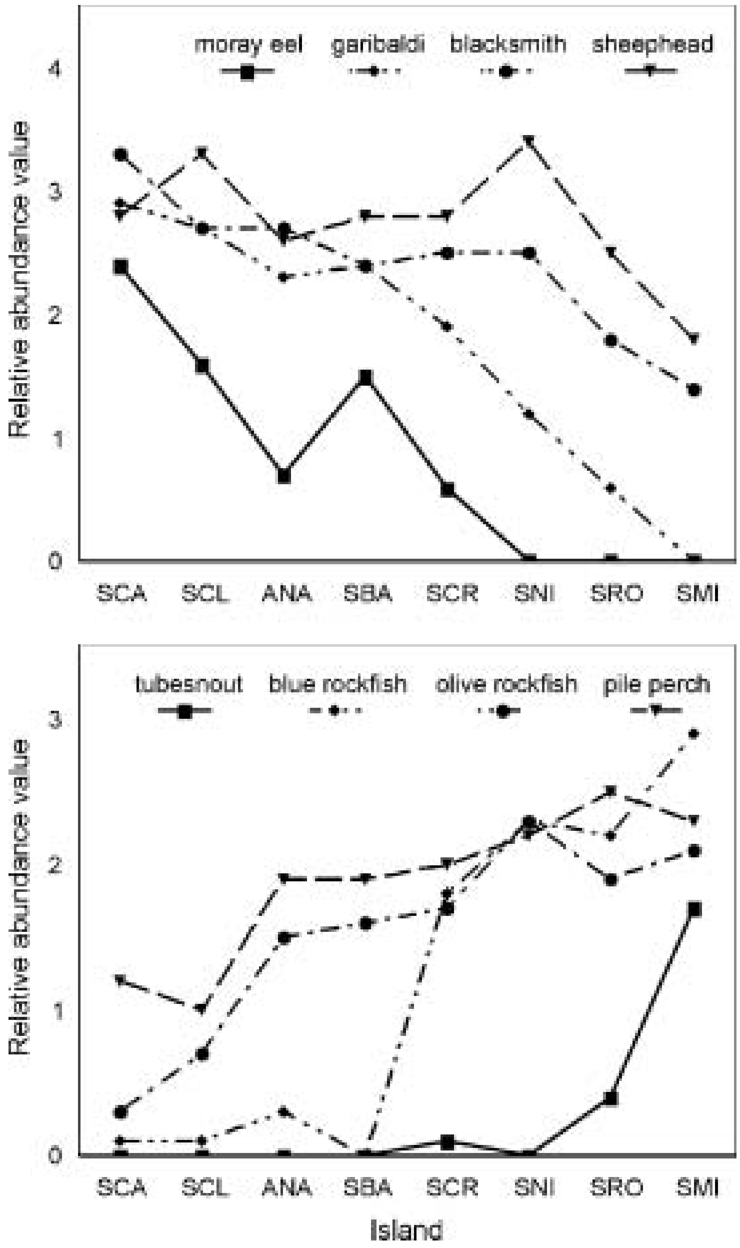

FIGURE 9-10 Relative abundance scores for selected species of fish with southerly distributions (upper panel) and northerly distributions (lower panel) from 105 sites on eight southern California islands (Santa Catalina, SCA; San Clemente, SCL; Anacapa, ANA; Santa Barbara, SBA; Santa Cruz, SCR; San Nicolas, SNI; Santa Rosa, SRO; and San Miguel, SMI), 1978–1986. Adapted from Engle (1993).

help to determine the true bathymetric extent of some species of fish from rock and kelp habitats.

Macroalgae and Bottom Characteristics

The effects of macroalgae and bottom characteristics on fish assemblages are closely intertwined. Much of the initial research on kelp-forest fishes concerned the effects of kelp and kelp harvesting on fishes (Limbaugh, 1955; Quast, 1968a–f; Davies, 1968; North, 1968, 1971), and further research (see below) has continued to address this issue. The confounding factor in all of this research is the relatively strong dependence of kelp and other types of macroalgae upon the rock bottom for attachment. This makes it difficult to distinguish the effects of kelp from the effects of rock bottom on fishes. Because of this, we will initially address the relative effects of kelp (primarily *Macrocystis pyrifera*, and secondarily *Nereocystis luetkeana*) and bottom type on fishes together.

Limbaugh (1955), in addressing the effects of kelp harvesting on fishes, provided the first comprehensive description of the natural history of kelp-forest fishes. As in later studies, he compared areas with different combinations of habitat, including rocky and sandy areas with and without kelp. He described suites of species associated with the kelp canopy, bottom (kelp-bed rock bottom and kelp-bed sand bottom), and midkelp region and discussed his conclusions regarding habits and habitat requirements of many species. In his qualitative analysis, he concluded that most species of fish that occur in kelp forests are bottom species that are "completely independent of kelp" but allowed that some species seek shelter in the kelp canopy as adults, that a few species deposit eggs on kelp (and on other substrates), and that juveniles of some species occur in kelp.

Quast (1968b,c) used quantitative sampling as well as the presence and absence of species from areas of differing habitat to evaluate further the effects of bottom type and kelp on the species composition and abundance of fishes. He concluded (Quast, 1968b, p. 43) that "Substrate character seems of primary importance to the rocky inshore fishes, while the presence or absence of kelp is secondary." He noted that several species (such as California sheephead and blacksmith) are abundant in areas of high-relief rocky bottom, whether or not kelp is present, and that areas of kelp with low-relief rock or sandy bottom lack many species and have a lower total standing crop than areas of high-relief rocky bottom (Quast, 1968b,c). However, he also noted that areas of low to moderate bottom relief with kelp supported larger standing crops of fishes than those without kelp (Quast, 1968b,c,f). Envisioning the kelp forest as a "giant filter" for coastal zooplankton, Quast (1968b,f) thought that kelp served inshore fishes primarily though the collection of plankton by attached invertebrates and through its effect as a point of visual orientation, allowing several species of fish to extend their range into the water column.

Ebeling et al. (1980a) surveyed fishes in bottom and kelp-canopy habitats differing in bottom depth, bottom type, and kelp density off Santa Barbara and Santa Cruz Island. Because the south-facing coast off Santa Barbara is somewhat protected from oceanic swells, kelp forests there sometimes grow on sand or low-relief rocky bottom, facilitating the comparison of kelp-forest fish assemblages over high-relief and low-relief substrates. However, kelp was present in most samples from high-relief rocky bottoms. Their analysis distinguished five "habitat groups" of fishes: a "kelp-rock" group of species from high-relief rocky bottoms in kelp forests; a "canopy" group that was associated with the kelp canopy, relatively independently of bottom type; an "inner marginal" group associated with shallow water and surfgrass inshore of kelp forests; a "commuter" group of species that showed no strong habitat association, but which moved throughout the water column and a "bottom" group associated with the rock bottom on the outer edges of kelp forests. Species from the "kelp-rock," "commuter," and "bottom" groups often occurred together, forming the core of the benthic, epibenthic, and midwater column species typically seen over rocky bottoms in kelp forests. The species composition in any location was seen as responding continuously to several habitat variables. They concluded that areas of kelp over low-relief rocky bottom supported kelp-canopy species and generalist species but that higher relief was required for a number of species. Like Quast (1968b,c,f), they found that the presence of kelp over low-relief substrate did enhance density and diversity of species. They also found that in bottom transects, fish density and species diversity increased with both bottom depth and bottom relief. The relationships of density and diversity with bottom relief did not reach asymptotes; instead, they reached their highest values at the greatest values of bottom relief. In this study, bottom relief was scored on a subjective 1–5 scale that reflected both reef height and bottom rugosity, but neither of these parameters was measured directly. Because kelp was present in essentially all samples over moderate to high-relief rocky bottoms, it was impossible to determine whether kelp enhanced the rock-reef habitat for members of the "kelp-rock" group.

Stephens and Zerba (1981) reported on surveys of the breakwater at King Harbor, a high-relief rock reef without kelp, located in Southern California. Although their discussion did not focus primarily on fish–habitat relationships (other than the effect of temperature stratification), their results describe a diverse and abundant fish fauna containing a large number of species that are common in kelp forests. These include species that one might expect to find on a rock reef, including benthic and epibenthic species (such as various surfperches, garibaldi, painted greenling, and opaleye) typically associated with rocky bottoms in kelp forests and water-column species (such as blue rockfish and blacksmith) that also use rock bottoms for shelter. The fish fauna also included other species that are often associated with kelp even in the absence of a high-relief rocky bottom (such as kelp bass, señorita, and halfmoon), and even species that are frequently associated strongly with kelp (such as kelp perch and giant kelpfish). Their data indicate that many members of the "kelp-rock" and "commuter" groups of Ebeling et al. (1980b) can be found on rock bottoms that lack kelp, as can some members of the "canopy" group.

Larson and DeMartini (1984) surveyed fishes in a cobble-bottom kelp forest and an adjacent kelp-free site of similar bottom type near San Onofre, California. The cobble bottom here offered little variation in bottom height and little fish-sized bottom shelter. It was periodically inundated or scoured by sand, so there was little growth of attached algae and invertebrates on the rocks. Several species that depend on a rocky bottom for shelter or food were absent or uncommon at this site (such as blacksmith, opaleye, garibaldi, painted greenling, benthic rockfishes, and some surfperches). The species present in the kelp forest were kelp-canopy species (such as kelp perch, halfmoon, and giant kelpfish), bottom and/or water-column species that were less reliant on a high-relief rocky bottom (such as kelp bass, señorita, and perhaps California sheephead), and species that seem to prefer low-relief bottom habitats (such as barred sand bass and white seaperch). The abundance and biomass of nearly all of the species except barred sand bass were substantially greater in the kelp forest than in the kelpless cobble site. It appears that the presence of kelp had a great influence on the fishes at San Onofre and provided habitat for a large number and biomass of species, particularly those inhabiting the water column.

Stephens et al. (1984) reported on surveys of fishes of Palos Verdes during the recovery of the kelp forest there and during a major shift in oceanic climate. They found that the reef-kelp habitat at Palos Verdes supported a less diverse and less abundant fish fauna than the kelp-free but high-relief breakwater at King Harbor. Only a few species seemed to increase in abundance in concert with the regrowth of the kelp bed at Palos Verdes. Benthic counts of kelp bass increased, but so did counts at King Harbor. From the added counts of kelp bass above the bottom at Palos Verdes, they concluded that kelp bass might have increased in abundance in response to the growth of the kelp forest. Kelp perch increased at Palos Verdes but also increased at King Harbor. Other species, including kelp rockfish and various surfperches, did not increase in abundance with the development of the kelp bed at Palos Verdes. The effects of altered ocean climate (regime shift) may have obscured the relationship of these species with kelp after 1977.

Patton et al. (1985) carried out an extensive survey of sites within the Southern California Bight that included different combinations of bottom relief and kelp abundance. They found a saturating (asymptotic) effect of reef height on the abundance of "oxyphilic" (rock-loving) species and on species density. Kelp density seemed to have no effect on fish density or species density over high-relief rock bottoms and had a saturating effect on fish density and species density over low-relief bottoms, especially when sites with sand bottom and kelp were included. In a cluster analysis, the effects of kelp on species composition could be distinguished regionally for high-relief rocky bottoms, but substrate composition and geography accounted for deeper levels of clustering.

Bodkin (1988) examined the effects of *Macrocystis* on the density and species composition of fishes near Pt. Piedras Blancas in central California by clearing kelp from a 1-ha area.

TABLE 9-2

Pearson Correlation Coefficients Between Fish Counts and Kelp Abundance on Santa Cruz Island, 1996

	Bottom Transects	*Canopy Transects*
Kelp bass	0.338	0.820?
California sheephead	− 0.572	
Señorita	0.031	0.706
Blacksmith	− 0.272	− 0.384
Garibaldi	− 0.438	
Halfmoon	− 0.649	− 0.565
Opaleye	0.229	0.624
Black perch	0.119	
Striped seaperch	0.391	
Pile perch	− 0.279	
Rubberlip seaperch	0.509	
Kelp perch	− 0.455	0.551
Kelp rockfish	0.922*	0.871?
Olive rockfish	0.609	0.732
Black-and-yellow rockfish	0.352	
Treefish	− 0.216	
Painted greenling	− 0.462	
Rock wrasse	0.033	

NOTE: Mean kelp scores were made subjectively on a scale of 1 to 5. Fish were counted at five sites on the north shore of Santa Cruz Island, in 2.5 minute video transects conducted as in Ebeling et al. (1980a,b) near the bottom and in the kelp canopy (or at the depth the kelp canopy would have been). Significance levels: * ($p < .05$); ? ($.05 < p < 0.1$). From Larson, Alevizon, Niesen, and Clark (unpublished data).

The effect of kelp removal was substantial in the midwater zone, where kelp provided the only substrate and point of orientation, but was small in the benthic/epibenthic zone. Juveniles of rockfish and adults and subadults of blue rockfish, olive rockfish, kelp rockfish, and señorita decreased in abundance relative to controls in midwater transects. Overall, the biomass declined substantially after kelp was removed in the experimental area. This study was carried out over a high-relief rocky bottom.

DeMartini and Roberts (1990) compared fish density in areas of differing kelp density at San Onofre, an area of low-relief cobble bottom. Fish density showed a significant, positive relationship with kelp density for at least one life stage in 11 of 14 species evaluated. Total fish density and biomass increased significantly with kelp density. The latter relationship was nonsaturating; it applied, even if the samples with very low kelp density were excluded from the analysis. Like others, they concluded that the presence of kelp might have a stronger effect on fish abundance over a low-relief bottom than over a high-relief bottom because kelp is the primary feature providing structural heterogeneity in such habitats.

Holbrook et al. (1990) compared the abundance of selected species of fish in areas of differing *Macrocystis* density at Santa Cruz and Santa Catalina Islands. Like DeMartini and Roberts (1990), they specifically addressed the effects of *Macrocystis* on different life stages, but in addition they addressed indirect effects of *Macrocystis* on fishes through its effect on understory algae. Some species and life stages (such as kelp perch, giant kelpfish, kelp rockfish, and young-of-year of kelp bass) showed strong positive relationships with kelp density; some seemed to require a threshold density of kelp to be present. The density of adult kelp bass was unrelated to kelp density. Different species of benthic surfperch appeared to respond either positively (black perch, pile perch) or negatively (striped seaperch) to kelp density, as apparently influenced by their dependence on features of bottom cover. Kelp appeared to inhibit foliose understory algae, which is used as a substrate for foraging by striped seaperch, but cover of benthic "turf," which is used by black perch and pile perch for foraging, increases in the absence of foliose understory algae.

Larson and colleagues (unpublished data) repeated the surveys of Ebeling et al. (1980b) at Santa Cruz Island, investigating the effects of climate change and other factors on fishes there. They found a substantial decline in the abundance of kelp, which in 1996 was restricted to only a few sites on the north side of Santa Cruz Island. They sampled five sites, two with essentially no kelp, one with sparse kelp but a continuous kelp canopy, and two with relatively dense stands of kelp. All sites had the high-relief rocky bottom typical of Santa Cruz Island (Ebeling et al., 1980a). In bottom transects, the mean abundance of most species at a site was weakly correlated (positively or negatively) with the mean kelp-density score at a site (table 9-2). Kelp rockfish showed a strong, significant positive correlation with kelp density over sites. In canopy transects, most species showed large (though not significant) positive correlations with kelp-density score (table 9-2). The aggregate of these correlations indicates that in the water column, species composition and abundance responded strongly to the presence of kelp. For these species, total abundance at a site (integrated from the surface to bottom) may be greater in areas of kelp even if their abundance on the bottom is independent of kelp density.

Although the kelp forests of southern California are dominated by *Macrocystis, Nereocystis* beds occur in more exposed sites in central California and are the only types of offshore kelp beds in northern California. In general, far less has been published to date on the fishes of central and northern California rock reefs and kelp forests than on those of southern California. Burge and Schultz (1973) provided descriptions of the fish fauna of Diablo Cove but did not specifically evaluate the effects of habitat on the fish assemblage there. Miller et al. (1967; summarized also in Miller and Geibel, 1973) contrasted the sportfish catches on exposed reefs in clear water with those at more sheltered reefs in turbid water. Miller and Geibel (1973) reported on scuba-based surveys of fishes in rock-reef and kelp-forest habitats near Monterey. They described the assemblage and the habitat associations of several species. In a relatively small-scale (0.5-ha) kelp-canopy removal experiment, they found no significant changes in adult density but did find a displacement of juvenile rockfish from the kelp canopy to the bottom. Bodkin's (1988) *Macrocystis* removal experiments near Pt. Piedras Blancas were described before. Bodkin (1986) has also provided the best comparison to date of fish assemblages in *Macrocystis* and *Nereocystis* forests. In surveys near Pt. Piedras Blancas and Big Creek, he found that species composition and species diversity differed very little between the two types of kelp forests but that several species were more abundant, often markedly so, in *Macrocystis*. These included blue, olive, kelp, and black rockfishes in the midwater and gopher rockfish, kelp rockfish, striped seaperch, and painted greenling on the bottom. He concluded that the following factors may contribute to the differences in fish abundance in the two types of kelp forests: (1) increased food availability for blue rockfish during seasons when they consume algae; (2) the perennial nature of *Macrocystis* forests; (3) differences in abiotic conditions such as wave surge and sand scour, which affect the occurrence of *Macrocystis* versus *Nereocystis* and may also affect fishes directly; and (4) the differing physical structure of *Macrocystis* and *Nereocystis* in the midwater and canopy regions.

The effects of other brown algae that provide vertical structure such as *Egregia menziesii*, *Cystoseira osmundacea*, *Pelagophycus porra*, and understory brown algae species such as *Pterygophora californica*, *Laminaria farlowii* and *L. setchelli*, *Eisenia arborea*, and *Desmarestia ligulata* have not been investigated extensively. Ebeling and Laur (1985) found that juvenile surfperch decreased in abundance when the understory of *Pterygophora californica* and *Laminaria farlowii* was reduced either naturally or experimentally. Stephens et al. (1984), however, found that fish density was low in the midbed region of the kelp forest at Palos Verdes, where *Pterygophora californica* was abundant. Likewise, the "kelpless cobble" site of Larson and DeMartini (1984), where the abundance of benthic and epibenthic species was lower than at the site with a *Macrocystis* canopy (see above), was dominated by *Pterygophora*. Rather than serving as a point of visual orientation, like *Macrocystis* and other brown algae with vertical structure, dense stands of *Pterygophora* may inhibit visibility within a meter of the bottom for benthic and epibenthic fishes. In addition, *Pterygophora* may inhibit the growth of foliose algae and "turf" (Foster and Schiel, 1985), upon which benthic species of fishes may depend for foraging. We have observed that juvenile rockfish settle in *Cystoseira* in Monterey Bay, and in general, small fishes may orient toward any large structure.

Benthic drift algae, which are ultimately temporary but may persist for at least weeks, form an extension of the rock-reef and kelp habitat for some species of fishes (Vetter, 1998; Vetter and Dayton, 1999). Vetter (1998) found a number of fishes typically associated with rock reefs and kelp forests, including kelp bass, sheephead, blacksmith, señorita, pile perch, and black perch, near mats of drifting macrophytes near Scripps Canyon. These fishes often occurred in very high densities. We have also observed juvenile fishes, such as rockfish and white sea bass, associated with macrophyte detritus (Allen and Franklin, 1992; chapter 5).

In summary, the effects of bottom characteristics and macroalgae on fishes off California are complex and perhaps not completely resolved. Bottom characteristics clearly influence the species composition and abundance of fishes. Species may associate with rocky bottoms in a variety of ways, such as for shelter, for nesting sites, for prey that lives in or on rocks, for points of visual orientation, or for the attached algae or "turf" that provides shelter for fish or for fish prey. Because of this, different aspects of bottom characteristics may best describe the habitat needs of different species. Some may require shelter holes of particular size, some may require high vertical relief, some even associate with the rock–sand interface, and some may be quite generalized in their requirements. Improvements in the measurement of bottom characteristics may help to resolve questions such as whether fish abundance and diversity are saturating functions (Patton et al., 1985) or accelerating functions (Ebeling et al., 1980a) of bottom relief. Recent advances in remote sensing have facilitated new ways of describing habitat (Greene et al., 1999), and these methods have, in turn, been applied to characterizing of species–habitat relationships and to estimating of fish abundance (Yoklavich et al., 2000).

Although most work conducted in California shows that a high-relief rocky bottom is essential for a number of species of fish, the effect of *Macrocystis* on fishes is more complex. Over a sandy or low-relief rocky bottom, it seems clear that the presence of *Macrocystis* substantially enhances the diversity and abundance of fishes. As noted by DeMartini and Roberts (1990), a number of species with generalized habitat requirements will occupy an area of low-relief bottom if kelp is present. They suggest that kelp provides a point of visual orientation for a number of water-column species and that epibenthic, bottom-feeding species may benefit from prey produced in drifting kelp. The effect of kelp on fishes over high-relief rocky bottoms has been more difficult to determine. Clearly, a high-relief rocky bottom supports diverse and abundant assemblages of fishes. Nevertheless, some species depend to a great degree on kelp, even when a high-relief rocky bottom is present and even though they may occur in other habitats. These species include kelp perch, giant kelpfish, kelp clingfish, and perhaps kelp rockfish. In addition, young stages of several species associate strongly with kelp. On or near the bottom, abundances of many species are uncorrelated or only loosely correlated with kelp density. However, the abundances of some species increase in the water column over a high-relief rocky bottom when kelp is present, so the density of species measured over the entire water column may increase when kelp is present. We might tentatively conclude that some species depend strongly (although not completely) on kelp, even over a high-relief rocky bottom, and that other species may be more abundant when kelp is present, but that much of the fish assemblage over a high-relief rocky bottom is not dependent upon kelp. It would be good to resolve the nature of the relationship between kelp density and the species composition and abundance of fishes. Is fish density a saturating function of kelp density? Is there a lower threshold of kelp abundance for some species? What are the effects on fish assemblages of temporal variation in kelp density on various temporal scales? What happens seasonally, interannually, and perhaps interdecadally to fishes when kelp density fluctuates?

DeMartini and Roberts (1990) found that with a decline in the area of the kelp forest at San Onofre, fish became denser in the remaining kelp forest. Similarly, there have been indications of shifts from cleared to uncleared areas in kelp-removal experiments (Miller and Geibel, 1973, Bodkin, 1988). What do such shifts mean relative to the carrying capacity of kelp forests for fishes and to the nature of the relationship between kelp density and fish abundance? Some of these questions may be difficult to resolve, in part because of matters of spatial scale. For example, kelp-removal experiments, or comparisons of fish abundance or recruitment in areas with or without kelp, may depend on the choices available for fish within the ranges of their movements and perception. Finding that fish disappear from a small area that is cleared of kelp does not necessarily mean that those fish would never use an area without kelp because they may simply have chosen between available alternatives. Levin and Hay (2002) examined the effect of the spatial scale of study on the relationship between fishes and *Sargassum filipendula* in the South Atlantic Bight. Similar studies of California could be useful. In any case, these are important questions in assessing populations of fishes in nearshore areas off California.

Overview of Habitat Functions for Fish Assemblages

The structure of the reef/kelp habitat serves a number of functions for fishes, and the heterogeneity of this structure provides opportunities for niche diversification. Together, these factors account for the high density and diversity of fishes associated with this habitat (Bond et al., 1999). Some of the more important functions provided by the reef/kelp habitat to the fish assemblage are shelter, orientation, food availability, and nesting sites for the fish assemblage.

Shelter is one of the most important functions provided by the reef/kelp habitat. Shelter is especially important to small species and to the young-of-year of many larger species but is also important to larger species that associate with the substrate. The notion of "shelter" is actually complex and can work in a number of ways. Most obviously, hard structures can provide physical protection from predators. Here, crevices, burrows, and caves in rock and other solid structures can prevent a predator from gaining access to potential prey. Second, an immobile substrate can provide physical shelter from wave surge. For example, black-and-yellow and gopher rockfish are found in more protected positions as wave surge increases (Larson, 1980a). Third, both hard and soft substrates can serve as objects behind which fish can hide, escaping visual detection by potential predators or prey. For example, newly settled kelp rockfish hide among the stipes and blades of *Macrocystis* in the kelp canopy and dart for shelter when approached by potential predators (Nelson, 2001). Closely related to the role of substrate in hiding fish, the substrate may provide a cryptic background that conceals a fish, even if it is not hidden behind an object. This function is important in both concealing potential prey from their predators, like kelp perch that are concealed by kelp from potential predators (Anderson, 1994, 2001), and in concealing ambush predators, such as giant kelpfish, from potential prey.

Steele (1996, 1997, 1998, 1999) conducted one of the more thorough experimental analyses of the influence of predators and shelter abundance on mortality, using two species, bluebanded and blackeye goby. Behrents (1987) previously suggested that the recruitment success and survivorship of bluebanded gobies depend on shelter availability. Steele (1997) showed that predation halved survivorship in bluebanded gobies, but survivorship increased with shelter availability, with or without predator pressure (Steele, 1999). In contrast, shelter increased the survivorship of blackeye gobies only in the presence of predators. Survivorship on small patch reefs also increased in both species with distance from larger reefs (Steele, 1996). This suggests a predatory effect, which was confirmed for a variety of blennies in recent King Harbor recruitment studies (Stephens and Pondella, unpubl. data). Recruitment of bluebanded gobies was strongly positive to the presence of conspecifics (Steele, 1997) but not blackeye gobies (Steele et al., 1998). Both species showed asymptotic survivorship based on species specific density characteristics, and bluebanded gobies showed reduced growth in the presence of predators. These data suggest that the effect of shelter is important to settlement survivorship and is species specific. In this case, the bluebanded goby is a very small brightly colored, territorial species that displays on open reefs but retreats to protective shelters for survival. By contrast, the blackeye goby is larger and protectively colored for its sand reef habitat, and numerous adults may occupy the same shelter.

In tube dwelling species, such as the mussel blenny, *Hypsoblennius jenkensi*, and the yellowfin fringehead, *Neoclinus stephensae*, the presence of adults depends on available burrows (Stephens et al., 1970). Recruitment (settlement) may occur in burrow-free habitat, but postrecruitment mortality or migration occurs subsequently. The ability of competent reef fish larvae to select specific habitats (shelter sites, etc.) has not been demonstrated in these species. The absence of young-of-year in inappropriate habitat sites could result from either habitat selection or postsettlement mortality.

Shelter is required as a resting site for the adults of some species. For example, the blacksmith, an important diurnal planktivore, is missing from reefs without available nocturnal shelter sites. Some labrids (rock wrasse and señorita) shelter at night by burying in soft substrate adjacent to the reef. Shelter sites are the basis of territorial behavior in many small, shelter-using species (blennies, gobies, clinids, etc.). Shelter or nesting sites also anchor the territories of a number of larger species as well, such as garibaldi (Clarke, 1970), black-and-yellow and gopher rockfish (Larson, 1980b,c; Hoelzer, 1987), black perch (Hixon, 1981), giant kelpfish (Coyer, 1982), painted greenling (DeMartini, 1985, 1987), and possibly treefish (Haaker, 1978).

Reefs and kelp provide relatively stable visual cues that allow fishes to orient to positions in and above the substrate. This feature is not found in pelagic or soft substrate (sand, mud) habitats. Much of the diversity of the reef fish assemblage is due to the differing features in the reef habitat: sand fringe, rock–sand interface, reef slope, reef crest, algal layering, and canopy. Each of these areas includes morphological or biotic features that further subdivide it. Many species are restricted to specific areas (sites). Orientation to such sites may involve species-specific habitat preference, competition, or fortuitous timing and history.

The reef/kelp habitat affects food availability in many ways. Most algae growing on a reef require attachment to a hard substrate, and a limited number of reef fish use this resource directly (Horn, 1989). Invertebrate organisms feed or shelter in the algae, and they represent the greatest food resource for most reef fishes (see chapter 13). Many epibenthic species that do not directly seek shelter in the reef are pickers or winnowers of this resource (Laur and Ebeling, 1983), and nocturnal planktovores feed on zooplankton that emerges from the substrate at night (Ebeling and Bray, 1976; Hobson and Chess, 1976). Reef structure also affects water currents, concentrating planktonic organisms and making them more available to midwater feeders (Bray, 1981). Other species that reside on the reef may feed on adjacent soft substrate (DeMartini et al., 1994). The reduction in prey density in fringing areas may force longer feeding migrations by these residents. Finally, the presence of abundant and diverse reef fishes allows their exploitation by meso- (primarily *Paralabrax* and species of *Sebastes*) and macrocarnivores (largely elasmobranchs, white sea bass, lingcod, giant sea bass, and groupers). The importance of macrocarnivores to this system is poorly understood (Pondella and Allen, 2000) and may be highly modified due to fishing pressure.

The nesting site is most often identical to the shelter site, especially for small cryptic or territorial species (gobies, blennies, kelpfishes, ronquils, pricklebacks, gunnels, clingfishes, and sculpins). Of the larger reef species, most are water-column spawners (basses and groupers, chubs, croakers, grunts, etc.) or viviparous (surfperches and rockfishes) (see chapter 24). Some larger species also have demersal eggs and usually parental care, i.e, damselfishes, toadfishes, wolffish, sculpin (*Scorpaenichthys*), and greenlings, many of which nest at their shelter sites like the smaller species.

Roles of Reef and Kelp in Recruitment and Survival of Young-of-Year Fishes

Recruitment of fishes to rock reefs and associated kelp beds may occur in a number of ways, although the mechanisms are not clearly understood for most species. Most commonly, passive drift may carry late larval stages to the reef vicinity, where settlement takes place (Cowen, 1985). In other species (perhaps chubs, giant kelpfish, or rockfishes), actively swimming late larvae or pelagic juveniles may follow gradients in perceptual cues or internal waves to the reefs. In still other species, larvae produced on the reef may have behavioral mechanisms to retard the drift process, keeping them in the general area for subsequent settlement (Marliave, 1986; Stevens et al., 1987). In the case of livebearers such as embiotocids, the relatively mature young-of-year are born on the reef occupied by the adult. In other species, individuals migrate to the reef from other places where they settled or were born. Shiner perch, *Cymatogaster aggregata*, exhibit this behavior.

Once young-of-year individuals have established residence on the reef, survival depends on their behavioral abilities and the protection supplied by the reef, kelp, and epibenthic cover. Two interesting differences have been noted in settlement: some species settle primarily to sites occupied by conspecifics (bluebanded goby; Steele, 1997), whereas others settle in habitats in the reef/kelp region that are not occupied by adults of that species and then migrate later to adult habitats. The distributions of postlarval, settled fishes is likely to be a combination of habitat selection by the fish and postsettlement mortality. Habitat selection seems clear in some species.

Kelp seems to play a role in settlement of some species associated with a reef/kelp habitat. Carr (1989) reported selective settlement of late larval kelp bass to kelp fronds at Santa Catalina Island in the Southern California Bight, followed by movement of settled young-of-year to the rock reef. Several species of rockfish (kelp, black-and-yellow, gopher, and copper) also seem to settle preferentially in the kelp canopy, at least when a canopy is available (Hoelzer, 1988; Carr, 1991; Nelson, 2001). However, although species such as kelp bass and these rockfishes do seem to use kelp when it is present, the consequences of a large-scale lack of kelp are still not clear. For example, in the absence of kelp at King Harbor, Redondo Beach, young-of-year kelp bass recruit to the intertidal portion of the breakwater and subsequently move to the breakwater base where they associate with patches of foliose algae. These territorial young-of-year may hold position for many months, later forming aggregations of subadults, which may emigrate. In cases such as this, it would be interesting to compare the number of larvae that initially settle in areas with and without kelp (within the range of perception and choice for settling fish) and the subsequent survival of those that settle in alternative conditions.

Settled juveniles of many other species show restricted habitat distributions. Rockfish show a number of specializations in habitat (Carr, 1991; Love et al., 1991). Many young-of-year fishes occupy warm shallow tidepools at settlement (opaleye, black perch, pile perch, and zebraperch) and subsequently develop preferences similar to those of adults, leaving the pools for their subtidal habitat and exhibiting ontogenetic shifts in temperature selection (Norris, 1963; Schrode et al., 1982; Ehrlich et al, 1978). A more in-depth discussion of these processes is presented in chapter 15.

Activities of Fishes in Reef Habitats

Residency, Seasonality, and Movement of Kelp/Reef Fishes

Temperate reefs have a greater seasonal component of productivity than tropical reefs, which affects the structure and continuity of the fish assemblage. Additionally, whereas coral reefs are generally isolated habitats, sublittoral rocky reefs may extend for miles with little habitat break. These two factors should affect the way species occupy temperate reef habitats (Ebeling and Hixon, 1991). Unfortunately, these aspects of reef fishes are not well described for California fishes because most communitywide studies are carried out once a year. An alternative concept would describe reef assemblages as temporary assemblages with many key species moving between reefs and along the coastline searching for food and shelter and remaining at a site only as long as habitat quality is sustained. In such a model, the genetic structure of such populations should not reflect local specializations, and the assemblage should be bounded by regional physical gradients and the physiological limits of its component species within the limits of their ecological flexibility. Movements by adults may supplement larval drift, producing panmictic California fish populations. The limited population genetic work on California reef fishes may support this premise (Halderson, 1980; Beckwitt, 1983; Tranah and Allen, 1999; Bernardi, 2000).

Much of our knowledge of reef fish biology is based on information from coral reef fishes (reviews by Ehrlich, 1975; Sale, 1991). Our early (1950–60s) ideas of assemblage interactions, territoriality, recruitment, and stability are centered on these data because little work in temperate communities was available. Temperate rocky reefs or kelp beds are known primarily from summer–fall studies (Ebeling and Hixon, 1991). But as "seasonality increases from the tropics . . . through the cold temperate zones, the stronger seasonal variation in the higher latitudes elicits greater, albeit predictable, responses in the reef fish assemblages" (Ebeling and Hixon, 1991). What can we infer is occurring in these fish assemblages during the colder, less productive months? The major question regarding temperate assemblages is, "What response does the assemblage have to seasonal changes in productivity and climate?" Do assemblage members modify their behavior to cope with these regular occurrences (e.g., change their diets; Love and Ebeling, 1978), or do they search for more favorable sites?

To illustrate the difficulty and magnitude of this problem, consider sportfishing data from isolated reefs such as Naples Reef (off the Santa Barbara coast) and power plant entrapment data from the well-studied system of King Harbor, Redondo Beach. In both systems, hundreds to thousands of fishes are removed annually. Yet these reefs maintain high standing stocks and easily outperform other reefs in fish abundance. To attempt to address this problem, from 1975 through 1977, we (Stephens et al., unpublished data) tagged more than 2000 fish of 34 species captured in fyke nets set along the King Harbor breakwater. Tagged fish were released adjacent to the capture site. We recorded sightings of tagged fish along the breakwater as well as returns and losses to intake entrainment. Diver sightings of tagged fishes diminished rapidly; few fishes were sighted after 4 months and only one fish at 7 months. Loss to entrainment occurred rapidly (usually within a few days of tagging), whereas fishers recaptured fish up to 14 months later (Stephens, unpublished data). No significant movements were recorded in these data, but the absence of tagged fish suggested movement off the breakwater site or tag loss. Similarly, DeMartini et al. (1994) tagged fish on an isolated artificial reef off Del Mar to follow growth patterns in an 8-month study (April–November 1989). The observed median period at liberty for tagged fish was 6 months. Certainly some fishes are residents on reefs (Clarke, 1970; Larson, 1980; Hixon, 1981; Lea et al., 1999; Lowe et al., 2003). However, if studied at all, the residence of most fishes has not been tracked for long periods of time and certainly not for their entire life spans or over large spatial areas, leaving this as an important aspect of future studies (chapter 20).

One possible explanation for these processes is that fishes move based on "ideal free distribution" (MacCall, 1990). As resources in an "ideal free distribution" decrease, fish should search for increased "habitat quality." Similarly, as fish are removed from a system with high resource value, one might expect movement onto the reef from less valuable habitats. This theory may explain why loss of fishes at relatively high rates from Naples Reef and King Harbor does not elicit drastic decreases in abundance. Perhaps these fishes are quite mobile, and these observations indicate linkage along the lines of metapopulation theory.

Seasonal changes in fish assemblages have rarely been studied in temperate regions due to poor scuba study conditions in winter and spring (Ebeling and Hixon, 1991). Thus we have limited knowledge of the seasonal movements of rocky reef fishes, and this is summarized in chapter 21. In addition to seasonal movements, fishes have daily activity cycles that are genetically encoded. These cycles are entrained by light intensity and/or tides (Wooton, 1990; Thorpe, 1978). On subtidal reefs, most species are either diurnal or nocturnal, although activities such as feeding may be enhanced during crepuscular periods. Temperate species show less specialization than tropical assemblages for activity periods, though tropically derived taxa such as wrasses and damselfish show remnants of these specializations. There are fewer nocturnal teleosts on our temperate reefs and many elasmobranchs are nocturnal. Daily activity cycles are largely associated with feeding strategies (see chapter 13). The reef is a dynamic place as we move through nocturnal, diurnal, and crepuscular periods; chapter 21 discusses these processes.

Interannual Variability of Reef Fish Assemblages

Few long-term studies of interannual variability in reef/kelp fish assemblages have been carried out. The longest such study is that of Hobson at Catalina Island, which began in 1973 as an annual survey and still continues. Unfortunately, however, an analysis of this long-term data set has not been published. The surveys at King Harbor and Palos Verdes Point by Stephens and colleagues began in 1974 and include a continuous series of quarterly transects by depth as well as monthly larval samples, recruitment and young-of-year surveys, and cryptic fish samples. This continuing 28-year study is the baseline for assemblage variability in southern California (Stephens and Zerba, 1981; Stephens et al, 1984, 1994; Holbrook et al., 1994, 1997; Holbrook and Schmitt, 1996; Pondella et al., 2002; Stephens and Pondella, 2002). Although fish recruitment and mortality are critical factors for understanding the population dynamics of reef fishes, temperature and productivity appear to be important driving factors in these processes. The King Harbor and Palos Verdes studies began near the end of the cool cycle of the Pacific decadal oscillation (PDO) (Hare and Francis, 1995; Mantua et al., 1997) which began in 1946 and ended in 1976 to 1977, in concert with the small ENSO event in 1977 to 1978. A warm phase of the PDO occurred subsequently, although it may have ended in the mid to late 1990s (Chavez et al., 2003). As of 2004, King Harbor data had not yet shown a faunal shift associated with the return of cooler temperatures. However, the fish assemblage did undergo a major faunal shift correlating with the shift from a cool to a warm regime in 1977 (Stephens and Zerba, 1981; Stephens et al., 1994). Two dominant planktivores, *Sebastes mystinus* and *Cymatogaster aggregata,* disappeared or became rare with this temperature shift, and species of the largely tropical wrasses (Labridae), damselfishes (Pomacentridae), and sea basses (Serranidae) became more important members of the assemblage. During the early 1980s, the increase in warm temperate fishes reached a maximum, and the great El Niño of 1982 to 1984 affected the densities of many species. Since the mid 1980s, there has been a general decline in reef fishes (Stephens et al., 1994). This decline is observed in larval abundance (Stephens and Pondella, 2002) as well as in adults (Holbrook et al., 1997; Brooks et al., 2002).

Although the density of many species changed significantly in the last three decades, the overall density and species richness of the assemblage has shown no long-term trends. The assemblage at King Harbor had a significantly higher number of species and species per transect in five fully sampled years prior to 1980, during the cold-water period and transition, than after 1980, but the decline was a stepwise change with the advent of the warm cycle (Holbrook et al., 1997). After 1980, no trend was apparent. At Palos Verdes, no trend is apparent from the onset of the studies. This suggests that there was some overall consistency in the "community" even with major changes in the densities of individual species, and this might suggest that the assemblage was operating at close to its biotic potential. One problem with many "long-term" data sets is that they rarely include more than a few species of interest. In that case, decreases in species densities, which may represent normal decadal variability, may be interpreted as a decremental trend. Data on "core teleosts" from King Harbor and Santa Cruz Island (Holbrook and Schmitt, 1996) show such a decrease from 1985 to 1992. That same data set prior to 1985 would have shown an increasing or stable assemblage, and since 1992 to 2001, would also appear relatively stable, whereas data for the whole period appear stable after about 1980 (20+ years).

Brooks et al. (2002) analyzed the above data sets as well as impingement data from southern California Edison's coastal electric generating plants to see if fish declines noted between 1977 and 1993 were consistent across trophic levels, modes of reproduction, extent of geographic range, benthic versus pelagic food webs, and habitat. They found strong concurrence in these data and relate the declines to a productivity shift that began in 1977. Productivity would also explain the decline in larval abundance during the same period (Stephens and Pondella,

2002) and a decline in juvenile survivorship of surfperches (Pondella et al., 2002). Brooks et al. (2002) suggest that only a regime-change reversal would be expected to change this pattern. Such a change is apparently occurring as young-of-year surfperch are increasing at their study site as well as in King Harbor (A. Brooks personal communication; D. Pondella unpublished data). This hypothesis will be tested with the continued progress of these research programs. The changes reported here underscore the necessity of continued long-term monitoring.

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