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CHAPTER 20

Movement and Activity Patterns

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Introduction

Few aspects of fish behavior have been of greater interest to humans than movement and activity patterns. The rapid increase in our knowledge about where fish go and why has transformed us into the most efficient predator in the marine environment. At first, knowledge of movement and activity patterns of marine fishes was essential for human subsistence, but over time this information became vital to development and economic growth of nations. Unfortunately, a little knowledge can be a dangerous thing. Along with the rapid development in fishing technology, this knowledge of movement and activity patterns has resulted in over-harvesting of many marine fish species and has even led to wars between countries (Kurlanski, 1997; Parrish, 1999). On the other hand, this information can be valuable for fisheries management. For example, information on temporal and spatial aspects of spawning aggregations can be used to prevent excessive harvesting of species at a time and location where they may be most vulnerable. Knowledge of fish movements is essential to understand and model stock structure and design marine reserves, yet obtaining this information poses many challenges.

Nevertheless, from an academic standpoint, knowledge of fish movement and activity patterns may offer unique insight into the ecological role fish play in marine ecosystems. Understanding the mechanisms behind the drive to move, orient to environmental and social cues, or regulate where fish go and when, is essential for quantifying fish population dynamics, community structure, and distribution. Understanding these mechanisms can also be beneficial in understanding how these behaviors have evolved as well as how these patterns have influenced form and function in marine fishes.

What defines a movement pattern in fishes? In order to contemplate the ultimate (evolutionary) mechanisms behind why and when fish move, one must first understand the proximate (causatory) mechanisms that enable fish to exhibit these movement patterns. Most fish movements are directed or intentional, and thus require the fish to orient to some environmental or social cue. Fish use a variety of sensory information to detect and orient to these cues; however, basic orientation does not require the fish to travel anywhere. Nevertheless, in many cases, orientation to some cue provides the means by which a fish can make a directed movement (e.g. patrol its home range, follow prey, guard its territory, and migrate).

In addition, there are spatial and temporal components to fish movements that can vary considerably over geographical area and time span, and a wide variety of abiotic and biotic factors can affect these components. While almost all fishes exhibit some degree of ontogenetic shift in space utilization as they mature, as adults the degree of movement or area used may vary depending on the species and location. For example, some fishes such as gobies are highly residential and may not move more than a few meters over the course of their adult lives, whereas highly migratory fishes such as salmon shark (*Lamna ditropis*) or blue shark (*Prionace glauca*) may move thousands of kilometers in a single season.

The timing of movements or activity patterns may vary considerably among fish species as well as individuals. While most biological cycles in fishes are regulated or maintained by exogenous cues such as light, lunar phase, tide, salinity or temperature, some deepwater fishes live in habitats where these cues are greatly reduced or absent. Do they exhibit rhythmic patterns of activity, and if so, how do they keep time? Other fishes such as lie-and-wait or opportunistic predators may apply a more energetically conservative approach to movement and only become active if prey are present. Obviously, there are plenty of examples of fishes that exhibit activity patterns over daily, monthly, or seasonal time scales. In some cases the timing of movements of fishes is relatively fixed and tightly programmed, such as in seasonal spawning migrations, while other movement patterns such as those related to feeding may be more plastic due to variations in availability of food or presence of predators.

Variations in movement and activity patterns can occur over broad temporal and spatial scales among individuals of the same species. Some individuals of the same species show little movement, while other individuals are more transient. This intraspecific variability may explain much of the long-range dispersal events for some species in California waters, particularly during El Niño periods. Some individuals may exhibit high site fidelity and specificity for part of their life, but then exhibit a radical change in home range due to competition, decline in habitat quality, or increase predation pressure. Much of the variation in these types of behaviors for species presumably has been shaped through selection as the result of trade-offs between feeding, reproduction, and predation risk (Covich, 1976; Pyke, 1983).

To begin to understand the evolution of these behaviors and the mechanisms that affect the movement and activity patterns of marine fishes, one might start by asking the question—why do fish move at all? From an energetic standpoint, movement is costly and therefore should not be exhibited unless there is some intrinsic value to the fish. Considering the rich diversity of marine fishes in California waters and the variety of ecosystems and communities they inhabit, it becomes obvious that there is a great and varied need for fish to move. In this chapter we will address methods for quantifying movement and activity patterns of California marine fishes and discuss some of the proximate and ultimate mechanisms that may have led to the evolution of these behaviors.

How Can You Quantify Where Fish Go and When?

Our knowledge of the movement and activity patterns of marine fishes has grown rapidly over the last few decades due to advances in technology. The development of new tools and techniques has expanded our understanding of where fish go and when. However, there is still a lot we do not know and new technology is evolving to help answer questions about hard to study species. In order to understand what we really know about fish behavior, it is important to carefully examine the methods that are used to determine movement and activity. Certain methods may be useful in addressing questions about dispersal, but may be inappropriate or inadequate for answering questions about fish home range. In addition, there are often trade-offs between the number of fish that can be sampled and the quality of data obtained.

Fishing

Most of what we know about fish movement and activity patterns comes from fishing (or catch) data. Finfish have been systematically harvested from coastal waters for thousands of years. During this time, fishers have made careful observations of where and when they catch the most fish. The accumulation of these data over time has provided a vast knowledge base on when fish can be found in certain habitats and locations, as well as their activity periods. However, catch data are most useful in estimating spatial and temporal distributions of fishes and their dispersal over large geographical areas and time. For example, catch data from commercial fisheries in California have been used to determine geographic distributions of many fish species (Miller and Lea, 1972).

However, like many methods, catch data can also be ambiguous and misleading due to inherent biases in the method. The main limitations of this method are attributed to issues related to catchability, size selection, and data collection accuracy. For example, just because a fisher does not catch any fish at a particular location does not necessarily mean that there are no fish there. It is possible that fish are present, but may not be caught using that particular method. Thus, without being able to physically detect the fish at that time, one might conclude that there are no fish there at all. It is also possible that the method of fishing being used is size selective and may not allow for catch of a certain size. This may be common with hook and line or gillnet fishing methods, which tend to select for larger fish and may lead to the conclusion that juveniles are not present in that habitat. Because most catch data are fishery-dependent (generated by commercial and sport fisheries), landings and catch locations are provided by fishers who may not be forthcoming in revealing their favorite fishing spot. As a result, positional information on fish catch may be lacking in accuracy, therefore further reducing the resolution of the method for determining movement patterns. In addition, commercial and sport fishers are very good at optimizing take, which results in biased sampling. However, fishery derived catch data have been calibrated by using scientific fishing methods. Scientific fishing generally employs the same types of fishing techniques and gear as used by commercial and sport fishers, but uses controls and random sampling techniques to more fairly assess fish distribution and abundance.

When coupled with tagging or marking of fish, catch data can yield important information on growth, size distribution, mortality, dispersal rates and distances. Marking fish to quantify their movement patterns started as early as the 1600s and tagging methods have varied widely over the years (McFarlane et al., 1990). Large-scale tag and release programs in California for highly mobile pelagic species such as tunas, billfishes, and sharks have yielded important information about dispersal and migration, particularly in relation to their movement across Economic Exclusion Zones (EEZ) (Laurs and Lynn, 1977). Most tagging studies require tagging large numbers of fish to ensure a sufficient return rate. In some cases there are intense fisheries that increase the rates of recapture of target species and facilitate the collection of data. The International Pacific Halibut Commission (IPHC) has been tagging Pacific halibut (*Hippoglossus stenolepis*) in the Bering Sea since 1925, tagging over 350,000 and recapturing 35,000 fish as of 1990. This 60 year tagging program has demonstrated that juvenile Pacific halibut disperse farther than adults and that mature fish annually migrate thousands of kilometers from spawning to feeding grounds (Trumble et al., 1990). In addition, tagging studies of kelp bass (*Paralabrax clathratus*) in southern California have shown increased dispersal distances for juveniles and greater site fidelity of adults (fig. 20-1) (Collyer and Young, 1953; Young, 1963). As a general rule, most fish tagging programs exhibit recapture rates of 3–10%, which suggests that a lot of fish must be tagged in order to obtain enough data to quantify movements.

Caution must be used when interpreting tag and recapture data. First, tag and recapture data only indicate where the fish was tagged and the location it was recaptured. In many tag and recapture studies, a large percentage of the recaptured fishes are found close to the location where they were originally tagged. One might assume from these findings that the fish do not travel far, and thus may have a small home range. It is also possible the fish had traveled thousands of kilometers, but returned to the site of initial capture. This brings about another important point about the ambiguity of catch data. Some fish may be more susceptible to capture during certain seasons, and thus may be more likely to be caught in one location even though they used other areas where they are not caught. This also influences the effectiveness of tag and recapture as a tool to examine dispersal or migration due to effects of catchability.

Second, there are other experimental artifacts of tag and recapture studies such as tag retention, physiological and behavioral impacts from catch and handling, effects of the

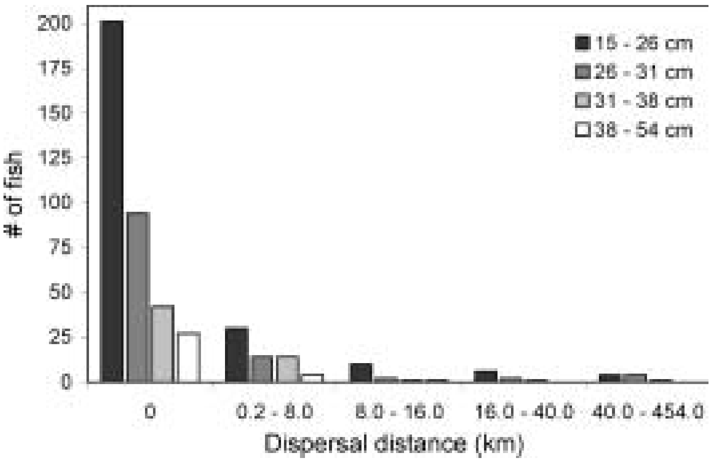

FIGURE 20-1 Dispersal distances of four size classes of kelp bass, *Paralabrax clathratus*, tagged with standard identification tags at Santa Catalina Island. After Young (1963, p. 361).

tags themselves, and underreporting of recaptured fish—all of which can influence estimates of movement patterns. Therefore, tag and recapture studies should be preceded with preliminary tag retention and growth effect studies to determine how often tags might be shed by fish and to quantify the effects of tagging on the fish's health. Lack of participation by fishers can also hamper data collection. Many fishers may be reluctant to turn in tags for fear that additional information may result in more restrictions on the fishery. Catch data, and tag and release studies have been the largest sources of information about movement and activity patterns of fishes, despite their lack of spatial and temporal resolution and the impact it has had on many populations.

In Situ Monitoring

Aside from catch data, few other methods have provided more detailed information on behavioral patterns of fishes than *in situ* observations made via snorkeling, scuba, remotely operated vehicles (ROVs), or manned submersibles. Early direct observations of fish behavior were made from the surface along coastal habitats such as tide pools, lagoons, and shallow coral reefs. The development of scuba in the 1950s provided fish biologists with a powerful tool for directly observing fishes underwater. Scuba allowed researchers to observe the types of habitats fish use, how they interact with other fishes, and how and when they feed and mate. For example, most of what we know about California reef fish behavior comes from scuba studies. Although scuba has provided more resolution and fine-scale information on fish movement and activity patterns, this method is limited to shallow waters (<30 m) and short observation durations (1–2 hour dives). Another logistical problem with scuba diving involves poor water conditions (cold, turbid water, surge), especially north of Point Conception (e.g., studies of the blue rockfish, *Sebastes mystinus* by Hobson and Chess, 1988). Study sites are understandably selected for their optimal diving conditions and we know far less about fish activities in less hospitable areas. These logistical problems were humbly summarized by Ebeling and Hixon (1991). In addition, there is some evidence that fish behavior is influenced by diver presence (Stanley and Wilson, 1995; Kulbicki, 1998) and nighttime observations may be problematic due to the use of lights and more restricted vision. Research divers have always strived to increase the amount of time they could spend underwater observing fishes; however, the dive time is greatly limited by air supply and nitrogen gas accumulation in the blood and tissues of the diver. A valuable diving system that was available in the mid 1980s at the Wrigley Marine Science Center at Santa Catalina Island involved surface-supplied tether gear, which provided divers an unlimited supply of air, voice communication, warm-water circulation, and a decompression bell. This system enabled prolonged bottom time for various projects involving reef fish (e.g., Bray et al., 1988). To provide divers even more observation time, several underwater research laboratories (SeaLab, Habitat, Hydrolab) have been established over the years that allow divers to live underwater and make longer dives at deeper depths without the burden of daily decompression. By placing these underwater laboratories on coral or rocky reefs, researchers have been able to monitor fish behavior over longer periods of time (Johnson and Ruben, 1988). Nevertheless, some fishes are more wary of divers, who tend to be noisy due to exhalation of bubbles and equipment. Recent developments in rebreather diving technology have increased the amount of time a diver can spend underwater observing fishes by more carefully regulating the mixture of gases the diver breathes at different depths, allowing divers to venture significantly deeper (~150 m). Most importantly, this technology seems to be less disturbing to many fishes and allows divers to get closer to hard-to-study species because there are no exhalation bubbles (Pyle, 1996; Lobel, 2001; Pyle, 2001).

Direct observations of deepwater fishes have come from ROVs and manned submersibles (e.g., PISCES subs), which can go to much greater depths and allow researchers to observe fishes for longer periods of time than standard scuba will allow. These studies have provided some of the first detailed observations of fishes rarely seen alive. Video collected during dives can be archived and reviewed by others at later dates and provide a hard record of observations, not always afforded by diver observations. The use of parallel laser sights attached to cameras can be used to quantify lengths of fishes being observed. Much like diver observations, ROVs and submersibles also are likely to influence fish behavior particularly because bright lights are often needed to see fish in the deep sea. It is possible that the light might attract or repel fish, thereby reducing the effectiveness of this technique for assessing whether fish are normally present in the habitat or not. Because of the relatively short durations of dives and the high cost of this type of deepwater research, determining movement and activity patterns of deepwater fishes using direct *in situ* observations is logistically more difficult than for shallow water species.

Coupling of direct observations with tagging studies can greatly facilitate data collection on movement patterns. For example, Matthews and Reavis (1990) tagged rockfish underwater and used diver surveys to subsequently look for tagged fish. Tagging fish underwater reduces barotrauma and handling stress that may result in high mortality rates and lower recapture rates (Parrish and Moffitt, 1992; Adkison et al., 1995; Starr et al., 2000). In addition, surveying for tagged fish via scuba allows for multiple visual recaptures and more accurate descriptions of the recapture location can be made. Using this technique, Matthews and Reavis (1990) found significantly higher recapture rates (48%) compared with other conventional tagging studies on rockfish (~2–3%) and that the rockfish species they observed showed relatively high site fidelity and the ability to home after being displaced up to 6 km away. The main limitations of this technique are that it can only be done over small geographical areas and the method may not be feasible for highly mobile species that have large home ranges. Even by combining methods of tag and recapture and direct observations, there are still problems with resolution of position and influences on behavior from the presence of a diver, ROV or submersible. Another technique used for direct observation that is growing in popularity is the use of remote cameras that can be fixed and camouflaged on the substratum. These cameras can use time-lapse photography to sample fishes in the vicinity or video cameras can be used to record movements and activity. These cameras have an advantage in that fish habituate to their presence, whereas they may not to a diver or ROV. These cameras are generally limited to daylight hours when ambient light is available, but CCD chip cameras sensitive to infrared and visible light, coupled with infrared illumination at night, may represent a significant breakthrough in the study of fishes at night, at least at close range (Holbrook and Schmitt, 1999).

Remote Sensing Techniques

Because methods such as fishing and resulting catch data are limited in spatial resolution and *in situ* observations are limited in duration and by influences of the technique on the fish's behavior, there has been a need for less intrusive, more accurate means of quantifying fish movements. The development of remote sensing techniques to monitor fish movements underwater has been promoted largely due to the shortcomings of these other methods. A variety of remote sensing technologies have evolved over the last 50 years, including sonar, LIDAR, radio and acoustic telemetry.

SONAR

The earliest form of remote sensing technology came in the development of sonar as a way to monitor the location and movement of fishes (MacPhee, 1988). Sonar uses a pulsed acoustic signal ranging from 12–500 kHz produced from a hydrophone attached to a boat to detect objects of differing densities in the water column or on the seafloor. Because fish possess tissues that vary in density compared with seawater, some of the pulsed sound signals that hit the fish get reflected back to the boat. The electronics of the sonar can determine how far away the fish is from the boat and where the fish is relative to the seafloor (fig. 20-2a). Sonar systems have become so sophisticated that researchers (and fishers) can now identify fish to species and approximate size based on the acoustic signal that is reflected back to the boat. High-resolution sonar (e.g., side-scan, scanning, and multi-beam sonar) has been used to track schools of fishes and even determine swimming speeds of large individuals (Harden-Jones, 1973). In addition, these types of sonar can be used to count fish as well as monitor their movements through the water column. Sonar has been used to monitor the vertical movements of fish relative to prey, thermocline, or deep scattering layer (Robinson et al., 1995; Stanley and Wilson, 1995). This method is most useful in monitoring an entire school of fish, but is not very effective for monitoring movements of individuals.

LIDAR

Another technique similar in principle to sonar is the use of LIDAR (LIght Detection And Ranging) systems. These systems employ the use of a plane or helicopter-borne laser to shine a beam of light into the water and then measure the spectral characteristic and intensity of the light that is reflected back. LIDAR can be used to identify and follow fish that are found near the surface or in shallow water (<40 m) based on the light reflective properties of their skin (Gauldie et al., 1996) (fig. 20-2b). Much like sonar, this method is best for following schools of fishes and not individuals. In addition, it is expensive and is limited to fish found in shallow, clear water.

TELEMETRY

Telemetry is another method that can be used to quantify the movement and activity patterns of fishes. Unlike sonar and LIDAR, which detect the reflection of a sound or light signal off a fish, telemetry relies on detection of a radio or acoustic signal emitted from a transmitter attached to the fish. This technique enables monitoring of movements of an individual fish and provides better spatial resolution for geo-positioning, and therefore allows for determination of home range size, habitat utilization, and environmental preferences. Radio telemetry uses pulsed high frequency radio signals (MHz) as the carrier signal. Although radio waves readily pass through air and freshwater, they are rapidly attenuated in seawater. As a result, radio telemetry is not typically used for marine fishes. Acoustic or ultrasonic telemetry uses pulsed, lower frequency sound (12–250 kHz) as a carrier signal. Because lower frequency sounds attenuate less in seawater, acoustic telemetry offers the best application for marine fishes. Transmitters are usually attached to the outside of the fish but can also be surgically implanted into the musculature or body cavity (Holland et al., 1993; Holland et al., 1996; Meyer et al., 2000). Fine-scale geographical movement can be determined by following the acoustic signal generated by the transmitter attached to the fish (fig. 20-2c).

Due to the large, bulky size of early electronics, the first applications of acoustic telemetry were used for studying the movement patterns of large fishes such as sharks (Nelson, 1990). Much of what we know about diel movement patterns of blue sharks, shortfin mako sharks (*Isurus oxyrinchus*), Pacific angel sharks (*Squatina californica*), and leopard sharks (*Triakis semifasciata*) comes from acoustic telemetry studies (Sciarrota and Nelson, 1977; Standora and Nelson, 1977; Holts and Bedford, 1993; Ackerman et al., 2000). As the technology improved and electronics became miniaturized, studies on smaller species have ensued. Acoustic telemetry tracking has been used to quantify the diel movement patterns and home ranges of smaller nearshore fishes such as kelp bass and California sheephead (*Semicossyphus pulcher*)(Lowe et al., 2003; Topping, 2003), and monkeyface pricklebacks (*Cebidichthys violaceus*) (Ralston and Horn, 1986).

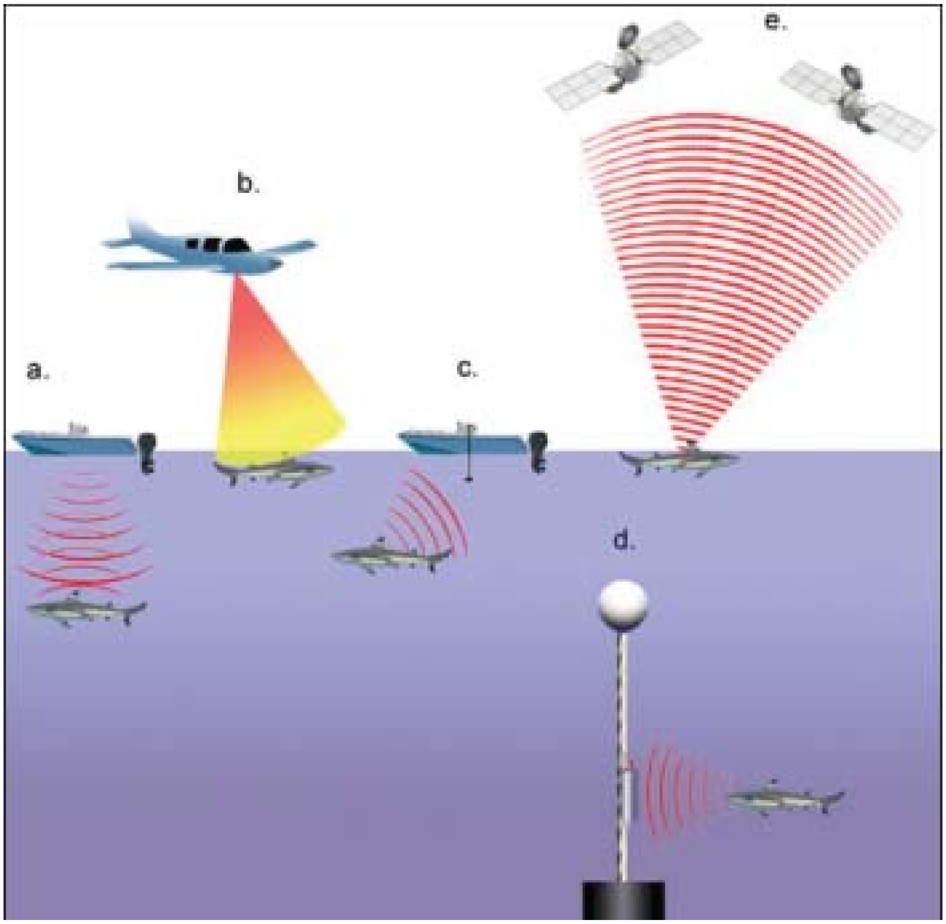

FIGURE 20-2 Depiction of remote sensing methods used to determine the movement patterns of fishes. Fig. 2a and 2b represent passive remote sensing methods, whereas fig. 2c–e represents active remote sensing methods based on whether the detection signal is generated from a device on or in the fish itself. (a) sonar, (b) LIDAR, (c) acoustic telemetry tracking, (d) acoustic telemetry monitoring, and (e) satellite telemetry. (Illustration by K. Anthony).

In addition, various sensors can be added to the acoustic transmitters that can relay information such as the fishes' depth in the water column, body temperature, heart rate, water temperature, tail beat frequency, and swimming speed (Lowe et al., 1998; Lowe and Goldman, 2001). By coupling these sensors with the ability to geographically position the fish, it is possible to examine movement patterns in three dimensions relative to environmental factors. For example, by using acoustic transmitters that sense depth and water temperature, researchers have found that blue and mako sharks spend most of their time swimming in the mixed layer of the water column, but occasionally dive through the thermocline (Sciarrota and Nelson, 1977; Holts and Bedford, 1993; Nelson et al., 1997) (fig. 20-3a). These movement patterns are very different than those observed for a megamouth shark (*Megachasma pelagios*) that was tracked by Nelson et al. (1997) off the coast of southern California. This shark remained relatively deep in the water column (~150 m) during the day, but moved to within 15 m of the surface at night (fig. 20-3b). Goldman (1997) fed acoustic transmitters with temperature sensors to adult white sharks (*Carcharodon carcharias*) at the Farallon Islands to monitor diurnal movement patterns and body core temperature. White sharks were found to maintain an average elevated body temperature of 29°C regardless of the ambient water temperature, providing direct evidence of endothermy in this species.

Although acoustic telemetry tracking has significantly increased our ability to quantify the movement patterns of fishes relative to their environments, this technique is very labor intensive and is restricted to short durations (few hours to a few days). The development of hydrophone arrays and acoustic transmitters with longer battery life has increased the duration of fish movement monitoring. Acoustic listening stations have been used to study site fidelity in fishes (fig. 20-2d). These stations constantly listen for fish that are carrying individually coded acoustic transmitters. As the fish swims by the listening station, it records the fish's identification code, the time and date that it was detected, and duration of the stay. By placing an array of these monitors around an area, it is possible to monitor larger-scale movement patterns and site fidelity. Coded transmitters allow for a large number of fish to be tagged and tags can last up to several years. Movement patterns and site fidelity of deepwater bocaccio (*Sebastes paucispinis*) and greenspotted rockfish (*Sebastes chlorostictus*) in Monterey Bay, California were determined over a 1–2 year period using an array of acoustic listening stations placed along the canyon (Starr et al., 2000).

Another derivation of this technology allows for more precise positioning of a fish within a given area, again using an array of hydrophones. By placing a triangle or polygon array of hydrophones on the seafloor and measuring the time it

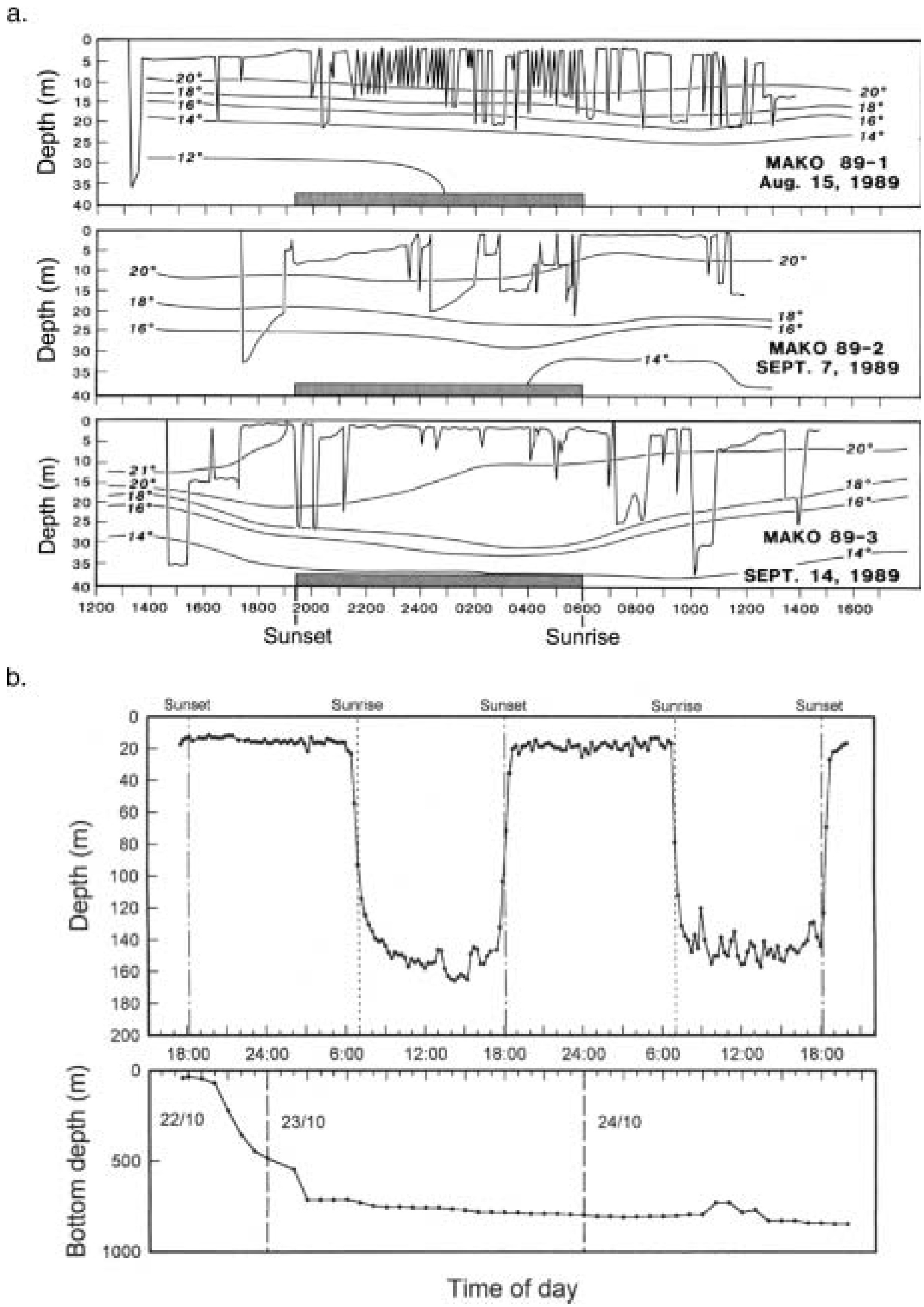

FIGURE 20-3 Vertical movement patterns of shortfin mako, *Isurus oxyrinchus,* and a megamouth, *Megachasma pelagios*, shark. (a) vertical movement patterns of shortfin mako sharks acoustically tracked in the southern California Bight. After Holts and Bedford (1993, p. 140). (b) vertical movement patterns of a megamouth shark acoustically tracked in the southern California Bight. After Nelson et al. (1997, p. 100).

takes for the acoustic signal produced by a transmitter within the array to reach each hydrophone, it is possible to determine the precise position of the fish (±1 m) within the array. This automated geographical positioning system is particularly useful in examining fine-scale movement patterns over relatively small geographical areas. For example, Ralston and Horn (1986) used a geo-positioning hydrophone array to examine tidal related movements of the monkeyface prickleback. Using this array, they found that these fish venture up into the intertidal zone as the tide rises, but then return back to their home rock after foraging. This system has also been used to monitor foraging and social behavior of white sharks around an elephant seal rookery (Klimley et al., 2001). A similar design has been used to look at movement patterns of abyssal rattails (*Coryphaenoides* spp.) attracted to a baiting station at 6000 m depth (Priede et al., 1991). While these systems have significantly reduced the labor involved in manual tracking, they are expensive and restricted to small geographical areas. If the fish moves outside the detection range of one of more of the hydrophones, it is not possible to derive a position.

Acoustic telemetry has greatly improved our ability to more accurately quantify movement patterns of fishes; however, it is still restricted for use in fine-scale, short-term movement patterns. This technology is not adequately suited for determining long-range migrations. Researchers have begun to develop and apply the use of satellite telemetry to quantify long-range movement patterns of highly migratory fishes. Satellite telemetry uses transmitters that emit radio signals to satellites, and because radio signals are quickly attenuated in seawater, satellite transmitters only work when they are at the surface. Although satellite telemetry has been primarily used on marine mammals and reptiles, it has been adapted for use on fishes by incorporating sensors that record light levels, depth, and water temperature. The transmitters have a data logger that records and summarizes the data, so that when the transmitter is at the surface the data can be downloaded to the satellite. However, the trick is getting the transmitter to the surface. Because very few species of fishes spend enough time near the surface to warrant the use of this expensive technology, researchers have developed timed-release mechanisms that allow the transmitter to be detached from the fish on a programmed time and date. The transmitter pops-up to the surface and downloads its information to a satellite (fig. 20-2e). Although these tags have provided long-term detailed data on the depth of the fishes and the water temperature they moved through, deriving accurate geographical positions has been problematic. In some cases, periodic positions are made when the satellites triangulate the position of the tag while the fish is at the surface (fig. 20-2e); however, those instances may be infrequent. Light levels recorded by the tag along with remote sensing oceanographic data can be used to position the fish. For example, it is possible to determine the latitude and longitude of the fish by accurately determining the times of sunrise and sunset. While these two measures can be used to determine longitude, by knowing the length of the daylight period (day length) at the tag location, it is possible to determine latitude. Unfortunately, using light levels to determine these parameters can be confounded as the fish swims deeper and light is attenuated or if water clarity changes. Nevertheless, this method can be effective in demonstrating large-scale movements (over hundreds or thousands of kilometers). Pop-up satellite transmitters (PSAT tags) have been used to characterize the migratory movement patterns of pelagic tunas, billfishes, and sharks (Block et al., 1998; Block et al., 2001; Boustany et al., 2002). This technology has greatly enhanced our ability to quantify migratory movement patterns of open ocean fishes. It is far less labor intensive compared to acoustic telemetry tracking and can collect data over longer durations; however, it is limited in application due to the size and expense of the transmitters and positional accuracy.

Genetic Techniques

Another way to examine long-range dispersal and movement patterns over longer time periods is through the use of genetic markers. Genetic variability among different populations of fish can be used as a means of determining whether two populations located in different areas emigrate. If the two populations are genetically dissimilar then it is likely there is little movement between the two areas. This does not necessarily mean that fish do not move between these two areas at all; however, it does suggest that movement between the two areas is very minimal and/or the fish that move between the two areas do not interbreed. This particular method is very beneficial in examining long-term stability of dispersal pattern.

A wide variety of methods and technologies have evolved to quantify movement patterns of fishes and new methods are constantly being introduced. Due to the limitations of many of these methods, more than one technique may be needed to answer a question about movement or activity patterns of a fish.

Spatial Patterns—Where Fish Go

One approach that can be used to understand the evolution of space use patterns of fishes is through the use of cost-benefit models. Because of the inherent costs of locomotion (e.g., in expended energy, increased threat of predation), one might expect the cheapest and easiest thing for a fish to do is to remain in one place and move very little. However, even though the fish may be sedentary and its metabolic costs minimal, there may not be enough food or mates nearby or possibly there may be too many predators to justify this strategy. In this case, the costs will likely outweigh the benefits (Covich, 1976; Pyke, 1983), and as a result, fish will move. A wide variety of space use patterns can be seen within and among species of Pacific coast fishes that range from little or no movement to long-range migration. While some fishes may exhibit little pattern in defined space use, others show clear space use patterns over a range of scales. In addition, all fishes exhibit some ontogenetic shift in space use patterns, resulting in a change in habitat or the amount of space used. These ontogenetic shifts are likely attributed to changes in cost-benefit ratios as the fish matures.

Home Ranging

The area a fish uses on a regular basis is typically defined as a home range (Mace et al., 1983). The size of a home range may vary with the size of the fish, water temperature, inter- and intra-specific competition, habitat composition and quality, food, shelter, and mate availability. It has been hypothesized that the home range size of an organism increases with its energetic demand (Mace et al., 1983), yet there are situations where using less area may be more beneficial.

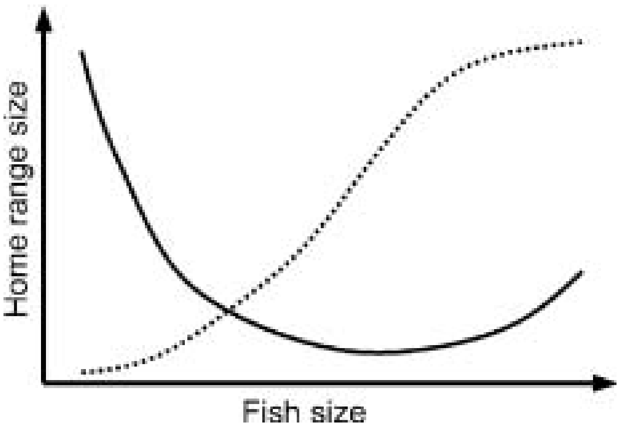

FIGURE 20-4 Cost optimization model of ontogenetic changes in home range sizes of territorial and non-territorial fishes. Dotted line represents predicted increase change in home range size with increase fish size of non-territorial fishes. Solid line represents predicted decrease change in home range size with increase fish size of territorial fishes.

In general, two cost-optimization models may explain ontogenetic changes in home range size observed in fishes, but they differ depending on whether or not the species is territorial. Non-territorial species might have small home ranges when they are young, but they might expand their home ranges as they get larger to accommodate greater energetic demands (fig. 20-4). This trend is likely reversed for territorial species, where juveniles often have large home ranges because they are too small to effectively defend their own territory and continuously get displaced by other territorial individuals. Eventually, they may get large enough to occupy and defend a small territory; and in many cases, these territories expand as the fish gets larger (fig. 20-4). These home range strategies have likely evolved to enable fishes to optimize energy intake based on the particular habitat type with which they may be associated.

High Relief Rock Substratum

From an ecological standpoint, complex habitats such as rocky reefs usually support a higher species diversity of fishes, due to the increased availability of substratum, shelter, and prey (Allen, 1985). Therefore, one might expect a large proportion of fishes that occupy these habitats to have small home ranges because of the greater availability of food and shelter (Barrett, 1995). In some cases, increased competition for limited resources in these small areas results in territorial behavior (Sale, 1971; Reese, 1973). While a territory is only that portion of the fish's home range that it will actively defend or exclude from other individuals, its territory size relative to the home range size may vary with competitor density, resource availability, or resource quality.

Many small, benthic, reef-associated fishes tend to exhibit small home ranges due to the availability of high quality essential habitat and resources (Sale, 1971). The blackeye goby (*Rhinogobiops nicholsii*) is commonly found at the interface between rock and sand substrata. These gobies have small home ranges and establish territories around primary shelters in the rock or holes in the sand. In a manipulative field study, Kroon et al. (2000) found that blackeye gobies had home ranges that varied in size from 0.01–1.18 m^2 and that larger fish usually held larger territories within their home range than do smaller individuals (table 20-1). Home range sizes decreased by 35% during breeding season. They found that if they removed a territory holder or added new habitat in the form of an artificial reef, the space was quickly recolonized by other blackeye gobies. Based on these findings, they concluded that suitable shelter habitat was limited. The importance of shelter habitat for blackeye gobies was further supported by a study done by Steele (1996) who found that predators such as kelp bass and barred sand bass impact blackeye goby survivorship by up to 75%. Thus, for the blackeye goby, home range size appears to be more constrained by the risk of predation rather than requirements for foraging. Therefore, it must be more beneficial to defend a good shelter than to move from area to area trying to find shelter along the way. In addition, the contraction of home range size during breeding season indicates a shift in the cost-benefit ratio towards more closely guarding nests versus increased foraging space, which suggests that food is not as limited as quality nest location.

While complex habitats offer more resources and thus increased species diversity, this higher diversity may also be accompanied by increased competition (summarized by Ebeling and Hixon, 1991). Therefore, competition between species may drive evolutionary changes in space use patterns. For example, two sympatric, closely related species of blennies, rockpool blenny (*Hypsoblennius gilberti*) and mussel blenny (*Hypsoblennius jenkinsi*), exhibit different space use patterns. Rockpool blennies typically inhabit the rocky intertidal and subtidal cobble, while mussel blennies are found subtidally and occupy *Serpulorbis* clam tubes and mussel beds. Stephens et al. (1970) found that rockpool blennies have a larger home range, moving up into intertidal areas (up to 15m) with the rising tide, whereas mussel blennies are territorial and rarely moved more than 1 m from their hole. Because rockpool blennies are the larger of the two blennies, it may have fewer shelters available to it in the subtidal area than mussel blennies, and/or may be less susceptible to predation by exploiting food resources found in the intertidal areas. It is possible that these behavioral differences in space use evolved as a way of reducing competition between these two species or may simply be adaptations to prey availability or predation pressure.

Some rock-associated territorial fishes have small home ranges, but defend area based on food availability rather than shelter quality. The black and yellow rockfish (*Sebastes chrysomelas*) and gopher rockfish (*Sebastes carnatus*) are two closely related species found in shallow water rocky reef habitats (Love et al., 2002). In a field study at Santa Cruz Island off southern California, Larson (1980) found that individuals of both species had restricted home ranges (3–15 m^2) (table 20-1). The smallest rockfish had the largest home ranges and were not territorial. The largest fish, however, held territories and had larger home ranges than smaller territorial individuals. Consequently, territorial fish found in areas of lower prey density tended to have larger home ranges. Larson (1980) concluded that these two species of rockfishes were likely competing for shelters in the areas where food was most abundant. Because these rockfishes are larger than the blackeye goby, they are less susceptible to predation, but have higher energetic requirements. In this case, home range size may have been more determined by food availability than the quality of the shelter.

Interestingly, while most demersal, rock-associated rockfishes probably have relatively small home ranges, not all are

TABLE 20-1

Movement and Activity Patterns of California Marine Fishes—Species Are Arranged Alphabetically by Family

Species	*Common Name*	*Family*	*Habitat*	*Movement Patterns*		*Other Activity*	*Source*
				Home Range	*Migrations*		
Xeneretmus latifrons	Blacktip poacher	Agonidae	Soft bottom			Nocturnal (GA,M)	(Allen 1982, Bond et al. 1999)
Albula vulpes	Bonefish	Albulidae	Soft bottom			Diurnal (U)	(Bond et al. 1999)
Anoplopoma fimbria	Sablefish	Anoplopomatidae	Soft bottom			No diel (GA,M)	(Allen 1982, Bond et al. 1999)
Atherinops affinis	Topsmelt	Atherinopsidae (Atherinidae)	Mixed			Diurnal (DO,GA)	(Hobson et al. 1981, Bond et al. 1999)
Leuresthes tenuis	Grunion	Atherinopsidae	Mixed		Tidal (SO,N)	Diurnal (U)	(Bond et al. 1999)
Rathbunella hypoplecta	Stripefin ronquil	Bathymasteridae	Rocky			Diurnal (U)	(Bond et al. 1999)
Porichthys myriaster	Specklefin midshipman	Batrachoididae	Mixed		Seasonal (OT)	Nocturnal (GA,OT, M)	(Fitch and Lavenberg 1975, Allen 1982)
Porichthys notatus	Plainfin midshipman	Batrachoididae	Mixed		Seasonal (OT)	Nocturnal (GA,M, OT)	(Allen 1982)
Hypsoblennius gentilus	Bay blenny	Blennidae	*Zostera* beds	>15 m radius (DO)		Diurnal (DO)	(Stephens et al. 1970, Bond et al. 1999)
Hypsoblennius gilberti	Rockpool blenny	Blennidae	Rocky, intertidal	15 m radius (DO)		Diurnal (DO)	(Stephens et al. 1970, Bond et al. 1999)
Hypsoblennius jenkinsi	Mussel blenny	Blennidae	Rocky	1 m (DO)		Diurnal (DO)	(Stephens et al. 1970, Bond et al. 1999)
Prionace glauca	Blue shark	Carcharhinidae	Open ocean (pelagic)	Nomadic	Ontogenetic, diel (AT), seasonal (TO, TR)		(Sciarrota and Nelson 1977, Tricas 1979)
Hydrolagus colliei	Spotted ratfish	Chimaeridae	Mixed			Nocturnal (OT, GA,M)	(Allen 1982)
Gibbonsia elegans	Spotted kelpfish	Clinidae	Rocky			Diurnal (DO,GA)	(Hobson et al. 1981, Bond et al. 1999)
Heterostichus rostratus	Giant kelpfish	Clinidae	Rocky, kelp			Diurnal (DO,GA)	(Hobson et al. 1981, Bond et al. 1999)
Chitonotus pugetensis	Roughback sculpin	Cottidae	Soft bottom			No diel (OT, GA,M,)	(Allen 1982)
Clinocottus analis	Woolly sculpin	Cottidae	Rocky, intertidal		Tidal (U)	Tidal (U)	(Love 1996)
Icelinus quadriseriatus	Yellowchin sculpin	Cottidae	Soft bottom			No diel (OT, GA,M,)	(Allen 1982)
Leiocottus hirundo	Lavender sculpin	Cottidae	Sand-rock ecotone			No diel (DO,GA)	(Hobson et al. 1981)
Leptocottus armatus	Pacific staghorn sculpin	Cottidae	Soft bottom			Nocturnal and tidal (GA)	(Tatso 1975, Love 1996, Bond et al. 1999)

Oligocottus maculosus	Tidepool sculpin	Cottidae	Rocky, intertidal		Tidal (SO,N,T)	Tidal (SO,N,T)	(Green 1971)
Orthonopias triacis	Snubnose sculpin	Cottidae	Rocky, intertidal			Nocturnal (U)	(Bond et al. 1999)
Ruscarius creaseri	Roughcheek sculpin	Cottidae	Rocky intertidal and subtidal			Nocturnal (U)	(Bond et al. 1999)
Scorpaenichthys marmoratus	Cabezon	Cottidae	Rocky		Ontogenetic (U)		(O'Connell 1953)
Symphurus atricauda	California tonguefish	Cynoglossidae	Soft bottom			Nocturnal (GA,M)	(Allen 1982, Bond et al. 1999)
Brachyistius frenatus	Kelp perch	Embiotocidae	Inshore, water column, kelp			Diurnal (GA, DO, AO)	(Bray and Ebeling 1975) (Hobson and Chess 1976, Hobson et al. 1981)
Cymatogaster aggregata	Shiner perch	Embiotocidae	Mixed		Seasonal (DO)	Diurnal (DO,GA)	(Hobson et al. 1981, Stephens and Zerba 1981, Shrode et al. 1983)
Embiotoca jacksoni	Black perch	Embiotocidae	Rocky subtidal		Seasonal (DO)	Diurnal (DO,GA)	(Ebeling and Bray 1976, Terry and Stephens 1976, Ellison et al. 1979, Hixon 1980, 1981, Bond et al. 1999)
Embiotoca lateralis	Striped seaperch	Embiotocidae	Bays, rocky subtidal			Diurnal (DO, GA)	(Ebeling and Bray 1976, Hixon 1980)
Hyperprosopon argenteum	Walleye surfperch	Embiotocidae	Inshore, water column			Diurnal (<60 mm SL), Nocturnal >60 mm SL (DO, GA)	(Ebeling and Bray 1976, Hobson and Chess 1976, Bond et al. 1999)
Hypsurus caryi	Rainbow seaperch	Embiotocidae	Rocky subtidal		Seasonal (DO)	Diurnal (DO, GA)	(Ebeling and Bray 1976, Terry and Stephens 1976, Ellison et al. 1979, Bond et al. 1999)
Brachyistius frenatus	Kelp perch	Embiotocidae	Inshore, water column, kelp			Diurnal (GA, DO, AO)	(Bray and Ebeling 1975) (Hobson and Chess 1976, Hobson et al. 1981)
Micrometrus minimus	Dwarf perch	Embiotocidae	Inshore, water column			Diurnal (DO,GA)	(Ellison et al. 1979)
Phanerodon furcatus	White seaperch	Embiotocidae	Inshore, water column		Seasonal (DO)	Diurnal (DO,GA,AO)	(Bray and Ebeling 1975, Terry and Stephens 1976, Ellison et al. 1979, Bond et al. 1999)
Rhacochilus (Damalichthys) vacca	Pile perch	Embiotocidae	Rocky subtidal		Seasonal (DO)	Diurnal (DO,GA)	(Ebeling and Bray 1976, Terry and Stephens 1976, Ellison et al. 1979)
Rhacochilus toxotes	Rubberlip seaperch	Embiotocidae	Rocky subtidal			Nocturnal (DO,GA)	(Ebeling and Bray 1976)
Zalembius rosaceus	Pink seaperch	Embiotocidae	Water column <10 m			Diurnal (GA,M)	(Allen 1982, Bond et al. 1999)
Fundulus parvipinnis	California killifish	Fundulidae (Cyprinodontidae)	Bays		Tidal (O,N)	Diurnal, tidal(O,N)	(Fritz 1975)
Acanthogobius flavimanus	Yellowfin goby	Gobiidae	Bays			Diurnal(U)	(Bond et al. 1999)
Clevelandia ios	Arrow goby	Gobiidae	Bays			Diurnal(U)	(Bond et al. 1999)
Gillichthys mirabilis	Longjaw mudsucker	Gobiidae	Bays			Nocturnal(U)	(Bond et al. 1999)

TABLE 20-1 (continued)

Species	Common Name	Family	Habitat	Movement Patterns		Other Activity	Source
				Home Range	Migrations		
Ilypnus gilberti	Cheekspot goby	Gobiidae	Bays			Diurnal(U)	(Bond et al. 1999)
Lepidogobius lepidus	Bay goby	Gobiidae	Bays			Diurnal(U)	(Bond et al. 1999)
Lythrypnus dalli	Bluebanded goby	Gobiidae	Rocky subtidal			Diurnal (DO,GA)	(Hartney 1989, Bond et al. 1999)
Lythrypnus zebra	Zebra goby	Gobiidae	Rocky subtidal			Diurnal (DO,GA)	(Hartney 1989, Bond et al. 1999)
Quietula y-cauda	Shadow goby	Gobiidae	Bays			Diurnal(U)	(Bond et al. 1999)
Rhinogobiops (Coryphopterus) nicholsii	Blackeye goby	Gobiidae	Subtidal and/cobble	0.01–1.18 m^2 (TO)		Diurnal (DO,GA)	(Hobson et al. 1981, Cole 1984, Bond et al. 1999, Kroon et al. 2000)
Anisotremus davidsonii	Xantic sargo	Haemulidae (Pristopomatidae)	Subtidal rock and sand			Nocturnal(U)	(Bond et al. 1999)
Xenistius californiensis	Californian salema	Haemulidae	Subtidal rock and sand			Nocturnal (DO,GA)	(Hobson and Chess 1976, Hobson et al. 1981, Bond et al. 1999)
Heterodontus francisci	Horn shark	Heterodontidae	Rock, sand, and kelp (benthic)	2148–17024 m^2 (AT)	17 km; ontogenetic, diel, seasonal (TO,TR, DO)	Nocturnal (AT,DO,AO)	(Nelson and Johnson 1970, Finstad and Nelson 1975, Strong Jr. 1989)
Girella nigricans	Opaleye	Kyphosidae	Rocky intertidal and subtidal			Diurnal (DO,GA)	(Ebeling and Bray 1976, Hobson et al. 1981, Bond et al. 1999)
Medialuna californiensis	Halfmoon	Kyphosidae	Water column, kelp			Diurnal (GA)	(Ebeling and Bray 1976, Hobson et al. 1981)
Halichoeres semicinctus	Rock wrasse	Labridae	Shallow rock and kelp (pelagic)			Diurnal (DO,GA)	(Hobson and Chess 2001)
Oxyjulis californica	Señorita	Labridae	Shallow rock and kelp (pelagic)		~500 m (TO)	Diurnal (DO,GA)	(Bray and Ebeling 1975), (Hobson and Chess 1976, Hartney 1996)
Semicossyphus pulcher	California Sheephead	Labridae	Shallow rock and kelp (epibenthic)	1000–23000 m^2 (AT)	Ontogenetic, diel (DO, AT)	Diurnal (DO,GA)	(Ebeling and Bray 1976, Cowen 1983, Hobson and Chess 2001, Topping 2003)
Alloclinus holderi	Island kelpfish	Labrisomidae (Clinidae)	Shallow rock			Diurnal (DO,GA)	(Hobson et al. 1981)
Paraclinus integripinnis	Reef finspot	Labrisomidae	Intertidal and shallow subtidal rock			Diurnal(U)	(Bond et al. 1999)
Carcharodon carcharias	White shark	Lamnidae	Coastal (epipelagic)	1.8–9.1 km^2 (AT)	4500 km (ST); ontogenetic, seasonal (TO)		(Goldman and Anderson 1999, Klimely et al. 2001, Boustany et al. 2002)
Mugil cephalus	Striped mullet	Mugilidae	Bays, nearshore surface			Diurnal(U)	(Bond et al. 1999)

Myliobatis californica	Bat ray	Myliobatidae	Sand/mud substratum (benthic)		Tidal, diel, seasonal (AT)		(Matern et al. 2000)
Chilara taylori	Spotted cusk-eel	Ophidiidae	Sand (benthic & epibenthic)		Diel (OT)	Nocturnal (DO,GA,M)	(Allen 1982, Hobson and Chess 1986)
Otophidium scrippsae	Basketweave cusk-eel	Ophidiidae	Sand (benthic & epibenthic)			Nocturnal (OT, DO, AO)	(Greenfield 1968)
Citharichthys sordidus	Pacific sanddab	Paralichthyidae (Bothidae)	Sand (benthic)			No diel(GA,M)	(Allen 1982)
Citharichthys stigmaeus	Spotted sanddab	Paralichthyidae (Bothidae)	Sand (benthic)		Seasonal (OT)	Diurnal (GA,M)	(Ehrlich et al. 1979, Allen 1982)
Citharichthys xanthostigma	Longfin sanddab	Paralichthyidae (Bothidae)	Sand (benthic)			Diurnal (U)	(Bond et al. 1999)
Paralichthys californicus	California flounder (halibut)	Paralichthyidae (Bothidae)	Sand (benthic)			No diel (GA,M)	(Haaker 1975, Allen 1982)
Hippoglossina stomata	Bigmouth flounder (sole)	Paralichthyidae (Bothidae)	Sand (benthic)			No diel (GA,M)	(Allen 1982)
Glyptocephalus zachirus	Rex sole	Pleuronectidae	Sand (benthic)			Nocturnal (GA,M)	(Allen 1982, Bond et al. 1999)
Lyopsetta (Eopsetta) exilis	Slender sole	Pleuronectidae	Sand (benthic)			No diel (GA,M)	(Allen 1982, Bond et al. 1999)
Microstomus pacificus	Dover sole	Pleuronectidae	Sand (benthic)		Ontogenetic (GA,M)	Diurnal (GA,M)	(Allen 1982)
Parophrys vetulus	English sole	Pleuronectidae	Sand (benthic)			Diurnal (DO,GA)	(Allen 1982)
Pleuronichthys (Hypsopsetta) guttulatus	Diamond turbot	Pleuronectidae	Sand (benthic)		Tidal (AO)	Diurnal, tidal(AO,GA)	(Lane 1975)
Pleuronichthys coenosus	C-O sole (turbot)	Pleuronectidae	Sand (benthic)			No diel (DO,GA)	(Hobson et al. 1981)
Pleuronichthys decurrens	Curlfin sole	Pleuronectidae	Sand (benthic)			No diel (GA,M)	(Allen 1982)
Pleuronichthys verticalis	Hornyhead turbot	Pleuronectidae	Sand (benthic)			Nocturnal (GA,M)	(Allen 1982)
Gambusia affinis	Mosquitofish	Poeciliidae	Bays (brackish)			Diurnal(U)	(Bond et al. 1999)
Chromis punctipinnis	Blacksmith	Pomacentridae	Shallow rock and kelp	~ 500 m (TO)	Ontogenetic, diel (DO,GA)	Diurnal (DO,GA)	(Ebeling and Bray 1976, Hobson and Chess 1976, Bray 1981, Hartney 1996)
Hypsypops rubicundus	Garibaldi	Pomacentridae	Shallow rock and kelp			Diurnal (DO)	(Clarke 1970)
Cheilotrema saturnum	Black croaker	Sciaenidae	Shallow rock and sand			Nocturnal(U)	(Bond et al. 1999)
Genyonemus lineatus	White croaker	Sciaenidae	Bays, sand (water column)			Diurnal (<100 mm SL) diurnal and nocturnal (>100 mm) (DO, GA, M)	(Allen 1982, Bond et al. 1999)

TABLE 20-1 (continued)

				Movement Patterns			
Species	Common Name	Family	Habitat	Home Range	Migrations	Other Activity	Source
Menticirrhus undulatus	California kingcroaker	Sciaenidae	Shallow sand (epibenthic)			Nocturnal(U)	(Bond et al. 1999)
Seriphus politus	Queen croaker	Sciaenidae	Sand/mud (epibenthic)		Ontogenetic, diel (DO,GA,M)	Diurnal (<100 mm), nocturnal (>100 mm) (DO,GA,M)	(Hobson and Chess 1978, Allen 1982, DeMartini et al. 1985, Bond et al. 1999)
Umbrina roncador	Yellowfin croaker	Sciaenidae	Shallow sand (epibenthic)		Diel (DO,GA)	Nocturnal (DO,GA)	(Hobson et al. 1981, Bond et al. 1999)
Thunnus alalunga	Pacific albacore	Scombridae	Open ocean (pelagic)	Nomadic	Ontogenetic, diel, seasonal (FO,TR)		(Laurs and J. 1977)
Scorpaena guttata	California scorpionfish	Scorpaenidae	Subtidal rock, sand			Nocturnal (GA,DO,M)	(Hobson et al. 1981, Allen 1982, Bond et al. 1999)
Cephaloscyllium ventriosum	Swell shark	Scyliorhinidae	Subtidal rock			Nocturnal (DO,GA)	(Nelson and Johnson 1970) (Tricas 1982)
Sebastes atrovirens	Kelp rockfish	Scorpaenidae (=Sebastidae)	Subtidal rock and kelp			Nocturnal (GA,DO)	(Ebeling and Bray 1976, Hobson and Chess 1976, Hobson et al. 1981, Bond et al. 1999)
Sebastes auriculatus	Brown rockfish	Scorpaenidae (=Sebastidae)	Shallow water, demersal	400–1500 m^2 (TO)	8 km (TO); ontogenetic		(Matthews 1990a)
Sebastes carnatus	Gopher rockfish	Scorpaenidae (=Sebastidae)	Shallow water, demersal (territorial) deeper than *S. chrysomelas*	2–10 m^2 (DO)	Ontogenetic (DO, GA)	No diel (DO, GA)	Ebeling and Bray 1976, Larson 1980, Hoelzer 1988)
Sebastes caurinus	Copper rockfish	Scorpaenidae (=Sebastidae)	Shallow water, demersal	10–4000 m^2 (AT, DO)	6.4 km (TO); ontogenetic, seasonal		(Matthews 1990a,b)
Sebastes chlorostictus	Greenspotted rockfish	Scorpaenidae (=Sebastidae)	Deep rocky reefs	0.58–1.6 km^2 (AT)	Ontogenetic (U)		(Love et al. 2002, Starr et al. 2002)
Sebastes chrysomelas	Black & yellow rockfish	Scorpaenidae (=Sebastidae)	Shallow water, demersal (territorial)	2–10 m^2 (DO)	50 m; < 1500 m (TO); ontogenetic	No diel (DO,GA)	(Ebeling and Bray 1976, Larson 1980, Hallacher 1984)
Sebastes dallii	Calico rockfish	Scorpaenidae (=Sebastidae)	Shallow subtidal rock, epibenthic			Diurnal (juveniles), nocturnal (adults) (GA,M)	(Allen 1982, Bond et al. 1999)
Sebastes diploproa	Splitnose rockfish	Scorpaenidae (=Sebastidae)	Recruit to drift kelp, deepwater (benthic)		Ontogenetic (GA,M)	Diurnal (juveniles), nocturnal (adults) (GA,M)	(Boehlert 1977, Allen 1982)

Sebastes elongatus	Greenstriped rockfish	Scorpaenidae (=Sebastidae)	Deep mud, cobble, rock			Diurnal (juveniles) nocturnal (adults) (GA,M)	(Allen 1982)
Sebastes flavidus	Yellowtail rockfish	Scorpaenidae (=Sebastidae)	Deep pinnacles (schooling, pelagic)	0.2–1.7 km (AT, DO)	22.5 km (TR), 3.7 km (AT)		(Carlson and Haight 1972, Pearcy 1992)
Sebastes jordani	Shortbelly rockfish	Scorpaenidae (=Sebastidae)	Water column			No diel (GA,M)	(Allen 1982)
Sebastes laevis	Cowcod	Scorpaenidae (=Sebastidae)	Deep rocky reefs			Diurnal (juveniles), nocturnal (adults) (GA,M)	(Allen 1982)
Sebastes maliger	Quillback rockfish	Scorpaenidae (=Sebastidae)	Shallow water, demersal	10–4000 m^2 (AT, DO)	6.4 km (TO); ontogenetic, seasonal		(Matthews 1990a, b)
Sebastes mystinus	Blue rockfish	Scorpaenidae (=Sebastidae)	Shallow to deep water, kelp, pelagic (schooling)	1.3 km	Ontogenetic, seasonal (DO,TO)	Diurnal(U)	(Miller and Geibel 1973, Bond et al. 1999)
Sebastes paucisipinis	Bocaccio	Scorpaenidae (=Sebastidae)	Deep rocky reefs	>12 km^2 (AT)	Ontogenetic (TR)		(Hartmann 1987, Love et al. 2002, Starr et al. 2002)
Sebastes rosenblatti	Greenblotched rockfish	Scorpaenidae (=Sebastidae)	Deep rocky reefs			Diurnal (juveniles), nocturnal (adults) (GA,M)	(Allen 1982)
Sebastes saxicola	Stripetail rockfish	Scorpaenidae (=Sebastidae)	Mud,cobble, (benthic, epibenthic)			Diurnal juveniles, nocturnal adults (U)	(Allen 1982, Bond et al. 1999)
Sebastes serranoides	Olive rockfish	Scorpaenidae (=Sebastidae)	Shallow water, pelagic, kelp/rock	800 m (DO,TR)	Ontogenetic (U)	Diurnal (<55 mm SL, inconsistent to 65 mm, nocturnal >65 mm)(DO,GA)	(Hobson and Chess 1976, Love 1980, Bond et al. 1999)
Sebastes serriceps	Treefish	Scorpaenidae (=Sebastidae)	Shallow rock			Nocturnal (GA)	(Hobson et al. 1981)
Sebastolobus alascanus	Shortspine thornyhead	Scorpaenidae (=Sebastidae)	Sand/mud substratum, deepwater (epibenthic)			Nocturnal(U)	(Bond et al. 1999)
Sebastolobus altivelis	Longspine thornyhead	Scorpaenidae (=Sebastidae)	Sand/mud substratum, deepwater (epibenthic)		Ontogenetic (OT)		(Wakefield and Smith 1990)
Paralabrax clathratus	Kelp bass	Serranidae	Shallow rock and kelp (pelagic)	40–11000 m^2 (AT)	Little in juveniles (TO); ontogenetic	Diurnal (DO,GA)	(Hobson et al. 1981, Hartney 1996, Bond et al. 1999, Lowe et al. 2003)

TABLE 20-1 (continued)

Species	Common Name	Family	Habitat	Movement Patterns		Other Activity	Source
				Home Range	Migrations		
Paralabrax maculatofasciatus	Spotted sand bass	Serranidae	Bays, shallow coast			Diurnal(U)	(Bond et al. 1999)
Paralabrax nebulifer	Barred sand bass	Serranidae	Sand, sand/ rock interface		Seasonal (FO)	Diurnal(U)	(Love 1996, Bond et al. 1999)
Sphyrna lewini	Scalloped hammerhead	Sphyrnidae	Deep water pinnacle (pelagic)	2.1–19 km (AT)	ontogenetic seasonal (TO)		(Klimley et al. 1988, Klimley 1993)
Squatina californica	Pacific angel shark	Squatinidae	Sand (benthic)		Diel (AT)	Nocturnal(AT)	(Standora and Nelson 1977)
Cebidichthys violaceus	Monkeyface prickleback	Stichaeidae	Rocky inter and subtidal (benthic)	2 m^2 (AT)	Tidal (AT)	No diel(AT)	(Ralston and Horn 1986)
Synodus lucioceps	California lizardfish	Synodontidae	Sand (benthic)			No diel(GA,M)	(Allen 1982)
Torpedo californica	Pacific electric ray	Torpedinidae	Sand, subtidal rock (at night)			Nocturnal (DO,AT)	(Ebeling and Bray 1976, Bray and Hixon 1978, Lowe et al. 1994)
Triakis semifasciata	Leopard shark	Triakidae	Rock, sand, mud, estuarine (epibenthic)	>6634 m^2 (AT)	~1.4–6.4 km ontogenetic diel, tidal seasonal (TO)		(Manley 1995, Ackerman et al. 2000)
Oxylebius pictus	Painted greenling	Zaniolepididae	Shallow rock			Diurnal(U)	(Bond et al. 1999)
Zaniolepis frenata	Shortspine combfisn	Zaniolepididae	Sand (benthic)			Diurnal(GA,M)	(Allen 1982, Bond et al. 1999)
Zaniolepis latipinnis	Longspine combfish	Zaniolepididae	Sand (benthic)			Diurnal(GA,M)	(Allen 1982)
Lycodes (Lycodopsis) pacifica	Blackbelly eelpout	Zoarcidae				Diurnal(GA,M)	(Allen 1982)

NOTE: Family names in parentheses indicate previously recognized nomenclature. Codes for evidence of behavior AO: aquarium observations; AT: acoustic telemetry; DO: diver observation; GA: gut analyses; M: morphological inference; OT: otter trawl; N: netting; SO: surface observations; ST: satellite telemetry; T: traps; TO: tag and observation; TR: tag and recapture; FO: fishery observation; U: unspecified territorial. Because, for most territorial organisms, territory size or space use is constrained by the amount of area they realistically can defend, non-territorial species should have larger home ranges than those that are territorial. Matthews (1990b) found home range sizes of shallow water copper (*Sebastes caurinus*) and quillback rockfish (*Sebastes maliger*) ranged from 30–1500 m^2, depending on the quality of the habitat (table 20-1). While it is not known whether these fish are territorial or not, they tend to have larger home ranges than territorial black and yellow and gopher rockfishes (3–15 m^2) studied by Larson (1980). Because Matthews (1990a) also found that fish moved seasonally from one location to another, these differences in home range size and space use between the two groups of rockfishes are most likely attributed to variability of food resources. In the case of copper and quillback rockfishes, it is possible that prey resources were more variable in the area where they were studied, thereby requiring the fish to have larger home ranges and reducing the benefits of being territorial. Similar observations have been made for two species of deepwater rockfishes in a Monterey Bay canyon. Starr et al. (2002) used an array of acoustic listening stations to quantify the movements of the demersal greenspotted rockfish and the more epibenthic bocaccio. They found that greenspotted rockfish used a much smaller area (0.5–1.6 km^2) than bocaccio, which more frequently moved beyond the study area (>12 km^2)(table 20-1). In addition, bocaccio exhibited more vertical movements and were thought to be moving along the ledge and rim of the canyon. Although it is unlikely that either of these species is territorial, the species most closely associated with the substratum had the smallest home range.

Like juvenile bocaccio, some rockfishes, such as yellowtail (*Sebastes flavidus*) and blue rockfish, are associated with rocky substratum, but are not demersal. These water column species form dense schools, usually around kelp beds or over rock banks and pinnacles. While there is much less known about the home range sizes of water-column rockfishes, one might expect there to be even larger home ranges for these species due to their decreased association with the substratum. In a tag and recapture study by Miller and Geibel (1973), juvenile blue rockfish tagged in shallow kelp bed habitats in central California exhibited little movement (~60 m) from their home reef. Juvenile blue rockfish tagged on deeper reefs were found to meander more along the reefs (~1.3 km) (table 20-1). They attributed those differences to possible variations in prey availability. Unfortunately, tag and recapture studies lack the resolution of acoustic tracking studies, so it is difficult to determine how realistic these methods may be in quantifying home range. In an acoustic telemetry study of yellowtail rockfish on an offshore bank, Pearcy (1992) found that these fish moved considerable distances over the bank (0.2–1.3 km) and made regular dives from 25 to 75 m depth (table 20-1). In comparison with their demersal congeners, yellowtail rockfish have significantly larger home ranges in both the horizontal and vertical plane. For these species, schooling may reduce predation risks, thereby reducing their dependence on shelters and allowing them more freedom to search out prey in the water column. Prey may be patchier in distribution and require the fish to move more to locate prey. Movements of these fish throughout the water column may enable them to locate prey that exhibit diel vertical migrations or may aid the fish in maintaining their position over the bank.

Although there are common trends in space use patterns among species, there is a large degree of variability observed in home range size within species and even individuals. Some fish home range studies have demonstrated that habitat quality significantly affects home range sizes of fishes. Matthews (1990a,b) found that copper and quillback rockfish had significantly smaller home ranges when occupying high relief habitats (<10 m^2) than when they were over low relief habitat (~4000 m^2). In addition, she found that the method used to quantify home range had a significant effect on area size estimates. Using a combination of visual underwater monitoring and acoustic telemetry, she found that acoustic telemetry measurements provided a more conservative measure of home range size. Lowe et al. (2003) observed similar trends in kelp bass acoustically tracked at Santa Catalina Island. Although there was no relationship in home range size with fish size, kelp bass residing under a pier showed significantly less movement (~40 m^2) than similar size kelp bass occupying native habitat (~8000 m^2) (table 20-1). Fish counts in these habitats indicate significantly higher densities of kelp bass in the vicinity of the pier than in natural habitats. This suggests that high quality habitats not only reduce the home range sizes of fishes, but can increase the densities of fishes as well. Kelp bass preferred this artificial habitat because it offered more shade, holes, and a light source that attracted prey at night. Although substratum availability may be limiting, the increased productivity of these habitats allows for greater fish density and less movement. Resource managers should keep this in mind when designing marine reserves. Setting aside areas of higher habitat quality could support larger numbers of fishes in a smaller area, potentially reducing the size requirements of marine reserves.

Low Relief Soft Substratum

If an inverse relationship exists between home range size and habitat complexity, then fishes that occupy low relief or soft substratum habitats should have larger home ranges than those found over rocky reef habitats. Unlike rock-associated fishes, flatfishes, sand basses, coastal sharks, rays, croakers, and some surfperches found over soft substrata have received less study in terms of their movement patterns and home range sizes. Most of the movement pattern studies done on this assemblage of fishes have primarily utilized tag and release methods to quantify the degree of movement of the species.

Tagging studies done on adult California halibut (*Paralichthys californicus*) suggest these fish show limited movement (~8 km) (Posner and Lavenberg, 1999). While these types of studies are most effective in quantifying dispersal and lack the resolution needed to determine home range size, observations by researchers such as Posner and Lavenberg (1999) provide evidence that sand-associated species, like halibut, move more than is typically seen in rock-associated species. This increased home range size is likely attributed to feeding requirements and food availability. Anecdotal observations of adult halibut based on fishing indicate California halibut may follow schools of anchovies and sardines, which can move over considerable distances (Love, 1996). While flatfishes appear lethargic and not highly mobile, large-scale movements are not uncommon. For example, studies of plaice (*Pleuronectes platessa*) in the English Channel have demonstrated that these flatfish move through out the entire channel (900 km) using tidal currents to assist their movements (Metcalfe and Arnold, 1997).

Many species of croakers (Sciaenidae) found over sand habitats exhibit greater diel movement than rock-associates species.

Using various fishing methods, Allen and DeMartini (1983) found that white croaker (*Genyonemus lineatus*) and queenfish (*Seriphus politus*) may exhibit considerable diel onshore/offshore movements, suggesting more extensive home ranges.

Many species of soft substratum fishes have been shown to exhibit longshore movement patterns. The round stingray (*Urobatis halleri*), a common benthic stingray found in nearshore waters in southern California, can occur in high density patches (20 rays/m^2) in bays and estuaries in the summer and fall months. Tag and recapture and acoustic telemetry studies have indicated that these rays move more than previously thought and appear to show seasonal site fidelity (Lowe et al. unpubl.; Vaudo, 2004). Therefore it is possible that these rays continually meander along the coast. The Pacific electric ray (*Torpedo californica*) is another highly mobile species that can be found over sand substratum. In an acoustic telemetry study (Bray and Lowe, unpubl.), rays were found to move at night, cruising over rock substratum bordering sand, but would settle and rest on sand substratum during the day. Rays exhibited a longshore movement from day to day. These types of space use patterns are similar to those observed for Pacific angel sharks. Pittenger (1984) acoustically tracked angel sharks around Santa Catalina Island and found they exhibited irregular movement patterns. Tagged angel sharks would spend several days in one area and then swim along the coastline at night, eventually circumnavigating the island (73 km). This type of longshore movement may be typical of many sand substratum oriented species (Love et al., 1986). Due to lack of habitat structure and more patchy food availability, many species commonly found over low relief soft substratum may have to move more to find food in this less complex habitat or to avoid predation.

Regardless of this trend, movement patterns of fishes vary depending on resource availability. A good example of this may be seen in some deepwater fishes. Priede et al. (1986; 1990; 1991) used acoustic tracking to monitor the movement patterns of abyssal grenadiers (*Coryphaenoides yaquinae*) attracted to a baiting station at 6000 m depth. Scavenging grenadiers were allowed to swallow bait containing acoustic transmitters and were subsequently tracked using an array of hydrophones deployed around the seafloor. They found that the fish moved more than 1 km away within 8 hrs after feeding at the baiting station. Based on these movement patterns, they concluded that a scavenging grenadier might move up to 3000 km/year in search of food. In contrast, the longspine thornyhead (*Sebastolobus altivelis*), a deepwater rockfish, is one of the most abundant fish at depths of 700–900 m in the Southern California Bight (SCB) and are found over sand/mud substratum, yet it is thought to move very little. Stomach content studies of this species indicate they feed on brittlestars (*Ophiopthalmus normani*), which litter the sea floor at depths where *Sebastolobus* are found (Neighbors and Wilson, chapter 14). In a bioenergetics study by Vetter and Lynn (1997), longspine thornyheads were found to have a very low metabolism and it was concluded that these fish may only need to eat 3 or 4 meals per year! Therefore, they may not have to move about to find food because their energy requirements are so low, and in this case food is readily available and abundant.

Open Ocean

Not all fishes show distinct home ranges. As one might expect, pelagic, open-ocean fishes, which may have little or no association with a substratum, may constantly be meandering about searching for food or mates. For example, movement studies of blue sharks and shortfin mako sharks in the SCB have provided little evidence for home ranging or site fidelity in these species (Sciarrota and Nelson, 1977; Holts and Bedford, 1993). Both blue and shortfin mako sharks have been observed swimming for kilometers without changing direction. Although it is possible that these tracking studies have been too short in duration to discern movement back to the area they were first tagged, standard tagging of these species also indicates they have high dispersal rates, which further indicates a lack of home ranging.

Similar small-scale movement patterns have been observed for yellowfin tuna (*Thunnus albacares*) in the SCB. In an acoustic telemetry tracking study, Block et al. (1997) found that small (8–16 kg) yellowfin tuna moved extensively over a 2–3 day period, traveling more than 70 km in the SCB. They also observed that these fish remained in the mixed layer of the water column, but made occasional dives through the thermocline. Compared with movements of yellowfin tuna studied in more tropical regions (Holland et al., 1990), yellowfin tuna at higher latitudes exhibit a more compressed vertical distribution due to the thermocline being at shallower depths (Block et al., 1997). Other pelagic species such as the ocean sunfish (*Mola mola*) may also fit into this category and lack a home range. Cartamil and Lowe (2004) tracked ocean sunfish in the San Pedro Channel and found continuous and directed movement over periods up to 48 hrs. Unlike pelagic sharks that may be searching for schools of mobile pelagic fishes and squids, ocean sunfish are thought to be planktivores, and feed primarily on gelatinous zooplankton, which vertically migrate daily and are transported by ocean currents. In addition, sunfish are seasonally abundant in southern California waters and are thought to migrate, possibly following blooms of pelagic zooplankton. Similar movement patterns have been observed for planktivorous sharks, such as whale sharks (*Rhincodon typus*). Eckert and Stewart (2001) used satellite transmitters to track the movement patterns of whale sharks in the Sea of Cortez. They found extensive movement of tagged sharks throughout the Sea of Cortez and had several sharks move across the Pacific. They suggested that the sharks' movements were influenced by oceanographic features corresponding with upwelling and increased plankton production.

Most open ocean fish movements appear to be correlated more with movements of water masses, which can vary with season, current, and decadal weather pattern. However, due to the vast three-dimensional habitat that most open ocean fishes occupy, finding patches of prey may require development of specific strategies and result in more movement. Dagorn et al. (2000) developed a computer model to examine the evolution of movement patterns of predatory pelagic fishes (tunas, billfishes, and sharks) based on prey availability. Existing behavioral data on movement patterns of these fishes, as well as distributions and patchiness of prey species were factored into the model. Prey density and availability were found to greatly influence the evolution of movement patterns for each species of fish. Therefore, many open ocean species lack defined home ranges and may be more appropriately defined as "nomadic" in that they simply search for environmental conditions most likely to contain prey patches. Moving along the edges of water masses and eddies and making dives through the thermocline may increase the rate with which open ocean fishes encounter prey.

MIGRATION—SPATIAL PATTERNS

Because of variability in resource availability or environmental conditions in most habitats, along with ontogenetic shifts in resource demands, it is not surprising that many species of fishes exhibit some sort of spatial movement pattern beyond that of typical home ranging. In its broadest sense, migration has been described as the undistracted movement an animal makes from one location to another, which can vary over a wide range of spatial and temporal scales (Dingle, 1996). The term "migration" has been used quite loosely throughout the fish literature, probably due to the difficulty in quantifying the movement patterns of individuals as well as the motivations for these movements. Nevertheless, there are numerous examples of spatial movement patterns of fishes that occur over various temporal scales, which may or may not meet the strict definition of a migration. For example, a fish may exhibit ontogenetic, seasonal (mating and reproduction), and diel (tidal, vertical, onshore-offshore) movements, all of which involve traveling from one habitat type to another. These movements may be influenced by the reproductive or developmental state of the fish, its susceptibility to predation, the availability of suitable food, or changing environmental conditions. In addition, because many of these movements may be bi-directional, fish must be able to find their way back to their original location, requiring an ability to home. The mechanisms that regulate these types of movements rely on a combination of innate and learned behaviors as well as the ability to use predictable information about environmental factors that would benefit moving (Dodson, 1988; Dingle, 1996). In this section, we will address the processes involved in these various types of movement and how they relate to a fish's spatial requirements.

Ontogenetic Related Movements

Because most species of fishes have a planktonic larval stage, many exhibit some ontogenetic movement from one habitat to another over the course of their lives. This is particularly true for demersal species of fishes such as flatfishes, some rockfishes, and labrids (Boehlert, 1977; Boehlert, 1978; Cowen, 1985; Brewer and Kleppel, 1986; Moser and Boehlert, 1991; Sakuma et al., 1999). For example, adult California halibut are commonly found over sand substratum on the shelf to depths of 90 m. Adults spawn throughout the year with a peak in winter and spring, which corresponds with a period of minimal offshore transport by currents (Lavenberg et al., 1986). Thus, the eggs and larvae remain over the shelf with the greatest densities found in waters less than 75 m deep, and the planktonic larval stage is relatively short (usually less than 30 d). Kramer (1991) suggested that transforming larvae may get pushed towards shore by being up in the neuston at night, but settling back down to the bottom during the day. Settled larvae may find bays and lagoons following longshore currents, and get transported into these habitats via tidal transport (Kramer, 1991). Juveniles emigrate from bays back to the open coastline after about one year, where they become more piscivorous as they mature. Kramer (1991) hypothesized that larval halibut move into the bays to escape predation pressure common along the coastline, but later leave the bays to obtain more oceanic prey such as anchovies, squid, and nektonic fishes.

California sheephead spawn from May through August, and their larvae spend 34–78 d in the plankton before settling out to the substratum (Cowen, 1985; Cowen, 1991). Sheephead larvae have been found many kilometers offshore, therefore their protracted larval duration may be necessary to allow the larvae to reach suitable habitat for settlement. There is some evidence that newly settled juveniles may be more abundant at deeper depths in nearshore environments, but they move to shallower depths as they mature (J. Caselle, pers. comm.). The opaleye (*Girella nigricans*) also undergoes a distinct ontogenetic shift in habitat use. They have a pelagic larval phase, which can be found out to 120 km offshore (Stevens et al., 1990). Preferring warmer water, pelagic juveniles (~2.5 cm) venture inshore and move into warm tide pools in the intertidal where they feed on invertebrates (Norris, 1963) (table 20-1). When these fish are about 7–15 cm long, they move out of the tide pools and into the subtidal zone where they form schools and shift their diets to algae.

Many species of rockfishes exhibit ontogenetic shifts in habitat use. For example, juvenile deepwater longspine thornyhead are found up in the water column at depths or 500–600 m for their first 18–20 months before settling to the bottom where they are found as adults (Wakefield and Smith, 1990). Some larval rockfishes may be carried hundreds of kilometers offshore, and thus remain in the water column for several months up to a year recruiting to pieces of drift kelp and floating debris (Moser and Boehlert, 1991). Eventually, these larvae settle out of the water column and utilize benthic habitats. Ovoviviparous female splitnose rockfish (*Sebastes diploproa*) release larvae from February to July and the larvae recruit to drift kelp. They emigrate from the surface to bottom depths greater than 180 m starting around July, which suggests these fish may be in the water column from 6 months to 1 year (Boehlert, 1977). Once splitnose rockfish settle they assume their adult habitat over sand/mud substratum. This represents the typical ontogenetic habitat shift observed in most rockfishes. Bocaccio form schools when they are subadults and exhibit greater movements; however, they become more sedentary as they get larger and tend to refuge more (Starr et al., 2002). Many species of rockfishes, settle out in shallow waters and the adults migrate deeper as they get larger (Love, 1980).

These ontogenetic movements may serve to minimize predation risks at more vulnerable stages of their life cycle, but shift to optimize feeding needs at another stage. In addition, this type of spatial movement is the primary dispersal mechanism for many species, yet it is still unclear what cues may induce settlement or to what extent dispersal may occur. Nevertheless, these migratory shifts exemplify the tradeoffs in cost optimization that fishes experience throughout their lives and how these tradeoffs shape their movement patterns and spatial needs.

Seasonally Related Movements

In temperate regions, seasonal migrations of fishes are common. Although these migrations are usually elicited based on seasonal environmental changes, the reasons for the habitat shift may vary. Certain species of pelagic predatory fishes such as California barracuda (*Sphyraena argentea*), Pacific mackerel (*Scomber japonicus*) and bonito (*Sarda chiliensis*) show seasonal shifts in habitat use. Using scientific fishing methods, Allen and DeMartini (1983) found that Pacific mackerel and bonito were more common inshore in summer and early fall months than during winter months. They also attributed some of these movements to possible longshore migrations. These inshore/longshore movements are likely attributed to the movements and concentrations of prey inshore during summer and fall months. Seasonal inshore and longshore migrations are common in many benthic species like the round stingray and the Pacific electric ray, which may only be found close to shore at certain times of the year. It is thought that rays congregate nearshore for mating and pupping purposes, as mature males and females are most common during later summer and fall (Babel, 1967; Bray and Lowe, unpubl.). Thus, some seasonal inshore migrations may facilitate the concentrating of potential mates.

Temperature can play a central role in influencing the seasonal movements and distributions of fishes. The fish assemblage inhabiting the artificial breakwater at King Harbor in Los Angeles experiences a structured and seasonally dynamic thermal regime caused in part by the proximity of warm water discharged from a power plant and cool water upwelled from a nearby submarine canyon. This setting provided Stephens and coworkers a unique opportunity to relate seasonal changes in fish distributions to water temperature (Terry and Stephens, 1976; Stephens and Zerba, 1981; Shrode et al., 1982; Stephens et al., 1994). The distributions of adult black perch (*Embiotoca jacksoni*), rainbow seaperch (*Hypsurus caryi*), pile perch (*Rhacochilus vacca),* and white seaperch (*Phanerodon furcatus*) shift to deeper cooler water during the late summer and fall, and return to shallower water when surface temperatures cooled. Subadults are more evenly distributed throughout the water column and do not vary seasonally. Juveniles appear in shallower warmer water than adults, suggesting an ontogenetic move to deeper water as they grow (Terry and Stephens, 1976). Laboratory studies, in which fish were placed in horizontal temperature gradients, indicate that the observed seasonal distribution patterns can be explained by thermal preferences, not depth *per se*. In addition to the rainbow seaperch, shiner perch (*Cymatogaster aggregata*), blacksmith (*Chromis punctipinnis*), and calico rockfish (*Sebastes dalli*), selected temperatures that were similar to temperatures where they occurred in the field (Shrode et al., 1982).

While it is thought that most rockfishes do not seasonally migrate (Love, 1980), a number of species have been shown to home after being displaced from their original site of capture (Carlson and Haight, 1972; Miller and Geibel, 1973; Hallacher, 1984; Matthews and Reavis, 1990; Matthews, 1990b; Pearcy, 1992) (table 20-1). The ability to home often implies the capacity to navigate or orient to landmarks, which are skills often used in migrations. For example, some rockfishes have been reported to move to deeper waters during winter months, particularly populations north of Point Conception, California. Miller and Geibel (1973) found fewer juvenile blue rockfish off shallow reefs in Monterey Bay during winter months and concluded that these fish may have been moving to deeper water to avoid turbulence due to winter storms. However, they also acknowledged that it was possible that the fish had not actually moved to deeper water, but they may have counted fewer fish due to the poor water conditions. Although there is no direct evidence of movement back and forth, the shift in abundances could indicate seasonal migratory movements. Not all seasonal movements of rockfishes are related to avoiding rough conditions. For example, the demersal California scorpionfish (*Scorpaena guttata*) apparently makes extensive migrations in late spring and early summer to spawn in groups; in this case, however, movements are vertical because the aggregations form in the water column during spawning (Love et al., 1987). Matthews (1990a) found that copper, quillback and brown (*Sebastes auriculatus*) rockfishes would move from low relief reefs in the winter to other suitable habitats. She hypothesized that this seasonal movement was related to the annual disappearance of kelp on these reefs. In this particular case, rockfish might be migrating to find suitable habitat, which is often accompanied by additional food.

Many pelagic fishes such as tunas, marlins, and sharks also make seasonal migrations for the purpose of mating and spawning. The SCB is thought to be an important pupping and nursery area for blue, shortfin mako, white, and common thresher sharks (*Alopias vulpinus*). Blue sharks are thought to migrate south in spring and summer months to mate, but venture north to pup and feed (Strasburg, 1958; Nakano, 1994). Common thresher sharks are also thought to show north-south seasonal migrations along the eastern Pacific through Baja, Mexico (D. Holts, pers. comm.). Pacific bluefin tuna (*Thunnus thynnus*) have been found to swim across the Pacific. Tunas tagged off California and Mexico have been recaptured off Japan (7500 km) and bluefin tagged off Japan have been recaptured off California and Mexico (Clemens and Flittner, 1969). Although these tagging data do not indicate whether these are seasonal migrations they do imply bi-directional movement between the two locations. Similar seasonal migrations have been suggested for Pacific albacore tuna (*Thunnus alalunga*). Laurs and Lynn (1977) used commercial catch data and tag and recapturing information to quantify the seasonal migration of Pacific albacore. They found that these tunas may be following transition zone waters as they move east during summer months. Future studies using satellite telemetry tags will undoubtedly help answer questions about migration routes and oceanographic correlates for these pelagic fishes.

Studying the movement patterns of large predatory fishes such as white sharks poses distinct challenges. The occurrence of white sharks at the Farallon Islands, California during fall months has been correlated with the arrival of juvenile elephant seals, which haul out on the island at this time of year. Goldman and Anderson (1999) acoustically tracked adult white sharks around the Farallon Islands during daylight hours and found that they repeatedly use certain areas near the seal haulout areas. The areas covered ranged from 1.84–4.34 km^2 and the size of the daytime home ranges increased with the size of the shark. As winter arrives and the seals leave, so do the sharks. Although the same sharks were found to return to the Farallon Islands every year, of six adult white sharks tagged with pop-up satellite tags at the Farallon Islands one was found to travel to the Hawaiian Islands and back and three were detected in open ocean off Baja, Mexico (Boustany et al., 2002). While white sharks have been previously documented in Hawaii, these findings indicate that they may behave more like pelagic sharks than previously thought. Nevertheless, it is still not clear whether these oceanic movements are related to breeding migrations or following prey—there have been anecdotal observations of white sharks following migrating humpback whales near the Hawaiian Islands.

Tidally Related Movements

Tidal flux provides an excellent cue for timing migrations, but also allows for increased access to habitat not normally accessible to many fishes. Some species of fishes, particularly those found in the sublittoral zone, make migrations into the intertidal zone during periods of high tide. For example, rockpool blennies migrate up into tide pools during high tides and then migrate back down to the subtidal zone when the tide is out (Stephens et al., 1970). This species has been shown to home back to its home pool after being displaced 45 m.

The monkeyface prickleback also undergoes tidal migrations, moving farther up into the intertidal zone with flooding tides (Ralston and Horn, 1986). As juveniles, these fish live in intertidal pools and are carnivorous, feeding on copepods, amphipods, isopods, and polychaetes. However, as they get larger they shift to an herbivorous diet, feeding on a wide variety of algae. Moving into the intertidal provides herbivorous adult fish access to more algae. Both Green (1971) and Williams (1957) observed that different species of sculpins (wooly sculpin, *Clinocottus analis* and tidepool sculpin, *Oligocottus maculosus*) migrate up into the intertidal pools as the tide flooded. Smaller individuals move the farthest, but usually at a distance less than 10 m. Other studies have shown that the intermediate-sized tidepool sculpin can home from a distance of up to 100 m, probably using olfaction (Khoo, 1974).

Some fish like the California grunion (*Leuresthes tenuis*) make a seasonal, tidal, spawning migration. Grunion time their spawning movements with high spring tides, which allow them to come up onto the beach and spawn in the sand. The eggs remain buried in the sand until the following spring tides, at which time the eggs hatch and the larvae are carried offshore (Walker, 1952; Speer-Blank and Martin, 2004).

Diel Related Movements

Diel migrations of fishes are particularly common because the rhythmic changes in light associated with day and night provide one of the best cues for setting biological clocks. Many fishes exhibit distinct changes in habitat use between day and night. While some species move into holes and shelters and become quiescent, others become active and move into the water column. Some species may move extensively during these diel habitat shifts regardless of their life stage. For example, many species of fishes exhibit diel vertical migrations even during their pelagic larval stage. Postflexion larval Pacific and speckled sanddabs (*Citharichthys sordidus* and *C. stigmaeus*) were found to vertically migrate from deeper water depths during the day through the pycnocline into shallower waters at night (Sakuma et al., 1999). Schools of northern anchovies (*Engraulis mordax*) have been shown to exhibit both vertical and onshore-offshore diel migrations (Allen and DeMartini, 1983; Robinson et al., 1995). Northern anchovy schools were found to move to deeper offshore waters during the day, but ventured inshore to shallower waters at night. Robinson et al. (1995) also found a strong correlation between anchovy movement and euphausiid abundance and concluded that anchovies may be exhibiting this diel migratory pattern as the result of following prey.

Even pelagic fishes that may exhibit little or no home range pattern still show diel movement patterns. For example, blue sharks tracked off Santa Catalina Island during winter months were found to move inshore at night and swim along the bottom, but would move back into offshore waters more near the surface during the day. This diel pattern was only observed during winter months and is thought to be attributed to the local abundance of prey inshore (squid—*Loligo opalescens*) at that time of year (Sciarrota and Nelson, 1977; Tricas, 1979). An opposite pattern of movement was observed in swordfish (*Xiphias gladius*) acoustically tracked in the Sea of Cortez by Carey and Robison (1981). Several swordfish were found to move inshore over a 91 m deep bank during the day and swim just above the bottom, whereas at night they moved offshore to open water and would swim near the surface. Carey and Robison (1981) hypothesized that these swordfish may be venturing inshore to feed on demersal fish moving on and off the bank, then venturing offshore to feed on abundant pelagic squid that would migrate towards the surface.

Obviously many of these types of migrations require the ability to orient to environmental cues or the ability to discern landmarks. While we have learned a lot about why fish move, when and where, we still know very little about how they achieve some of these impressive migrational movements. Space use patterns seem to be governed by tradeoffs between feeding, mating, and avoiding predation.

Activity Patterns—When Do Fish Move?

The high diversity of fish species off California results in a wide range of activity patterns. These patterns make up a time dimension of the niche that has presumably evolved in response to many selective forces.

Environmental situations, such as the availability of prey, nearness and activities of predators, level of the tide, etc., can affect activity levels of fish at a particular time and place. The broad patterns of California fish activities—when fish are prone to be active and inactive—also may be influenced by internal biological clocks. We will first provide a review of the wide range and nature of activity patterns displayed by California marine fishes with an emphasis on subtidal rocky reefs and surrounding areas. Later, we will briefly consider the control of these activity patterns by external and internal factors.

It is important to understand the vocabulary used to describe activity patterns. The commonly used terms relate to environmental rhythms created by the rotations of the earth and the moon. These terms include diel (24-hr day), diurnal (daytime), nocturnal (nighttime), crepuscular (dawn and dusk), tidal (one high and one low tide), semilunar (twice per month), lunar (each month), and annual (year). We will avoid the term “daily” because of its inconsistent usage. Although daily normally refers to diel, authors occasionally use it when describing only diurnal activities.

Activity patterns are usually inferred from five general sources of information: 1) direct observations of location and behavior; 2) monitoring individuals using remote sensing methods (i.e., sonar, LIDAR, telemetry); 3) examination of gut fullness of fish collected throughout the diel period; 4) knowledge of the diel availability of prey; and 5) inferences from morphology. Most of these methods are adequate for species that display consistent and obvious rhythmic behavioral patterns.

For other species, none of these methods provides a comprehensive picture. For example, while direct observations may reveal patterns of planktivores or herbivores, they are less useful for making inferences about study sit-and-wait predators (e.g., some rockfishes) that rarely move. Remote sensing studies tend to be restricted to fairly large fish and resolving ability may vary considerably depending on the species being studied and methods used. Gut content analyses can be ambiguous in situations where diel patterns in fullness are not evident. Species like the blacksmith consistently have food in their guts during the day and early evening but have empty guts just before dawn. In such situations, it can be inferred that it takes less than 24 hr for a food bolus to pass though the fish, enabling a crude estimate of feeding times. On the other hand, species like the giant kelpfish (*Heterostichus rostratus*) have items in their guts in both day and night collections (Hobson et al., 1981). In such cases, additional knowledge of movement and digestive rates of food in the gut, or knowledge about the diel habits of their prey, is required before feeding times can be estimated.

We raise several precautionary notes before summarizing the activity patterns of some California fishes. First, many fish are opportunistic. For example, the walleye surfperch (*Hyperprosopon argenteum*) feeds mainly at night as evidenced by the relatively full guts of individuals collected at night, but empty guts of individuals collected during the day (Hobson and Chess, 1976). Nevertheless, walleye surfperch are often caught on baited hooks during the day by shore fishers (Frey, 1971). The activity of cuskeels (Ophidiidae) is another example. These fishes normally bury in sand during the day and emerge at night (Greenfield, 1968; Hobson and Chess, 1986a); however, when the water is extremely turbid, they appear above the sand during the day and assume their nighttime behavior (Greenfield, 1968). Thus, a fish species might show overall general patterns of activities but the pattern can be altered under the appropriate environmental conditions. Second, as reported in the section above entitled, *Ontogenetic migrations*, activity patterns may change as fish age. In many cases where studied, juveniles are diurnally active while the adults may be nocturnal. Various rockfishes (*Sebastes* spp.) are examples of this pattern (table 20-1). Third, behavior might vary substantially among individuals. For example, a small number of subtidal reef fishes engage in removing ectoparasites and scales from other fish species. The best-known California example is the señorita (*Oxyjulis californica*) (Hobson, 1971). Careful observations on the rock wrasse (*Halichoeres semicinctus*) by Hobson (1976), and zebraperch (*Hermosilla azurea*) and opaleye by DeMartini and Coyer (1981) indicate that a few individuals of these species also clean—and these individuals do so frequently. This suggests that specialization can occur among individuals within a species. Thus, pooling individual behaviors to characterize a species' activity pattern masks these complex, but more realistic pictures of fish behavior. Cleaning behavior is discussed in detail in chapter 22.

With these reservations in mind, we examined the literature to gain insight on the activity patterns of California marine fishes. This information is summarized in the column labeled Other Activity in table 20-1. The longest activity pattern in table 20-1 is tidal; longer patterns mainly involve large-scale movements (see above and the Migrations column in table 20-1) or reproduction, which is covered elsewhere (DeMartini and Sikkel, chapter 19). Seventy-nine of the 105 species with activity data in table 20-1 demonstrate clear diel patterns (51 primarily diurnal, 28 primarily nocturnal). An additional 10 species (one embiotocid, two sciaenids, and seven sebastids) display mixed patterns, with the juveniles being active during the day and the adults being active at night. We suspect that additional studies of younger life-history stages will reveal that many other species also shift their activity patterns as they age. Most of the detailed information on activity patterns involves fish that inhabit subtidal rocky reefs—and our summary reflects this bias. Our survey is not complete but hopefully covers research on the most conspicuous and intensely studied species.

Diel Activity Patterns on Subtidal Rocky Reefs

Since the advent of scuba, southern California has been a major focal point of studies of diel activities of subtidal fishes. Outside of the tropics, probably more is known through direct observation about the diel activities of fish inhabiting subtidal reefs and surrounding sand flats in southern California than in any other region. Because of this rich knowledge base, we focus on diel activity patterns in and around rocky-reefs. One of the first studies, by Nelson and Johnson (1970), described the nocturnal activities of horn sharks (*Heterodontus francisci*) and swell sharks (*Cephaloscyllium ventriosum*) off Santa Catalina Island. Since then, the daytime and nighttime activities of numerous fishes have been conducted, mainly in the southern California Bight. Most of the community-level studies have centered around Big Fisherman Cove, Santa Catalina Island (33°27′N, 118°29′W) (e.g., Hobson and Chess, 1976; Hobson et al., 1981; Hobson and Chess, 1986a) and at Naples Reef (34° 25′N 119°57′W) (e.g., Bray and Ebeling, 1975; Ebeling and Bray, 1976; Bray and Hixon, 1978). Naples Reef is 24 km west of the city of Santa Barbara and less than 50 km from the major zoogeographic boundary at Pt. Conception. Additional long-term studies of the daytime and seasonal distributions of fishes have been conducted along the rocky breakwater at King Harbor (33°50′N, 118°20′W) (Terry and Stephens, 1976; Stephens and Zerba, 1981; Shrode et al., 1982; Stephens et al., 1994).

In the following paragraphs, we describe the typical day and nighttime situation on rocky reefs at Santa Catalina Island and Naples Reef during clear and calm conditions (fig. 20-5a–d). We grouped the fishes according to broad foraging guilds (Ebeling and Hixon, 1991) because of the dominance of foraging behavior when fish are active.

Patterns in Feeding and Distribution

During the day, the water column is filled with aggregations of planktivorous fishes numerically dominated by blacksmiths (fig. 20-5a, c) but also juveniles of various species. At dawn, blacksmiths emerge from their nighttime shelters among the rocks and swim into the water column where they feed on zooplankton; at dusk, they descend from the water column and move into their nighttime shelters (Ebeling and Bray, 1976; Hobson and Chess, 1976; Bray, 1981). Smaller blacksmiths do not stray far from kelp or rocky cover; however, larger individuals may migrate hundreds of meters and gather where water currents bring in oceanic zooplankton (Bray, 1981). Other common midwater inhabitants are the picker-type microcarnivores, including señoritas and kelp perch (*Brachyistius frenatus*) and occasional omnivores, such as halfmoon (*Medialuna californiensis*) and opaleye. Closer to the bottom, many of the obvious activities are by large-bodied microcarnivores such as demersal surfperches, garibaldi, and by various juveniles. Several species of surfperches (Embiotocidae) are commonly found in rocky reefs off southern California (Hobson and Chess, 1976; Ebeling et al., 1979; Stephens et al., 1994). These species include the black perch, rainbow seaperch, and the pile perch. An additional species, the striped

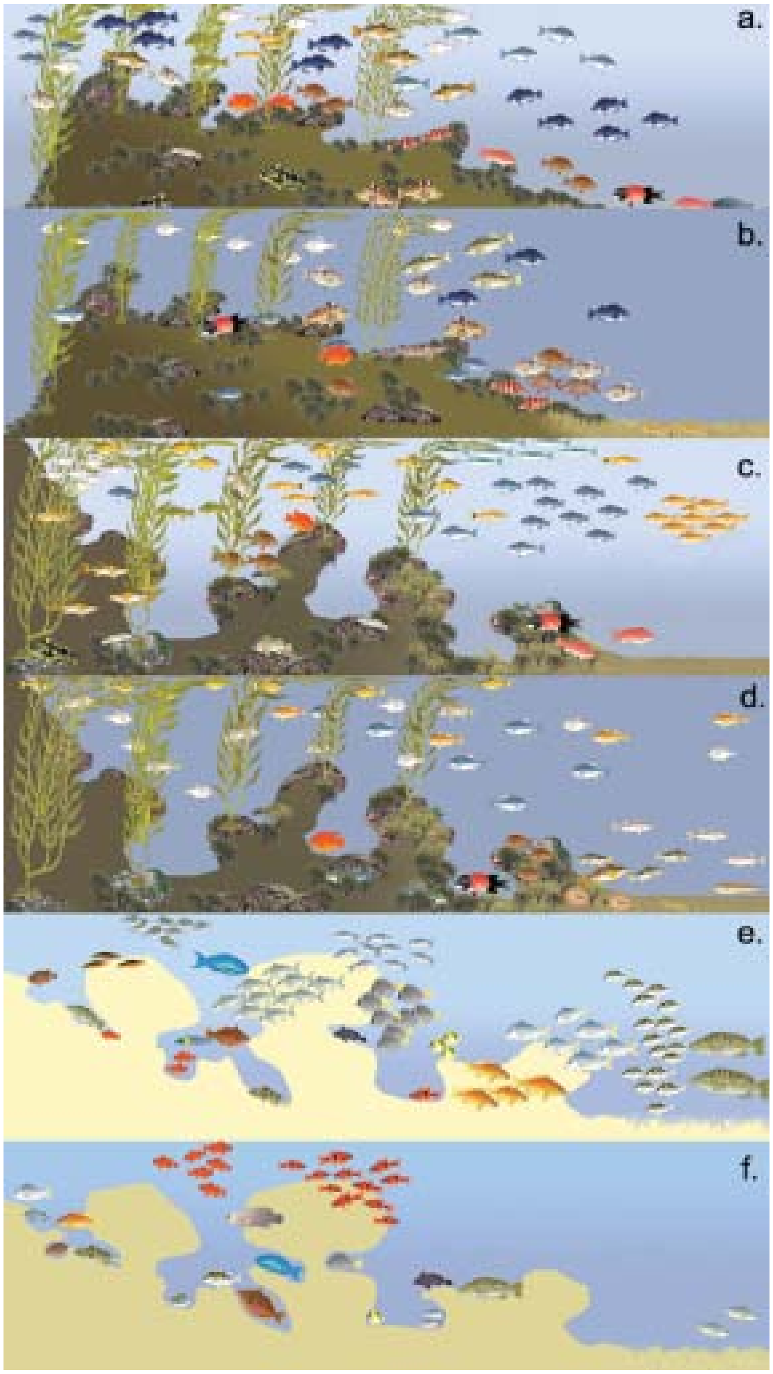

FIGURE 20-5 Depiction of day-night shifts in fish activity and water column distributions over rocky reefs. (a) Naples Reef day, (b) Naples Reef night, (c) Santa Catalina Island day, (d) Santa Catalina Island night, (e) Bahia de Palmas, Baja California, Mexico day, (f) Bahia de Palmas night. Fig. 20-5a after Ebeling and Hixon (1991); fig. 20-5e, f after Hobson (1965). (Fish drawings by L. Allen and illustration by K. Anthony.)

seaperch (*Embiotoca lateralis*) becomes abundant from Santa Barbara northward. Diving observations and gut analyses indicate that most of these feed mainly during the day (Ebeling and Bray, 1976); at night these fishes are inactive but often remain exposed just above the bottom. Other conspicuous fishes that are diurnally active are the opaleye, halfmoon, and juveniles and subadults of the kelp bass (fig. 20-5a–d).

Along the bottom, careful observation has shown that many smaller benthic reef fishes are also diurnally active. Blackeye gobies typically position themselves at the rock-sand interface, where they periodically dart out and snap zooplankton or benthic prey; at night, they take shelter in rocks and do not feed (Hobson et al., 1981). Brightly colored blue-banded gobies (*Lythrypnus dalli*) and the more reclusive zebra goby (*Lythrypnus zebra*) feed during the day, mainly on benthic prey (Hartney, 1989; Hobson and Chess, 2001). Some of the larger macrocarnivores (such as kelp rockfish *Sebastes atrovirens*) may sit motionlessly on rocks or hang among kelp fronds. Holes and crevices may be occupied by California morays (*Gymnothorax mordax*), zebra gobies, and a few demersal rockfishes *Sebastes* spp., but in general are not heavily occupied (fig. 20-5a,c).

The nighttime picture of fish activity is more subdued. Fewer fishes occupy the water column and more fishes occur in rocky shelters. This vertical day-night pattern was observed qualitatively at Santa Catalina Island by Hobson et al. (1981) and quantitatively off the Santa Barbara mainland by Ebeling and Bray (1976). One of the most abundant midwater nocturnal fishes is the walleye surfperch, which school inshore during the day and migrate offshore at night to feed on emergent zooplankton (Ebeling and Bray, 1976; Hobson and Chess, 1976). Another embiotocid, the rubberlip seaperch (*Rhacochilus toxotes*) is nocturnally active off Santa Barbara (Ebeling and Bray, 1976). Notably, both the walleye surfperch and rubberlip seaperch have enlarged eyes compared to other embiotocids of comparable body size.

Most of the fish at night are either positioned quietly right above the bottom (e.g., most surfperches), nestled in benthic algae (e.g., rock wrasse), or are in rock shelters. California sheephead typically rest under overhangs or in rocky crevices although they have also been seen fully exposed on the substratum (Hobson and Chess, 2001). Rock wrasse spend the night under sand or rocks or amid benthic algae (as summarized in Hobson and Chess, 2001). Señoritas spend the night underneath the sand. Diving and aquarium observations at dusk indicate that señoritas first descend to a sandy patch, roll on their sides just above the substratum, then swim into the sand headfirst with a flick of the caudal fin (Bray and Ebeling, 1975). They remain buried in sand throughout the night, as evidenced by aquarium observations and the lack of reported sightings at night during numerous night dives (Bray and Ebeling, 1975; Ebeling and Bray, 1976; Hobson et al., 1981; Hobson and Chess, 1986b; Hobson and Chess, 2001).

The horizontal distributional pattern of some fishes in the water column also differs between night and day. The blacksmith, a numerically dominant daytime planktivore, forages on oceanic zooplankton transported by water currents. Adult fish gather at the incurrent end of offshore reefs (Bray, 1981) or at the mouths of coves and headlands along the shore (Hobson and Chess, 1976; Bray, pers. obs.). While the actual feeding location can vary, according to tides and other determinants of nearshore currents, the result is a clumped spatial distribution of fish at certain locations above or near the reef. At night, however, the midwater planktivores such as the walleye surfperch are more dispersed throughout reefs instead of being aggregated at the incurrent end. This difference in spatial distribution of fish in the water column is likely due to the distribution of their prey. Unlike the oceanic zooplankters that make up the diet of diurnal fish, the zooplankters eaten by nocturnal fish are resident forms that emerge from the substratum at night. These zooplankters are broadly distributed throughout the reef and avoid currents that would sweep them away (Hobson, 1991).

At night, more fishes occupy open sand habitats than during the day (Hobson and Chess, 1986b) (fig. 20-5d). These species include the spotted cuskeels (*Chilara taylori*), walleye surfperch, shiner perch, yellowfin croaker (*Umbrina roncador*) and horn shark. At Abalone Cove on the Palos Verdes Peninsula in Los Angeles County, we have also seen substantial numbers of California scorpionfish dispersed over the sand at night where we have not seen them during the day (Bray and Lowe, pers. obs.).

Most of the fishes that appear over sand flats at night spend the day elsewhere, resulting in crepuscular migrations. An exception is the spotted cuskeel, which remains buried in sand during the day and emerges to feed in the same habitat. Hobson and Chess (1986a) hypothesized that the diel activity patterns of fishes over sand flats is possibly due to the nocturnal increase in prey availability at night and a decrease in number of predators.

Patterns of Egestion and Excretion

While most obvious and well-documented diel activities in California reef fishes involve the feeding of diurnally-active fishes, this behavior also results in regular patterns of egestion of fecal matter and excretion of ammonium. In tropical reefs, large quantities of fecal material are released in the water column during the day by planktivorous fishes; much of this fecal material is consumed by other fishes before it reaches the reef's surface (Robertson, 1982). A similar phenomenon occurs above rocky reefs off California. Hobson et al. (2001) observed that halfmoon and señoritas consume the fecal material from planktivores, mostly blacksmiths. At least some the diurnal feeders also defecate at night. One line of evidence comes from comparison of the fullness and location of food items in the digestive tract. The gut fullness of many fishes collected throughout the diel period show a progressive filling of the foregut, stomach, and intestine as the day passes, followed by similar pattern of elimination at night (e.g., Ebeling and Bray, 1976; Hobson and Chess, 1976; Cowen, 1983). Although this evidence has been used to support visual observations that the fish are diurnal feeders, it also means that the fish egest fecal material at night. For example, Cowen (1983) reported that the intestinal tracts of California sheephead are empty at dawn; that, coupled with the observation that sheephead were never seen defecating during the daytime, led Cowen to conclude that they defecate at night. Blacksmiths follow a similar diel pattern of gut fullness, with full guts in the afternoon and empty guts at dawn (Hobson and Chess, 1976; Bray, 1981).

Nighttime defecation was confirmed when fecal material was found at dawn in pipes occupied by sheltering blacksmiths (Bray et al., 1981). The fecal material does not accumulate along the rocky reefs. Detritivores such as shrimps and other crustaceans consume the feces (Rothans and Miller, 1991). Tagging evidence indicates some blacksmiths tend to return to the same nocturnal shelter, so the fecal material egested in nocturnal shelters represents a food source to detritivores that is predictable in time and space (Bray et al., 1981). For more discussion of feeding and trophic interactions please see chapter 13. This is but one example in which the diel cycles of activity of fishes may affect other members of the reef community.

Another possible community-level impact of fish activities involves excretion of ammonium as a result of nitrogen metabolism. Ammonium levels are higher in the vicinity of schools of Atlantic menhaden (*Brevoortia tyrannus*) (Oviatt et al., 1972) and juvenile grunts (*Haemulon flavolineatum* and *H. plumieri*) (Meyer et al., 1983). Off California, ammonium levels are higher within and just downstream of blacksmith aggregations during the daytime, and in shelters occupied by blacksmiths at night (Bray et al., 1986). Ammonium is an important nitrogen source for many algae so the excretion by fishes might contribute to the nutrient status of primary producers in inshore communities.

Comparison between Study Sites

The intensive community-level studies at Santa Catalina Island and Naples Reef provide an opportunity to compare activity patterns at different locations within the southern California bight (Ebeling and Hixon, 1991; Helfman, 1993). The fish community at Santa Catalina Island shares similarities with counterparts on tropical reefs. Both reef communities have a diurnal and separate nocturnal shift of active fishes and both have daytime resting aggregations and twilight migrations of fishes (Hobson et al., 1981). The diel activity pattern of the rocky reef fish community at Naples Reef is not as distinct. At night, fewer species forage in the water column, fewer species take shelter, and no fish move from reef to sand flat to forage; overall, Naples Reef at night appeared to be loosely programmed (Ebeling and Bray, 1976).

These local differences in community activity are probably due to several reasons:

1. Methodology. The Santa Catalina Island studies consist of general observations at various study sites throughout all times day and night with a focus on crepuscular hours. This approach integrates activities over large expanses of space and time but also confounds direct comparisons between day and night. The Naples Reef study involved paired day-night counts of fishes along a fixed transect line. This method allows direct comparisons of day-night activities, but observations and conclusions are focused in a small area around the line.
2. Physiography. The bottom profile at many sites around Santa Catalina Island drops off steeply from shore resulting in a horizontally compressed mixture of habitats. In contrast, Naples Reef is 1.6 km offshore and the gradually sloping bottom profile between shore and the reef consists of sand and low relief rocks. Habitats are spatially segregated and fewer fish may migrate to the reef itself.
3. Zoogeography. The species composition on rocky reefs varies along the California coast (see zoographical summaries by Cross and Allen, 1993; and Hobson, 1994).

Even within the southern California region, the fish community differs between Santa Catalina Island and the cooler areas off the coast of Santa Barbara and the northern Channel Islands. Santa Catalina Island has more representatives of primarily tropical while Santa Barbara has more cold-temperate species (Hobson et al., 1981; Ebeling and Hixon, 1991). Point Conception, less than 50 km west of Naples Reef, is a major zoogeographic barrier for tropical affiliates (Horn and Allen, 1978; Hobson, 1994). Because the species with the most distinctive diel patterns are from primarily tropical families (e.g., pomacentrids and labrids), the overall distinctiveness between day and night decreases in locations where these families are rare or absent.

COMPARISON BETWEEN TEMPERATE AND TROPICAL REEFS

Because day-night activities of reef fishes have been studied at several tropical and temperate locations, it is also possible to the compare the activities of California fishes with those found in tropical reefs. For the comparison, we chose Hobson's study of fishes at Bahia de Palmas (23°40'N, 109°42'W) near the tip of Baja California. Bahia de Palmas is a broad (18 km) sandy bay dotted with rocky outcrops (Hobson, 1965). Corals exist in the region but do not form reefs. The fish fauna consists mostly of Panamic representatives from the south mixed with a smaller number of northern and endemic species (Hobson, 1968). The diel activities of fishes at Bahia de Palmas are similar to those described in other tropical regions although the species richness is lower than other tropical reefs (see below).

Day-Night Differences

The most distinctive diel activity patterns of reef fishes occur in the tropics (Starck and Davis, 1966, numerous papers by Ted Hobson; Collette and Talbot, 1972). During the day, the water column is occupied with various pomacentrids, labrids, and other species while the bottom is active with numerous fishes that feed on algae, sea grasses, and sessile invertebrates (fig. 20-5e). At night, many of these species take shelter deep in reefs, where they do not feed. These species are replaced by other fishes equipped with large eyes and mouths that enable them to feed on large zooplankters that emerge at night from the substratum (fig. 20-5f). Thus, the water column just above coral reefs has day and night shifts of fishes that replace each other over a diel period. The diurnal species are more derived and have feeding and digestive specializations for consuming small zooplankters or benthic algae, respectively. The nocturnal feeders species are more generalized taxonomically and eat medium-sized prey that are available only at night (Collette and Talbot, 1972; Ebeling and Hixon, 1991; Hobson, 1991).

Some California reef fishes show day-night differences in magnitude comparable to those in the tropics. Conspicuous diurnal species in this category include the two pomacentrids (garibaldi, *Hypsypops rubicundus* and blacksmith) and three labrids (California sheephead, rock wrasse, and señorita)—all temperate representatives of primarily tropical families. These fishes are active during the daytime and seek shelter at night (fig. 20-5a–d). However, the day-night differences of many other diurnally active reef fishes off California are more subtle. For example, diurnally active bottom feeders off California, such as several species of embiotocids, spend the night in the open rather than take shelter (fig. 20-5b, d). They remain semi-alert at night and slowly move away if disturbed by divers. Gut analyses indicate that most surfperch (Embiotocidae) feed only during the daytime (Ebeling and Bray, 1976; Hobson et al., 1981).

The day-night differences of some of the nocturnal fishes off California are also less distinct than those in the tropics. Many tropical planktivores that feed above reefs at night take shelter individually and in small groups in holes and crevices during the day. These species include squirrelfishes and cardinalfishes, and soldierfishes (fig. 20-5f). In contrast, of the Santa Catalina species that are nocturnally active in the open water column (e.g., walleye surfperch, queenfish and salema, *Xenistius californiensis*), none shelters in reefs during the day; instead, they spend the daytime in dense, inactive schools (fig. 20-5d) (Hobson and Chess, 1976; Hobson et al., 1981). Thus, a major difference in nocturnal tropical and temperate planktivores is that during the day, the species on temperate reefs do not completely vacate the water column; they form inactive schools rather than take shelter in the reef.

Ebeling and Hixon (1991) compared the number of species with distinct diel activity patterns in tropical and California reefs based on a literature review. Ninety-four percent of the tropical species have a distinct activity period compared to 84% of the Californian species. The percentage was similar for fishes that were diurnal (55% tropical versus 53% Californian) and nocturnal (31% tropical versus 34% Californian) (Ebeling and Hixon, 1991). Another more dramatic tropical-temperate contrast involves the species richness. The number of species with known activity cycles observed in tropical studies ranged from 53 at Bahia de Palmas to 159 species in the Florida Keys. Far fewer species were reported off southern California (37 species at Santa Catalina Island and 23 species at Naples Reef). Thus, one obvious explanation for the tropical-temperate differences in diel activity patterns reflects the well-known differences in species richness between the two regions.

Dawn and Dusk Changeover

The period during the diel cycle that has attracted particular interest in coral reefs is the evening and morning changeover. This is the time when the diurnal shift of fishes occupying the water column is replaced by the nocturnal shift (e.g., Hobson, 1965; Collette and Talbot, 1972; Hobson, 1972) Helfman et al. (1997) provide a nice summary of the four different stages that play out over coral reefs during the dusk changeover. *Stage 1*: migrations made along the bottom by diurnal fishes that forage in one location and shelter in another. Fishes involved in these migrations are the zooplanktivores (e.g., some serranids, butterflyfishes, damselfishes) and large herbivores (parrotfishes and surgeonfishes). *Stage 2:* sheltering in crevices, holes, or ledges by diurnally active species. The timing varies according to family. Labrids are the first to shelter, followed by pomacentrids and other fishes. *Stage 3:* quiet period, starting after sunset, during which the water column above the reef is largely vacant. *Stage 4*: emergence and migration of nocturnal fishes. Fishes once again populate the water column, but in this case the species are adapted to feeding on zooplankton that emerge from the substratum at night. These fishes include bigeyes, cardinalfishes, soldierfishes, and croakers. At dawn, the process is reversed, starting with the migrations of the nocturnal fishes towards their shelters. The order of appearance of diurnal fishes is reversed, with pomacentrids among the early risers and the labrids being among the last to appear (Helfman et al., 1997). This pattern has been reported in the Gulf of California (Hobson, 1965), Hawaii (Hobson, 1972), and the Caribbean (Collette and Talbot, 1972).

What drives this well-ordered pattern of events? The best explanation for the quiet period over coral reefs is the threat of predation by piscivores at twilight. There are several lines of evidence for this. Direct observations (e.g., Hobson, 1968) indicate that large predatory fishes are more active during crepuscular hours. Additionally, studies of visual pigments and the light environment (McFarland, 1991) indicate that the sensitivity of scotopic (low-light) vision of many fishes better matches the characteristics of twilight than the starlight or moonlight. The argument is an evolutionary one: the visual sensitivity of fishes is tuned in to the lighting conditions that result in maximized fitness. Natural selection has led to the optimization of photon capture at twilight because of the increased threat of predation by large piscivores at that time (McFarland, 1991). The sheltering and emergence behaviors before and after the quiet period preempt predation on many fishes during the most vulnerable time.

The dawn and dusk changeover among California reef fishes appears more drawn-out and less obvious. The most conspicuous difference according to Hobson et al. (1981) is the apparent lack of a clear "quiet period" that is so characteristic of tropical reef fishes. The most detailed description of the evening changeover of California reef fishes was reported by Hobson et al. (1981). At sunset, the major event off Santa Catalina Island is the migration of blacksmiths to their nocturnal shelters. At about 10 minutes after sunset, the migrating groups start breaking up as individual blacksmiths take shelter. Approximately 10 and 20 min after sunset, the last of the señoritas, rock wrasse, and California sheephead take shelter. It is also during this time that the first olive rockfish (*Sebastes serranoides*) appear in the water column. It is not until at least 30 min after sunset that the first queenfish and salema appear at their feeding locations. In comparison, between approximately 12 and 32 min after sunset at Kona, Hawaii, the water column is vacant, forming the quiet period (Hobson et al., 1981). The major point is that off Santa Catalina Island there is little evidence of a distinct quiet period. Instead, the water column is occupied throughout dusk by the overlap of diurnally and nocturnally active fishes.

Several explanations have been forwarded for the temperate-tropical differences in fish activities during crepuscular hours (summarized in Helfman, 1993). Because the most distinctive differences between day and night behaviors involve representatives from primarily tropical families, the tropical-temperate difference might result from a latitudinal decrease in the abundance of tropical derivatives (e.g., Ebeling and Bray, 1976). Alternatively, since the tropical changeover may be driven by the threat of twilight predation, perhaps predation is less prevalent during crepuscular hours off California (Hobson et al., 1981). Another explanation is that temperate fishes tend to be larger than tropical counterparts, so the threat of predation might be reduced. Also, the twilight period itself is more drawn out in temperate areas, resulting in a more gradual change in light levels (Helfman, 1981). The abrupt evacuation of the water column by fishes during twilight may be because their visual adaptation mechanisms are too slow to keep up with the ambient light changes. On the other hand, the slower change in lighting in temperate areas give fish enough time to adapt visually, thus, reducing the need to dramatically alter behavior during twilight (Helfman, 1993).

Biological Clocks

A central question in the study of activity patterns is whether their control is exogenous (outside of the organism) or endogenous (inside of the organism). A set of terms describes these patterns. Circa patterns generally refer to activity patterns that are influenced by an internal biological clock (Ali et al., 1992). "Circadian" refers to a diel pattern; other common terms include circatidal, circasemilunar, circalunar, and circannual. A rhythmic pattern that continues under constant conditions (i.e., a circa pattern, is termed "free running" and is under the control of an internal time keeper). This biological clock does not keep perfect time, however, and must be reset periodically with an environmental cue, termed a Zeitgeber (German for "time giver"). Thus, many rhythmic activities, such as circadian rhythms, require at least two components: an endogenous clock and an exogenous cue to reset it.

Research over the past century has revealed two patterns that depend on the period of the activities. Patterns that take place repeatedly in less than one day (termed "ultradian") are primarily endogenous. At the subcellular level, for example, these rhythms are tied to oscillations in biochemical and neurogenic activity rather than rhythmic external factors (Peters and Veeneklaas, 1992). Activities that are diel and longer may be under endogenous and/or exogenous control (Gerkema, 1992).

Endogenous biological rhythms of fishes are under control of the neuroendocrine system (Helfman et al., 1997). The hormone melatonin, secreted by the pineal organ on the dorsal surface of the brain, appears to be a widespread timekeeping molecule that controls many physiological and behavioral functions (Zachmann et al., 1992). Melatonin concentrations follow a circadian rhythm, with elevated levels occurring at night. Photoperiod is the probably the most important environmental cue but temperature also plays a role (Zachmann et al., 1992).

Numerous studies have demonstrated the presence of circa rhythms in fish. Most studies have involved freshwater species (Ali, 1992) and only a few studies have been conducted on California marine fishes. The swell shark and horn shark display a circadian rhythm, actively swimming at night and sheltering in rocks during the day. In the lab, swell sharks maintain a distinct circadian activity under constant lighting conditions with increased movements occurring at a time that normally correspond to onset of darkness (Nelson and Johnson, 1970). Initial studies showed that horn shark activity was exogenous, not circadian (Nelson and Johnson, 1970); however, later experiments under different lighting intensities indicate that horn shark movements exhibit drifting circadian rhythm (Finstad and Nelson, 1975).

Studies of relatives of California fishes demonstrate endogenous control of patterns. For example, the diel activity patterns of labrids appear to be circadian. The diel activity patterns of *Halichoeres chrysus* in the western tropical Pacific are similar to the rock wrasse off southern California: it is active during the day and hides in the substrate at night. Laboratory studies by Gerkema (2000) indicate that individuals maintain this free running behavior under constant dim illumination. There is similar evidence of a circadian rhythm in *Coris julis,* which buries in sand at night (in Gerkema, 1992). Based on the evidence collected so far, it seems reasonable to hypothesize that the diel activities of the labrids and probably other fishes off southern California are under similar endogenous control.

Do fish sleep? This interesting question was discussed by Reebs (1992). The answer depends on the definition of sleep. The electroencephalograms (EEGs) of mammals, recorded in the cortex, display characteristic patterns during sleep. Fish do not have a cortex so sleep cannot be measured with this criterion. However, aquarium studies of one labrid and eight species of parrotfishes indicate that at night these fishes displayed behavior similar to a sleeping mammal: diminished overall activity, decreased responsiveness to stimuli, decreased and irregular respiratory movements—and periodic eye movement (Tauber and Weitzman, 1969).

Why do fish sleep? Circadian patterns of sleep may allow fish to conserve energy. Additionally, anticipation of sleep might force fish to seek shelter during times when they may be particularly vulnerable to predation (summarized in Reebs, 1992). This latter idea has support in studies of the importance of predation on California reef fishes, especially during crepuscular hours (Hobson et al., 1981). However, this does not explain why certain fish remain in shelters throughout the night. Hobson concluded that predation was most intense during crepuscular hours and decreased towards the middle of the night. At Naples Reef and off the Palos Verdes Peninsula in Los Angeles County, however, Pacific electric rays enter rocky reefs after sunset and hunt for fish prey (Bray and Hixon, 1978; Lowe et al., 1994). The rays swim slowly above the reef substratum and have been observed close to exposed fish. The stomach contents of one Pacific electric ray collected at dawn on the sand flat adjacent the reef contained two kelp bass and one black perch–both species that do not take shelter in rocky crevices. Additionally, California moray eels commonly feed on fishes at night. Large sheltering fish might be protected by their size but smaller fishes along the bottom may be vulnerable. The presence of nocturnal predators may help explain why many fish remain in shelters throughout the night. The threat of predation may also force small individuals to shelter deep in tiny crevices, as evidenced by the emergence of small fish, not previously seen, after application of the anesthetic quinaldine (Bray, pers. obs.).

The apparent universal nature of biological clocks begs the question about their adaptive significance. The prevailing idea about the adaptive significant of biological clocks, reviewed by Gerkema (1992), is centered on anticipation and synchronization. Anticipation involves the initiation of various physiological and biochemical mechanisms in preparation for upcoming activities. For example, the semilunar spawning cycle of grunions is preceded by a whole sequence of physiological steps (e.g., gametogenesis) in advance of the actual spawning run. Synchronization involves coordination of activities with conspecifics (to engage in schooling, feeding or spawning aggregations, etc), avoiding other species such as predators, and adjusting to periodic changes in the physical environment (e.g., light, tides). Overall, the central theme to all of these examples is that biological clocks enable anticipation of regular, predictable events (Gerkema, 1992).

Summary

While it is impressive to see how much we have learned about the movement and activity pattern of California fishes, there is still a lot of questions left unanswered. There are a number of good examples that suggest that fishes most closely associated with complex habitats tend to move less than those more loosely associated with habitat; however, there also appears to be a large amount of variability in behavior between species and individuals. Nevertheless, the general differences in movements are likely associated with energetic tradeoffs between finding food and mates, and avoiding predation or unsuitable abiotic conditions. In addition, many of the same tradeoffs have likely influenced the evolution of activity patterns that we see in marine fishes.

The recent development of new technology and techniques has significantly furthered our knowledge of fish movement and activity and it is likely these advances will continue. Because of the economic importance of many marine fishes in California, the need to understand fish behavior has increased, particularly for its application in resource and fisheries management. While we have a better understanding of the proximate mechanisms that influence movement and activity pattern in fishes, we still do not thoroughly understand the ultimate mechanisms behind these behaviors. In addition, while there has been a lot of research done to examine the movement patterns of larger fishes, there is still relatively little known about movements and space use of small fishes. Further investigation of ontogenetic shifts in movement pattern of fishes might lend support of the cost optimization models postulated in this chapter. This information could be extremely valuable to resource managers in developing better fisheries management models and when establishing marine protected areas.

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