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CHAPTER 14

Feeding Mechanisms and Trophic Interactions

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Introduction

The composition of the present-day California marine fish fauna is largely a reflection of trophic interactions, as stated by Hobson (see chapter 2). The diversity and complexity of the fauna are at least in part a response to these interactions over evolutionary time scales. As such, many of the feeding behaviors and associated morphologies of fishes in California waters have been shaped and honed in response to selective pressures specifically related to feeding performance. Whatever paths of evolution have resulted in this rich and varied fish fauna, the array of extant species represents much of the amazing dietary diversity seen among ocean-dwelling species in general. Fishes encounter prey that varies enormously in degree of mobility, habitat location, and in size, structure, digestibility, and nutritional content. Not surprisingly, fishes including those living in the sea off California are generally opportunistic and exhibit a wide variety of ways to capture and process food to meet their energy and nutritional requirements.

In this chapter, we first organize the subject of food and feeding in fishes into three parts and variously draw our examples from members of the California marine fish fauna. In the first part, we discuss factors that determine diet including body shape and feeding behavior, identify types of food capture, and describe several kinds of feeding mechanisms.

Second, we recognize some of the major types of food items consumed by representative taxa of the California fauna and associate these taxa with standard trophic level designations (i.e., herbivores, carnivores, and omnivores). Third, we use generalized profiles of trophic relationships to portray the main feeding interactions among fishes occupying: 1) bay-estuarine, 2) inner and outer shelf, 3) rocky intertidal, 4) rocky reef and kelp bed, 5) epipelagic, and 6) deep midwater habitats. The chapter broadly integrates with the treatments of predation (see chapter 16) and competition (see chapter 17) in this unit on population and community ecology and variously with all chapters (see chapters 5–13) in the unit on habitats and associated fishes.

Feeding Mechanisms

Overview

Body shape is clearly an important part of the mechanism for bringing the predator close enough to the prey or food item for it to then be consumed. Fishes have evolved streamlined shapes that facilitate sustained swimming for chasing down prey, robust shapes for burst behaviors that take prey by surprise, and cryptic shapes for evading detection by the prey until it is too late. Once the prey is within range, specific morphologies for capturing or otherwise obtaining and processing the item come into play. These structures might include features of the jaws (such as the number, size, and shape of teeth, and jaw length and width), neurocranium and suspensorium (to facilitate rotation and expansion of the head), and gill arches (such as the addition of teeth, epibranchial organs, or pharyngeal mills). These morphologies should combine with physiological features that enhance food capture abilities, such as highly developed systems for taking advantage of visual, olfactory, electrical, and auditory signals, as well as other cues related to the detection of a pressure wave propagated through water. The specific behaviors that a fish uses to locate, capture, and process a food item make up another category of traits that have been shaped over evolutionary time in much the same way as the physical features of the fish. Behavior and morphology, then, can be thought of together as creating the feeding mechanism. The mechanism, or suite of mechanisms, that any given individual possesses will set the boundaries on what food items can be taken from the environment.

The types of interactions that shaped the system in the past continue to occur in the present. An individual fish is constantly responding in real time to an onslaught of interference that prevents it from simply eating all of the items of which it is capable. These interactions can occur between individuals and the environment and may include such processes as weather, currents, and tides, as well as physical features such as substratum type and topography, salinity, and temperature. Any or all of these processes or features may restrict where an individual finds itself on short (minutes) or long (days to months) time scales.

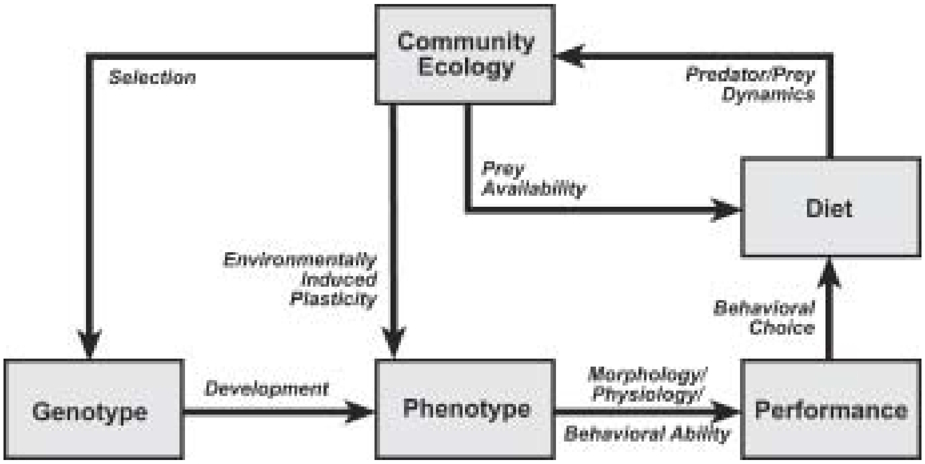

FIGURE 14-1 Possible scenario for how diet is determined. Implied in the Community Ecology Box are abiotic effects that impact interactions among species (after Ferry-Graham et al. (2004)).

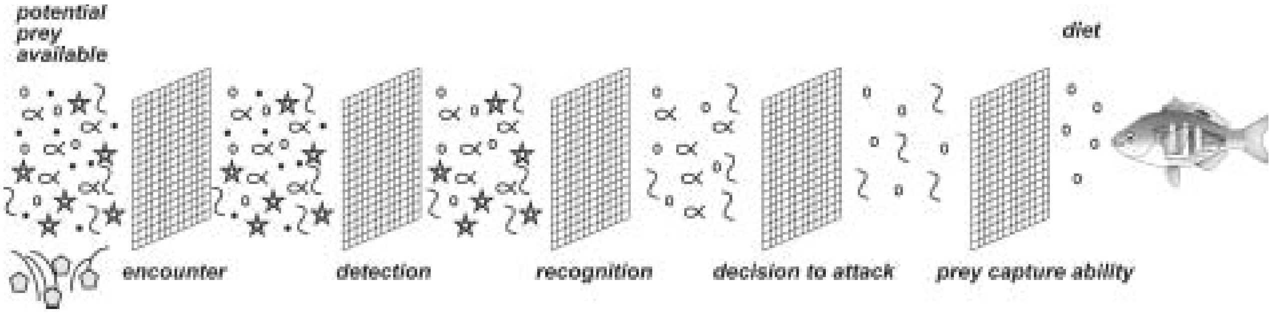

FIGURE 14-2 Schematic representing the set of factors that ultimately determine what an organism can eat and where they act in the process of foraging: *encounter* with prey, *detection* of the prey of the predator, *recognition* of the prey as something to eat, the *decision* to attack the prey, and, ultimately, the *ability* then to capture the prey successfully. Note that after each filter fewer types of prey remain available to the predator as a result of the exclusion of certain prey types. Prey types might be excluded because they are not *encountered* as a result of the part of the habitat used by the predator or the ecological interactions that restrict where the predator forages. Prey may not be *detected* or *recognized* because of sensory ability. Prey also may not be recognized as a result of behavioral learning (or a lack of it). The predator may *decide* not to attack the prey because of ecological interactions external to the prey item, such as predation risk, or because of behavioral cues that cause the predator to choose not to attack, such as they prey is too far away to be captured successfully. The *ability* to capture the prey successfully depends upon morphological, physiological, or behavioral capabilities. (After Ferry-Graham et al. (2004), and A. Cook, unpublished).

Interactions also will occur with other individuals of the same or different species in the form of predatory encounters and competition for food resources. These limitations force the fish to make choices about when and where to forage, what to try to eat and what to avoid, and, therefore, will restrict the diet to a subset of the available items.

Factors that Determine Diet

As ecologists, we tend to think of resource use, and feeding in general, as being shaped by the interactions of a species or an individual with both the environment and other community members. Clearly, such extrinsic interactions will partially determine which available prey items will ultimately become part of the diet. Nevertheless, the inherent abilities of the organism to capture and process prey also will affect diet and are determined by intrinsic factors such as organismal morphology or behavior. These extrinsic and intrinsic factors will act and interact to shape the diet of any given individual within an ecosystem (fig. 14-1). Some species have broad or generalized diets, containing a wide variety of prey items. Others have narrow diets composed of one or a few kinds of items, and are often said to be specialized. Species with broad diets may be composed of many generalized individuals each with broad diets, or of many specialized individuals each consuming different prey resources from the environment. Although each individual may consume a narrow range of prey, the population as a whole may appear to have a broad diet. The factors that determine diet in an individual or a species may be viewed as a series of filters that eliminates many potential prey and ultimately determines what an organism can and will eat (fig. 14-2).

Organisms must first encounter a potential prey item (fig. 14-2). Although this action ostensibly involves being in the right place at the right time, that place is determined in part by the extrinsic interactions experienced by the fish. For example, dispersal and recruitment will determine the environment in which a fish lives and forages and, therefore, will ultimately affect what items are available as potential prey for an individual or species. Both dispersal and recruitment will be shaped in part by environmental factors, such as currents and tides (see chapter 15). Similarly, avoiding competition (see chapter 17) will affect which prey are taken from those that are available. Dietary overlap between species or individuals is one mechanism thought to lead to competition, particularly when resources are limiting (Hardin, 1960; Alevizon, 1975; Hixon, 1980; Schmitt and Coyer, 1983; Schmitt and Holbrook, 1986; Holbrook and Schmitt, 1992). Competition may be reduced by the active avoidance of a particular prey by a species.

The above extrinsic forces acting on the fish, however, operate together with the intrinsic abilities of the fish. For example, a fish's swimming ability will determine whether it forages near shore or in open water. The foraging range of the fish will, in turn, affect which prey are encountered and can potentially be included in the diet. Similarly, the abilities of the fish to swim quickly may allow it to exclude other potential predators from a prey item (see chapter 17). These intrinsic features are further shaped by interactions with both the environment and other individuals and species over evolutionary time (Abrams, 1983; Robinson and Wilson, 1994); thus, extrinsic forces continue to play a large role in shaping diet. The intrinsic abilities of the fish ultimately, however, will determine where it can forage successfully, which will differ among individuals and species. The range of these intrinsic features, of course, is enormous among fishes, and extremes of body shape and travel distance can illustrate this point. For example, the streamlined and muscular bluefin tuna (*Thunnus thynnus*) swims continuously and migrates along coastlines of the northeastern Pacific and across the north Pacific basin participating in various food chains along the way (Bayliff, 2001). In contrast, the blunt and elongate monkeyface prickleback (*Cebidichthys violaceus*) swims only a few minutes per day, in a series of short forays, and even then within an area of only a few square meters of the rocky intertidal habitat (Ralston and Horn, 1986).

The second filter affecting diet is the fish's ability to detect the prey using visual, auditory, olfactory, or other sensory abilities (fig. 14-2). This filter, in large part, is determined by the intrinsic abilities of the fish. Prey detection, for example, in the blue shark (*Prionace glauca*) and albacore (*Thunnus alalunga*), two epipelagic fishes occurring in the northeastern Pacific with overlapping diets (see epipelagic trophic relationships, below), differs because the shark relies more on olfaction and electroreception than the tuna, which primarily uses vision (see Helfman et al., 1997). The predator must then recognize the prey as something good to eat, which may depend upon acquired knowledge or learning. Herbivorous fishes, for example, avoid eating unpalatable seaweeds, which probably involves a combination of evolved recognition and proximal learning, the latter especially if the seaweed community changes seasonally, or if a fish species such as the zebraperch (*Hermosilla azurea*) expands its range and encounters a different mix of potential algal dietary items (Sturm and Horn, 1998, 2001).

This recognition must be followed by a decision to attack the prey, which may be based upon an assessment of the prey's energy value or handling costs. The decision to attack also may be mediated by extrinsic factors such as risk to the predator of being attacked by a larger predator (the focus of chapter 16). Those who have studied and tried to observe the cryptic fishes of rocky intertidal habitats such as sculpins (Cottidae) and kelpfishes (Clinidae) know that they seldom appear or venture far from their protective base.

Ultimately, the predator then must possess the ability to capture the prey successfully. This ability will depend on the type of capture method employed, the suite of morphological features on hand for performing that type of prey capture, and the behavioral traits necessary to perform the action (discussed below). If a foraging fish is able to perform more than one type of prey capture behavior, then the fish must choose which behavior to employ in any given situation and in such a situation risks choosing inappropriately and missing its meal. Appropriate examples here are generalized feeders such as the topsmelt (*Atherinops affinis*), a silverside that feeds either on zooplankton or benthic prey in kelp beds or primarily on macroalgae and detritus in bays and estuaries (see Trophic Interactions below) or senorita (*Oxyjulis californica*), a wrasse that either picks moving prey from the water column or removes attached or encrusting animals from surfaces (see rocky reef and kelp bed trophic relationships, below)

The filters described in fig. 14-2, however, are not simply passive sieves; rather, they act and interact with one another creating a probability distribution at each juncture that determines which prey will remain at the next decision-making step (Ferry-Graham et al., 2004). The probability that a predator routinely encounters a certain prey item can affect the probability, for example, that the same predator will then recognize that prey item as something good to eat. Working in the opposite direction in fig. 14-2, the probability of a successful capture given the morphology of the predator may influence the likelihood that the predator decides to capture the prey item. Thus, fig. 14-2 represents a simplified series of steps that lie between a predator and its prey.

Such filters, nevertheless, represent criteria that distinguish among species and separate their diets. Potential prey may be the same for all species, but the prey that an assemblage or a guild of species encounters, however, will differ if the search behaviors of assemblage members are different. Prey detection may then depend, for example, upon the differing neurological abilities of the associated species, as might prey recognition. The decision to attack will depend at least in part upon the predator's ability to assess features of the prey and then to evaluate those features, effectively weighing them against some scale established in its evolutionary history or learned in its own lifetime. The decisions that are made and the ability to make those decisions can further separate species and their diets (Ferry-Graham et al., 2004). Ultimately, successful capturing and processing of any given item depend upon a suite of interacting factors that determine the abilities of the organism as distinct from its external influences (Ferry-Graham et al., 2004).

Types of Prey Capture

Several kinds of prey capture are employed routinely by fishes. These foraging modes include suspension and filter feeding, grazing and picking, active predation, and scavenging. Suspension and filter feeding encompasses an array of actions whereby small particles or organisms are strained or otherwise separated from the surrounding water using a porous structure, usually the gills and associated elements (fig. 14-3; Rubenstein and Koehl, 1977). Water may enter the fish's mouth and pass over the gills via one or both of two processes (Sanderson and Wassersug, 1993): 1) ram, where the fish moves through the water using forward locomotion thereby allowing large portions of water to enter the mouth, or 2) suction, where the water is drawn into the mouth through the expansive actions of the fish's head. Fish species that use suspension or filter feeding tend to obtain their energy near the base of the food

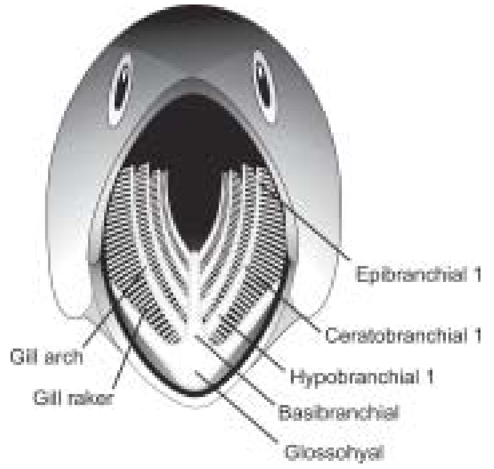

FIGURE 14-3 A head-on view of a generalized suspension feeding fish with the gill arches evident. The approximate locations of the bones that compose the branchial arches that are visible in this view are indicated: the glossohyal, the basibranchial, and hypobranchial 1, ceratobranchial 1, and epibranchial 1 on arch 1. See also figure 14-5. Drawing modified after Sanderson and Wassersug (1990) and Sanderson and Cheer (1993), with permission of S. L. Sanderson.

web and to reach either large population sizes, as in Pacific herring (*Clupea pallasi*), or large body sizes, as in the basking shark, *Cetorhinus maximus* (Sanderson and Wassersug, 1993).

Pickers and grazers tend to forage on attached prey items, although technically speaking, grazing may include any mode of feeding that facilitates herbivory, or general planktivory. Thus, open-water filter-feeders, such as northern anchovy (*Engraulis mordax*), that capture phytoplankton and (mainly) zooplankton may be considered grazers. Blacksmith (*Chromis punctipinnis*), which pick zooplankton from the water column (Bray and Ebeling, 1975), also could qualify as grazers in this broad sense. Grazers, however, are more often thought of as those species that bite, clip, or scrape from larger plant or algal material although herbivores are sometimes divided into species that graze, if sediment is ingested in the scraping or sucking process, or browse, if they bite or tear relatively upright macroalgae and rarely ingest any inorganic material (Horn, 1989). Based on this distinction for herbivores in California waters, striped mullet (*Mugil cephalus*) would be classified as a grazer, monkeyface prickleback as a browser, and zebraperch as a combination grazer/browser (Horn, 1989; Sturm and Horn, 1998). The senorita picks bryozoans off the surface of giant kelp (Bray and Ebeling, 1975) with behaviors similar to that of a grazing herbivore and thus can included in the picker and grazer category.

Picking also may be used to describe the behaviors used by fish to take small items that rest on but are not attached to the substratum. These small prey items remain largely stationary relative to the movements of the predator. Fish species that winnow prey also may be included in this category in the sense that they are selecting small prey by extracting them from a larger collection of items. The black perch (*Embiotoca jacksoni*), for example, scoops up large amounts of algal turf in its mouth and then uses repeated cyclic actions of the oral and pharyngeal jaws to separate nutritive from non-nutritive items, the latter of which are ejected from the mouth (Drucker and Jensen, 1991). Like suspension and filter feeders, pickers and grazers tend to feed low in the trophic structure, either as herbivores or primary carnivores.

Active predation typically encompasses the behaviors used to capture mobile prey items ranging from shelled invertebrates to other fishes. Predatory fishes tend to use one of several modes to locate prey and approach close enough to initiate prey capture. These modes (with examples) include: pursuit/chase (shortfin mako, *Isurus oxyrinchus*), group hunting (bluefin tuna), lurking (Pacific barracuda, *Sphyraena argentea*), lie-in-wait (angel shark, *Squatina californica*), disruptive coloration with slow approach (striped bass, *Morone saxatilis*), and luring prey (Pacific dreamer, *Oneirodes acanthias*). Once prey is selected, the remainder of the predatory event can be divided into two components (Cook, 1996): 1) the attack (which begins when the predator accelerates toward the prey and is linked intimately to the locomotor abilities of the predator) and 2) the strike (which is the part of the event that begins with the opening of the mouth and ends when the mouth closes) this part is tied more closely to the features of the head and jaws as related to prey capture. The strike typically consists of one of three methods of prey capture or a combination of these methods (Liem, 1980): 1) ram, where the predator swims to overtake the prey; 2) suction, as described above; and 3) manipulation, such as biting large pieces of flesh from a prey item. Predatory fishes that use these behaviors range from the small, intertidal mosshead sculpin, *Clinocottus globiceps* (Yoshiyama et al., 1996a,b) to the large, epipelagic white shark, *Carcharodon carcharias* (Tricas and McCosker, 1984) and occupy virtually all habitats including the deep sea (Gartner et al., 1997). As predators, these fishes tend to occupy the higher trophic levels in a food web.

Similarly, even though their prey is no longer mobile, scavengers may use the same modes of prey capture (i.e., combinations of ram, suction, and manipulation). Scavengers occur at almost all ocean depths, from white croaker (*Genyonemus lineatus*) in the surf-zone (Stephens et al., 1957) to rattails (Macrouridae) on the deep-sea floor (Pearcy and Ambler, 1974; Gartner et al., 1997; chapter 13).

Feeding Mechanics

Years of study have led to the general categories of prey capture and processing behavior briefly summarized in the previous section. These invaluable findings result from the careful description of how species capture prey; the quantification of literally dozens of variables has told us how features of the head and jaw move relative to one another on the predator and how the predator moves relative to the prey (e.g., Alexander, 1967; Alexander, 1970; Anker, 1978a,b; Liem, 1978; Liem, 1979). The modes of feeding by fishes as defined by their mechanics can be divided roughly into two categories: 1) those that rely on the activity of the oral jaws, such as suction feeding, ram feeding, and biting, and 2) those that rely on features of the pharyngeal jaws and other organs derived from the gill arches, such as suspension feeding and prey processing with these jaws.

BITING

Although any given fish generally can use ram, suction, or biting for prey capture to some extent, species that rely primarily on biting as a means of capturing prey are thought to possess functional morphological features that enhance that mode. Biting is best achieved with forceful closure of the jaw elements that facilitates removal of an item from a larger part or

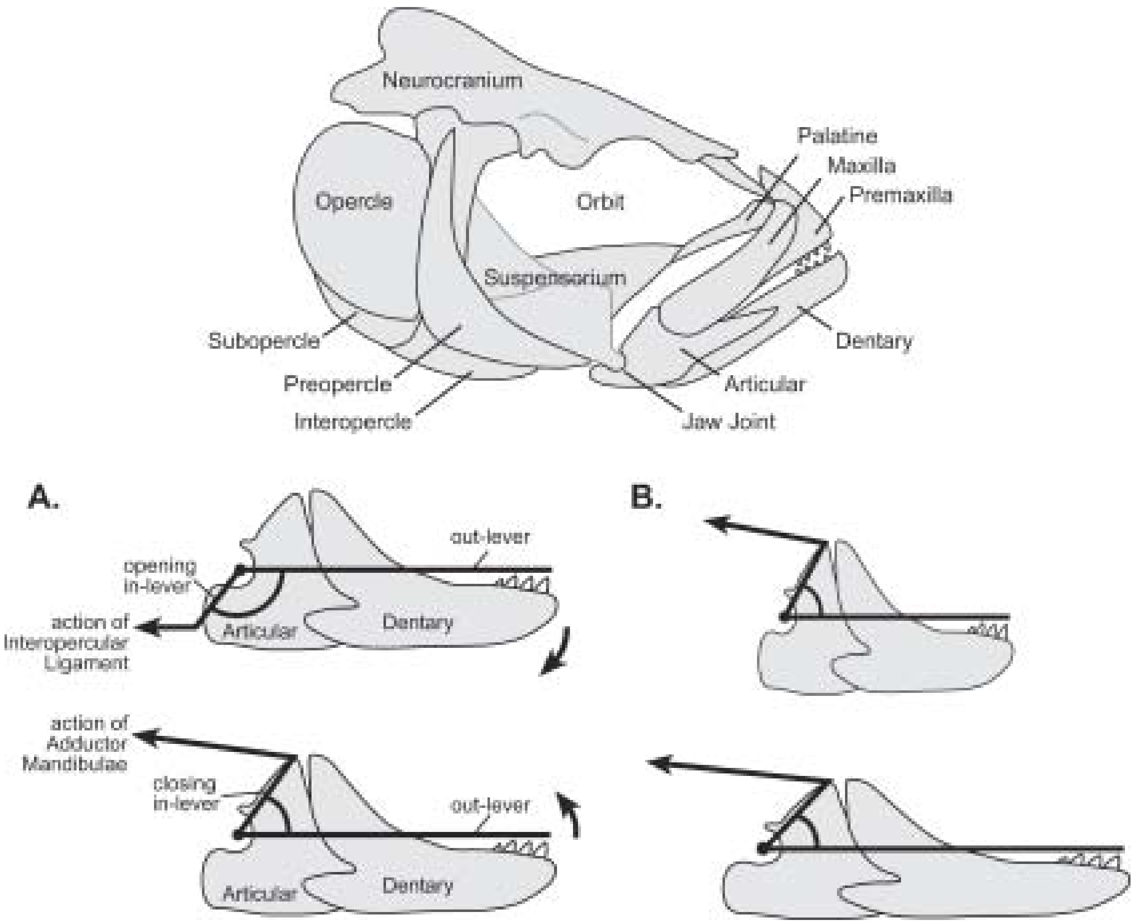

FIGURE 14-4 A highly generalized teleost skull with many of the superficial elements eliminated for clarity, such as details of the neurocranium and the orbital bones. Aspects of the upper (premaxilla and maxilla) and lower jaw (dentary and articular), suspensorium, and opercular series (opercle, sub-, pre-, and interopercle) are indicated. In A, generalized fish lower jaw with the opening (top) and closing (bottom) lever arms indicated. The jaw rotates about the fulcrum in response to an input force provided by the muscular actions drawn (force may be transferred by ligamentous connections). The direction of rotation is indicated by the arrow. The output force, used by the organism to obtain the prey, will be proportional to the ratio of the in-lever length to the out-lever length. Thus, as seen in B, a shorter out-lever, and relatively longer in-lever, will be better for producing the higher jaw closing forces useful for biting (top). A longer out-lever will be better for faster movements (bottom). Skull modified after Gregory (1933). Lower jaw drawings modified after Richard and Wainwright (1995), with permission of P. C. Wainwright.

from the surface to which it is attached. A number of seemingly reliable morphological correlates have been observed in biting predators. Biting and other manipulative modes of prey capture are often seen in predators possessing enlarged or hypertrophied jaw bones and musculature, which have been shown to enhance force production (Turingan and Wainwright, 1993; Turingan et al., 1995; De Visser and Barel, 1996).

Several studies, however, suggest that there is a trade-off in performance of feeding by suction when taxa are modified to enhance biting. For example, the structure of vertebrate musculoskleletal systems generally is thought to be constrained such that force production and speed of contraction cannot be maximized simultaneously. Architectural changes that provide for increased mechanical advantage during jaw closure come at the cost of jaw closing speed (Barel, 1983; Westneat, 1994). Also, morphological arrangements that facilitate biting may even decrease the capacity for head expansion and subsequent suction feeding ability (De Visser and Barel, 1996; Bouton et al., 1999). The traits associated with biting or suction feeding have been well studied, and, because these traits tend to be mutually exclusive, reasonable success has been achieved in predicting the primary mode of prey capture that will be used by a particular species and in a given situation. We know, for example, that more force is produced by a muscle with a larger cross-sectional area relative to a muscle with a smaller cross-sectional area. A large muscle mass, however, is difficult to move quickly, and long, slender muscles are better for producing rapid movements (Wainwright et al., 1976). A long muscle also can move the element to which it is attached over a larger angle than can a short muscle, thus producing larger movements (Wainwright et al., 1976). By the same token, longer bony elements also tend to be more often associated with speed rather than force (fig. 14-4). Thus, it follows that short, robust jaws are useful for producing force and eating hard prey.

SUCTION AND RAM FEEDING

Fish that are feeding on unattached prey also have to contend with the aquatic medium itself, which is dense and viscous relative to air. These characteristics of water pose a problem for aquatic predators whether they feed on tiny suspended particles or large active prey although the magnitude of the problem will vary with the size of the prey and the drag forces acting on the prey. As a fish moves through the water to capture prey, it will generate a bow wake that pushes the prey away unless the pursuing fish somehow compensates for its own forward locomotion. A feeding fish can either expand both the oral and opercular cavities, effectively creating a tube with openings at both ends that moves through the water with little resistance (a pure ram behavior), or some suction must be generated. Suction may be generated to draw the prey into the mouth, referred to as inertial suction, or may be used only to compensate for the bow wake, called compensatory suction (van Damme and Aerts, 1997). Suction is a common solution to the problem of dealing with the dense and viscous medium; in fact, nearly all fish species are thought to produce some suction. This reliance on suction is regarded as a major evolutionary constraint on the mechanics of fish feeding, and may well have led to the similarities in prey capture behavior that are seen across widely divergent aquatic taxa (Lauder and Pendergast, 1992).

Effective suction feeding depends primarily upon the ability to expand the head and draw water in from the surrounding area. The head is first compressed, forcing out any water inside of the oral cavity. The cavity is then rapidly expanded, creating a region of reduced pressure inside the mouth relative to the ambient pressure in the surrounding medium. Water flows into the region of reduced pressure through the open mouth. In the case of inertial suction, the prey item is trapped in this flow of water and therefore drawn into the predator's mouth. More rapid or larger expansion of the oral cavity helps to produce relatively more suction for prey capture (Liem, 1980). Then, of course, the mouth must close on or around the prey item in a timely manner to prevent the prey's escape.

Researchers have focused on only a few variables as predictors of whether a fish will rely primarily upon ram or suction to capture active prey. These predictors include morphological variables, such as oral cavity volume and mouth size, and behavioral variables, such as strike distance and velocity. Efficient suction feeders hypothetically should have smaller mouths, as this trait will tend to increase the velocity of water rushing into the mouth (Norton, 1991). Suction, however, is quickly dissipated and is not effective over large distances, so that suction-feeding fish are thought to strike very close to their intended prey (Cook, 1996). Arguably, then, suction feeding may be more useful in capturing stationary or less mobile prey (Norton, 1991; Norton, 1995). Correlations between mouth size and predator-prey distance seem to hold in the sculpin species in which such relationships have been tested. For example, small-mouthed species such as mosshead sculpin (*Clinocottus globiceps*) tend to have small predator-prey distances and lower attack velocities (Norton, 1991; Cook, 1996) and reduced success on elusive prey (prey that can escape via locomotion) as compared to larger-mouthed species such as smoothhead sculpin, *Artedius lateralis* (Norton, 1991). The smaller-mouthed species are assumed to produce more suction than the larger-mouthed species to capture the same prey, but this assumption has not been demonstrated. When offered multiple prey types, however, another scorpaeniform fish, the kelp greenling (*Hexagrammos decagrammus*), increases attack velocities and predator-prey distance in response to more elusive prey, behavioral changes thought to be associated with ram feeding (Nemeth, 1997a). More elusive prey also elicit greater sub-ambient pressure peaks in the oral cavity, indicating greater expansion of the head and presumably increased water velocity entering the oral cavity (i.e., greater suction produced in response to elusive prey (Nemeth, 1997b)). Larger intra-oral pressure changes were observed only in response to clinging prey that could grasp the substratum. In contrast, truly non-elusive prey elicited much smaller changes in intra-oral pressure (Nemeth, 1997b), suggesting that the use of suction is not reserved categorically for less mobile prey.

In terms of predicting whether predators are primarily ram or suction feeders, the accuracy of morphological indicators such as mouth size remains uncertain. Strictly speaking, if all other factors are held constant (e.g., rate of head expansion, amount of expansion behind the mouth), flow velocities should be higher through a smaller rather than a larger mouth opening. Making such a comparison, however, is challenging because of the difficulty of finding two fish species in which all other factors are the same and only mouth size changes. Recent findings clearly show that individual behavior will affect how the prey are captured, and species that appear to be better suction feeders may not actually use more suction than their counterparts when capturing the same prey (Wainwright et al., 2001). Thus, predicting whether predators will use ram or suction without actually measuring the amount of suction produced (i.e., through intra-oral pressure measurements) has become a difficult task.

SUSPENSION FEEDING

In the case of filter or suspension feeding, the structures within the fish head, such as the gill arches (fig. 14-3), frequently are assumed to be used to sieve items from the water (Rubenstein and Koehl, 1977). In fishes, sieving is typically facilitated by one or two rows of gill rakers that are present on each of the five gill arches (Sanderson and Wassersug, 1993). Particles that cannot pass through the pores of the sieve are trapped and ingested. Some fish may even be able to adjust the position of the arches to alter the pore size of the sieve (Hoogenboezem et al., 1990; Hoogenboezem et al., 1991).

Sieving, however, is only one mechanism of particle extraction. Particles also may be trapped on the gill elements through direct interception, inertial impaction, or gravitational deposition (Rubenstein and Koehl, 1977). The distinction between these three methods depends primarily on the size of the particles and secondarily on the velocity of the flow around the gill elements. Very small particles that are essentially without mass will be captured by a raker by direct interception if the particle passes close enough to that raker (less than one particle radius). If the particle is farther away from the raker, it will continue past the raker and not be captured. The paths of larger particles tend to follow the flow streamlines entering the mouth. If the particles are restricted to these streamlines, they will miss the rakers entirely. When fluid passes a raker, however, it tends to be diverted and accelerated. Because of their own inertia, larger particles will deviate from the streamlines in this region of accelerated flow and also will impact a raker if they pass within one particle radius. The intensity of inertial impaction will increase with increasing velocity, as well as with increasing raker diameter. Relatively large particles tend to sink as a result of gravity. If these large particles fall within one radius of a raker, they will be deposited. Gravitational deposition will increase with increasing particle size but reduced with increasing flow velocity.

The gill arches, however, may not be the only feature important for prey-trapping techniques. Several microphagous fishes possess epibranchial organs, a pair of diverticula that

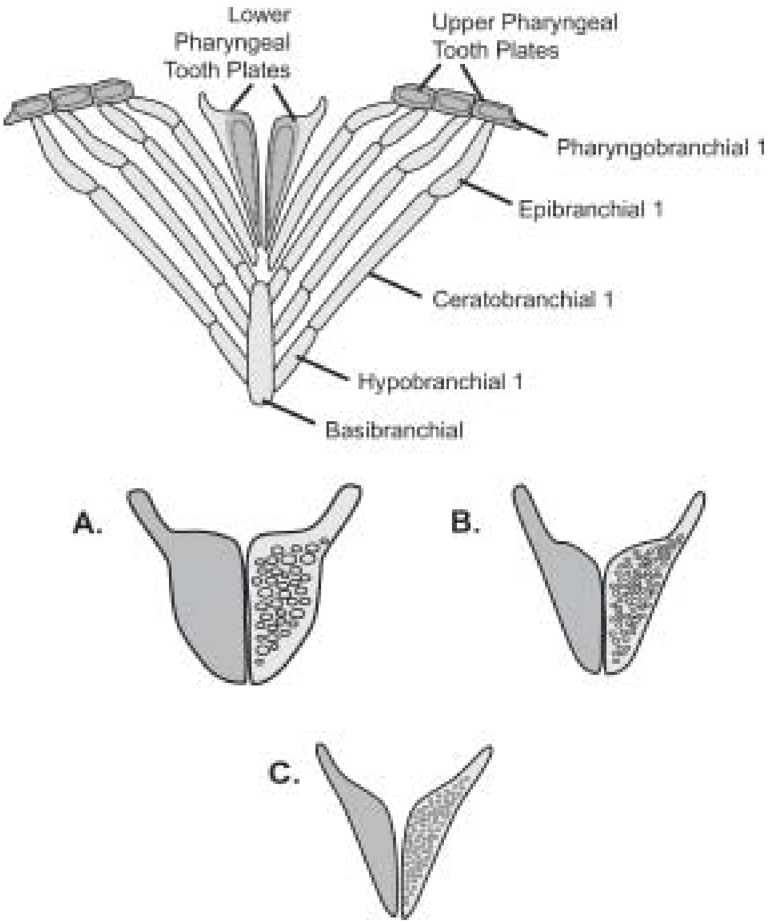

FIGURE 14-5 Generalized teleostean gill arches with details of the pharyngeal jaws indicated. Like some filter-feeding mechanisms, the pharyngeal jaws represent a series of modifications to the gill arches. The lower pharyngeal jaw is actually the fifth, or most posterior, ceratobranchial. The upper pharyngeal jaw comprises several pharyngobranchials. The size and shape of the tooth plates on these elements vary and are presumed to correlate with the types of prey processed by the jaws. A represents the dorsal surface of the lower pharyngeal jaw of a species that eats primarily hard prey, and always uses its pharyngeal jaws in a crushing pattern regardless of prey type in the lab (see Lauder, 1983). B represents that of a species that uses a crushing behavior only when hard prey are consumed. C represents that of a species that cannot crush hard prey. Details of the toothed surfaces of the lower pharyngeal jaws are shown on the right side of the jaw only. Gill apparatus modified after Collette and Russo (1985) and Cailliet et al. (1986). Lower pharyngeal jaw drawings modified after Lauder (1983) with permission of G. V. Lauder.

project from the pharynx above the esophagus. The gill rakers direct water flow towards these organs where food is trapped and formed into a bolus that then can be swallowed. Epibranchial organs are found in the Clupeiformes, Cypriniformes, Salmoniformes, Gonorynchiformes, and Osteoglossiformes (Sanderson and Wassersug, 1993). This list means that, in California marine waters, northern anchovy, Pacific sardine (*Sardinops sagax*) , Pacific herring, and the species of Pacific salmon (*Oncorhynchus* spp.) possess an epibranchial organ.

Stromateoid fishes, including Pacific pompano (*Peprilus simillimus*), which occurs in California waters, also are characterized by a type of epibranchial organ, which appears to be a specialization associated with macerating the jellyfishes and other gelatinous zooplankton that form a major part of the diet of many of the species (Haedrich, 1967; Horn, 1984).

Sanderson et al. (1991) used endoscopy and flow velocity probes to visualize the flow patterns inside the head of feeding Sacramento blackfish (*Orthodon microlepidotus*), a freshwater species, and revealed that water does not flow between the gill arch structures. Rather, water is directed to the mucus-covered roof of the oral cavity. Only through the quantification of the flow regime inside the actively feeding blackfish head was this novel technique for suspension feeding detected. In the Nile tilapia (*Oreochromis niloticus),* another freshwater species, strands of mucus hanging from oral structures are used to trap tiny particles such as bacteria in a technique called aerosol filtration (Sanderson et al., 1996). Whether any California marine fishes use this mechanism is unknown.

PREY PROCESSING BY PHARYNGEAL AND ORAL JAWS

Soft prey may be swallowed as soon as they are captured; however, hard prey, such as shelled invertebrates, often require additional physical processing. This further breakdown is achieved in many species of bony fishes by sequences of repeated crushing and shearing actions performed by the pharyngeal jaws (fig. 14-5). In truly durophagous species, the pharyngeal jaws and their associated musculature are extremely hypertrophied to enhance force generation or crushing ability, much like the biting predators described earlier in this section. Two California marine species, the pile perch (*Racochilus vacca*), which feeds on molluscs, crabs, and sand dollars (Limbaugh, 1955; Quast, 1968), and the California sheephead (*Semicossyphus pulcher*), which feeds on sea urchins, other echinoderms, and other hard-shelled invertebrates (Limbaugh, 1955; Cowan, 1986), both use their massive pharyngeal jaws to crush the shells of their prey (Brett, 1979; Hobson and Chess, 2001).

The hypertrophy of these jaws and their associated musculature is evolutionarily convergent across many families of fishes worldwide. Representative species can be found within the wrasses (Labridae, Wainwright, 1988), grunts (Haemulidae, Wainwright, 1989), croakers and drums (Sciaenidae, Grubich, 2000), jacks (Carangidae), and freshwater sunfishes (Centrarchidae, Wainwright et al., 1991). Extreme morphological modifications such as hypertrophied pharyngeal jaws are thought to have led to dietary specialization on particular prey types that cannot be eaten by unmodified fishes in the same habitat (Wainwright, 1988; Meyer, 1989; Wainwright, 1991). This limitation may be explain why such changes have evolved repeatedly in different fish families and in a myriad of habitats; such specialization may pose a distinct advantage when selection pressures lead to partitioning of resources within a community (Lauder, 1983).

Some species of fishes have well-developed oral jaws that also are used for crushing their prey. Oral jaw processing is most well-studied in the tropical pufferfishes (Tetraodontidae, Turingan and Wainwright, 1993; Ralston and Wainwright, 1997), butterflyfishes (Chaetodontidae, Harmelin-Vivien and Bouchon-Navarro, 1983; Motta, 1989; Sano, 1989; Cox, 1994), and parrotfishes (Scaridae, Gobalet, 1989; Bellwood and Choat, 1990; Alfaro and Westneat, 1999). These species take prey from coral reefs, often taking the coral itself, and thus require the ability to break down the food mechanically before it is transported into the gut. The California sheephead, among fish species in California waters, possesses well-developed oral jaws that are involved along with the pharyngeal jaws in crushing hard-shelled prey such as sea urchins (L. Ferry-Graham, pers. obs.). A number of chondrichthyans, such as the spotted ratfish, *Hydrolagus colliei* (Allen, 1982), bat ray *Myliobatis californica* (Karl and Obrebski, 1976), and horn shark *Heterodontus francisci* (Edmonds, 1999) consume hard-shelled invertebrates and possess either tooth plates or molariform teeth for processing such prey. The same performance trade-offs exist for oral jaw processors as for pharyngeal jaw processors and biting predators, and potentially the same advantages are offered in the form of dietary specialization relative to other community members.

Trophic Categories

The foregoing discussion of feeding mechanisms in fishes with frequent examples drawn from the California marine fauna provides the background for the second and third parts of this chapter. The diversification of ways in which fishes acquire and process food provides insight concerning the trophic levels that different fish species are expected to occupy in California waters. In turn, these two kinds of information lead to the general formulations of trophic relationships found among fish species in different marine habitats in California.

Herbivores

Fish species that consume phytoplankton, macroalgae (seaweeds), or seagrasses as a major part of the diet are rare in California waters as they are in all temperate zones in the world's oceans (Quast, 1968; Choat, 1982; Gaines and Lubchenco, 1982; Horn, 1989; Horn and Ojeda, 1999). As seen in the trophic relationships depicted in the next section, fish species with a majority of the diet comprising primary producers are found only in bay-estuarine, rocky intertidal, and rocky reef/kelp bed habitats. Fewer than 10% of the species in the assemblages occupying these habitats qualify as herbivores (Horn, 1989). In bays and estuaries, striped mullet and topsmelt can be considered as herbivores (Horn and Allen, 1985). Rocky intertidal habitats contain two herbivorous fish species in the monkeyface prickleback and rock prickleback, *Xiphister mucosus* (Barton, 1982; Horn et al., 1982; Horn and Ojeda, 1999), but other species including bald sculpin (*Clinocottus recalvus*), smoothhead sculpin, and reef perch (*Micrometrus aurora*) eat considerable amounts of algae (see chapter 8). In rocky reef and kelp bed habitats, the three most prominent consumers of macroalgae are halfmoon (*Medialuna californiensis*), opaleye (*Girella nigricans*), and zebraperch (Quast, 1968; chapter 9), with blue rockfish (*Sebastes mystinus*) also eating some macroalgae on a seasonal basis (Hallacher and Roberts, 1985). The reasons for the rarity of herbivorous fishes in temperate waters despite the often high standing stocks of macroalgae remain poorly known, but possible causes have been proposed (Choat, 1982; Gaines and Lubchenco, 1982; Horn, 1989; Harmelin-Vivien, 2002; Ferreira et al., 2004). Most likely among these possible explanations is that food-processing rates are more limited at the relatively low temperatures of the temperate and polar zones, which may impart the need for more energy-rich (i.e., animal) food sources in these higher latitudinal zones than in tropical waters (Harmelin-Vivien, 2002). Filter-feeding of phytoplankton and grazing and browsing on macroalgae represent the main feeding modes of herbivorous fishes in California marine habitats.

Detritivores

The degree that detritus contributes significantly to the sources of carbon remains poorly understood for most food webs involving fishes in California waters. Detritus perhaps plays its most prominent role as a carbon source in bay-estuarine habitats with their diverse array of primary producers, either in the water in the form of seagrass, phytoplankton, and macroalgae, or in the adjacent salt marshes in the form of marsh grass or other wetland vegetation. Striped mullet and topsmelt (Horn and Allen, 1985; Kwak and Zedler, 1997) probably are two of the most important detritivores in California bays and estuaries, but both species also consume microalgae and macroalgae, which confounds their role as consumers of detritus. The main feeding mode used by these two species for consuming detritus likely is suction feeding on the surface of soft-bottom bay-estuarine habitats. Detritus also contributes to the carbon source of fishes of inner and outer shelf and rocky intertidal habitats but indirectly through invertebrate detritivores.

Carnivores

The great majority of fish species in California marine habitats primarily consume animals, as they do in other marine habitats worldwide even on tropical reefs where herbivory is at its peak (e.g., Horn, 1989; Choat and Clements, 1998; Harmelin-Vivien, 2002). Crustaceans are the most abundant and frequently occurring items in the diets of fishes in all marine systems in California. This dominance as a food resource for fishes probably reflects the great abundance, wide size range but especially small size, and ubiquitous occurrence of crustaceans in marine habitats. Carnivorous fishes can be divided into three groups: 1) those that feed in the water column on zooplankton, 2) those that feed on the bottom or other surfaces, and 3) those that feed mainly on other fishes or larger invertebrates.

ZOOPLANKTON FEEDERS

The most well-known planktivorous fishes in California are the clupeoids in general, but, in particular, northern anchovy, Pacific sardine, and Pacific herring. Planktivory also occurs among a few species of rocky reef and kelp-bed fishes, among most species of vertically migrating midwater fish species, and in a few pelagic species of large body size, such as the basking shark in California waters. Zooplankton, not phytoplankton, makes up the bulk of the diets of planktivorous fishes, and crustaceans are the dominant members of the zooplankton community in all of these habitats. Filter-feeding and picking (by biting) are the principal feeding modes used by plankton-feeding fishes.

BENTHIC INVERTEBRATE FEEDERS

Species that eat bottom-dwelling invertebrates are the most diverse group of fishes associated with both soft substrata, as in bay-estuarine and inner and outer shelf habitats, and hard substrata, especially rocky intertidal and rocky reef and kelp-bed habitats. As in other marine systems, crustaceans are the most abundant and diverse members of the invertebrate assemblages in these bottom-oriented habitats. The range of structural and behavioral specializations for exploiting this diverse prey resource probably exceeds that of any other feeding group. Pickers such as kelp perch (*Brachyistius frenatus*) take individual invertebrates from surfaces, including kelp and other macroalgal surfaces, not just rock or sand substrata. Grazers include species such as black perch that feed on turf algae but select small invertebrate prey by winnowing from the larger collection of material. Essentially all types of feeding mechanisms, from biting to suction and ram feeding are represented among fishes that feed on bottom-associated invertebrates (see Norton, 1995). Fishes in which hard-shelled invertebrates are a major part of the diet usually possess well-developed oral or pharyngeal jaws to process these prey with shearing or crushing actions, as described in the previous section.

FISH FEEDERS

Fish species that prey on other fishes are represented in all California marine habitats (see Trophic interactions below) and are surprisingly abundant and diverse in some habitats considering that they feed at the third or fourth and sometimes even the fifth trophic level (Horn, 1998). Among the piscivores are generalized predators such as the three California species in the genus *Paralabrax*, kelp bass, *P. clathratus*, barred sand bass, *P. nebulifer*, and spotted sand bass, *P. maculatofasciatus* (see chapter 3), which use a burst of speed and suction feeding mainly to engulf their prey. More specialized fish predators engage a variety of behaviors and structures in capturing prey. For example, the California lizardfish (*Synodus lucioceps*), California scorpionfish (*Scorpaena guttata*), and California halibut (*Paralichthys californicus*) all ambush their prey from stations of camouflage on the bottom (Allen, 1982). Pacific viperfish (*Chauliodus macouni*), blackbelly dragonfish (*Stomias atriventer*), and Pacific dreamer ambush their prey in deep midwaters after luring the prey to within striking distance with luminescent devices (Gartner et al., 1997).

In marked contrast, the billfishes, including swordfish (*Xiphias gladius*) and striped marlin (*Tetrapterus audax*), combine high speed with a slashing or spearing bill to overtake and disorient or disable their prey (Helfman et al., 1997). In terms of feeding mechanisms, piscivorous fishes, many of which also include large invertebrates (e.g. squid, shrimp) in their diets, use biting, ram or suction feeding or a combination of these mechanisms as described in the previous section.

Omnivores

Some fish species in every California marine habitat consume a wide variety of prey, and these prey items often belong to different trophic levels. Thus, omnivory is common among these fishes, if, as is usual in ecology, omnivory is defined as feeding on more than one trophic level. The trophic relationships depicted in the next section (figs. 14-6–11) show that in many cases fishes are feeding on more than one trophic level even without portraying any ontogenetic changes in diet and trophic level that some species are known to undergo during their lives. Omnivory adds complexity to trophic interactions and tends to compromise the distinctiveness of trophic levels vertically (Persson et al., 1996). Sometimes omnivory is used in the more restrictive sense of referring to animals that ingest both plant and animal material, that is, feeding as a primary consumer or herbivore and on at least one higher trophic level. The prevalence of such fishes is apparent in both rocky intertidal and rocky reef/kelp bed habitats. A compilation of fishes by trophic category from three different California rocky intertidal habitats shows that omnivores accounted for 7–40% of the species based on having diets containing 5–69% algal material for inclusion (chapter 8). In a wider geographic survey, Gibson and Yoshiyama (1999) tallied 0–76% omnivores using the same criteria for inclusion. And, for kelp beds, Quast (1968) found that algae had the third highest utilization among species in his study even though only three of the 45 species examined were considered to be herbivores. As Horn and Ojeda (1999) stated, the frequent ingestion of algal material by a wide variety of presumably non-herbivorous species raises questions about the digestive specializations, if any, required for assimilating algal material and its role in the energetics of these fishes.

Trophic Interactions

Conceptual Background and Limitation

In this section, we present in broad and qualitative fashion some of the main trophic relationships involving the fish assemblages of six different habitat systems in California marine waters. These feeding interactions are not portrayed as food webs, even though they broadly resemble topological food webs. Food webs represent the variety of interconnected feeding or trophic interactions that occur in communities and the various ways in which energy passes through the populations composing the communities. Topological food webs focus on trophic relationships among organisms portrayed as links in the web. Such food webs are sometimes referred to as static food webs (Winemiller and Polis, 1996; Ricklefs and Miller, 2000) because only the presence or absence, not the strength, of the interactions is depicted, and no change in trophic relationships with growth of the individual participants nor change in age structure of the resources or consumers is portrayed. Even with these qualifications, our depictions do not qualify as topological food webs because we have not attempted to tabulate all the links within the community, and the fishes but none of the other organisms are identified to species. Moreover, no attempt was made to recognize guilds of consumers either of fishes or the other organisms shown. In a sense, our depictions resemble functional or interaction food webs, which identify the trophic relationships important to community structure (Ricklefs and Miller, 2000). The importance of each population in maintaining the integrity of the community by its influence on the

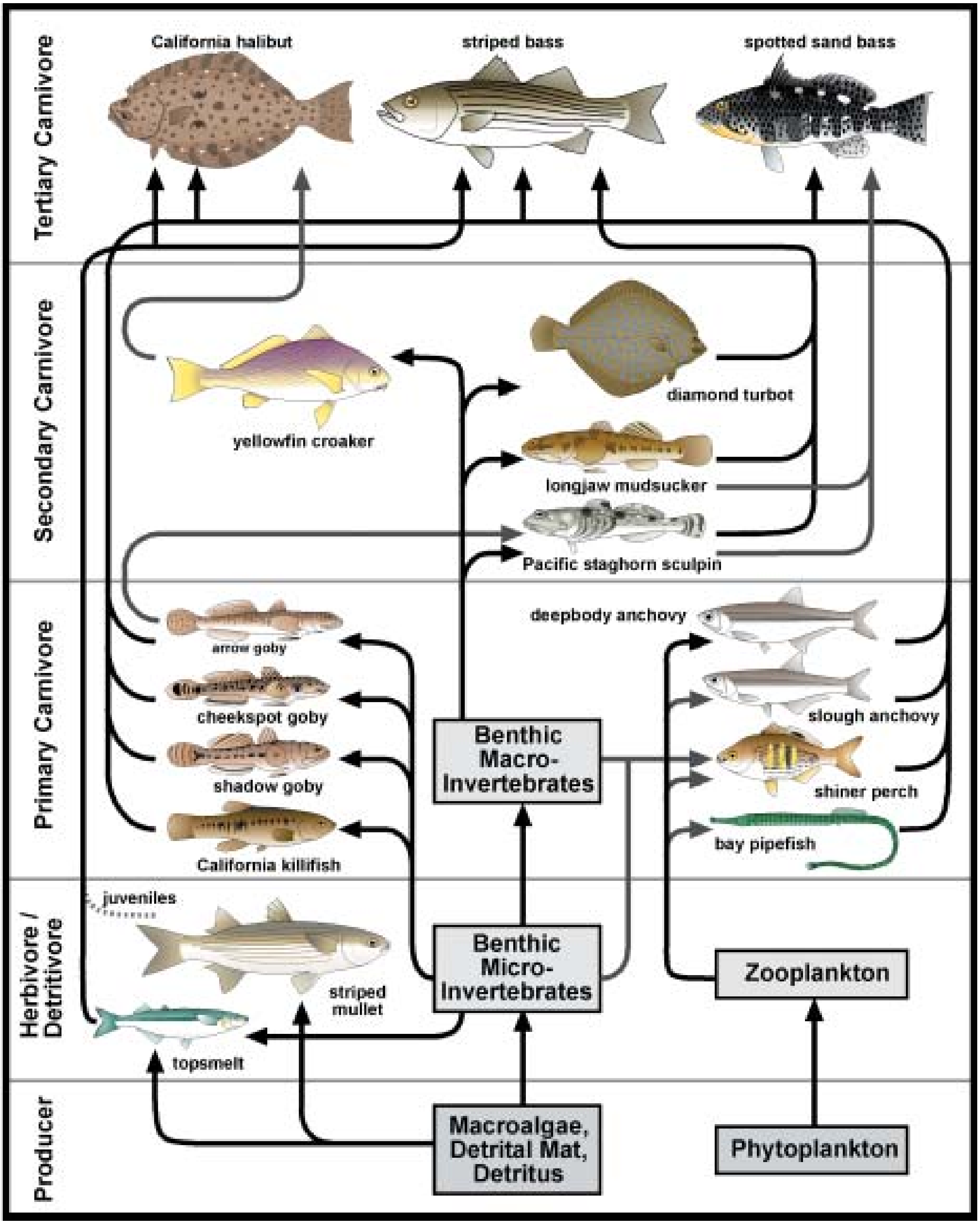

FIGURE 14-6 Trophic relationships of bay-estuarine fishes (after Cross and Allen, 1993).

growth of other populations is exhibited in such a food web and requires experimental manipulation to reveal such a role. Our illustrations do not qualify here either, but, even with these limitations, we maintain that the trophic relationships we show provide a broad consumer picture of some of the more common fish species in each system.

Bay-Estuarine Trophic Relationships

Bay-estuarine fish assemblages are recognized as being low in diversity but high in abundance and productivity with a small number of species showing numerical dominance (e.g., Allen and Horn, 1975; Haedrich, 1983; chapter 5). Feeding relation-

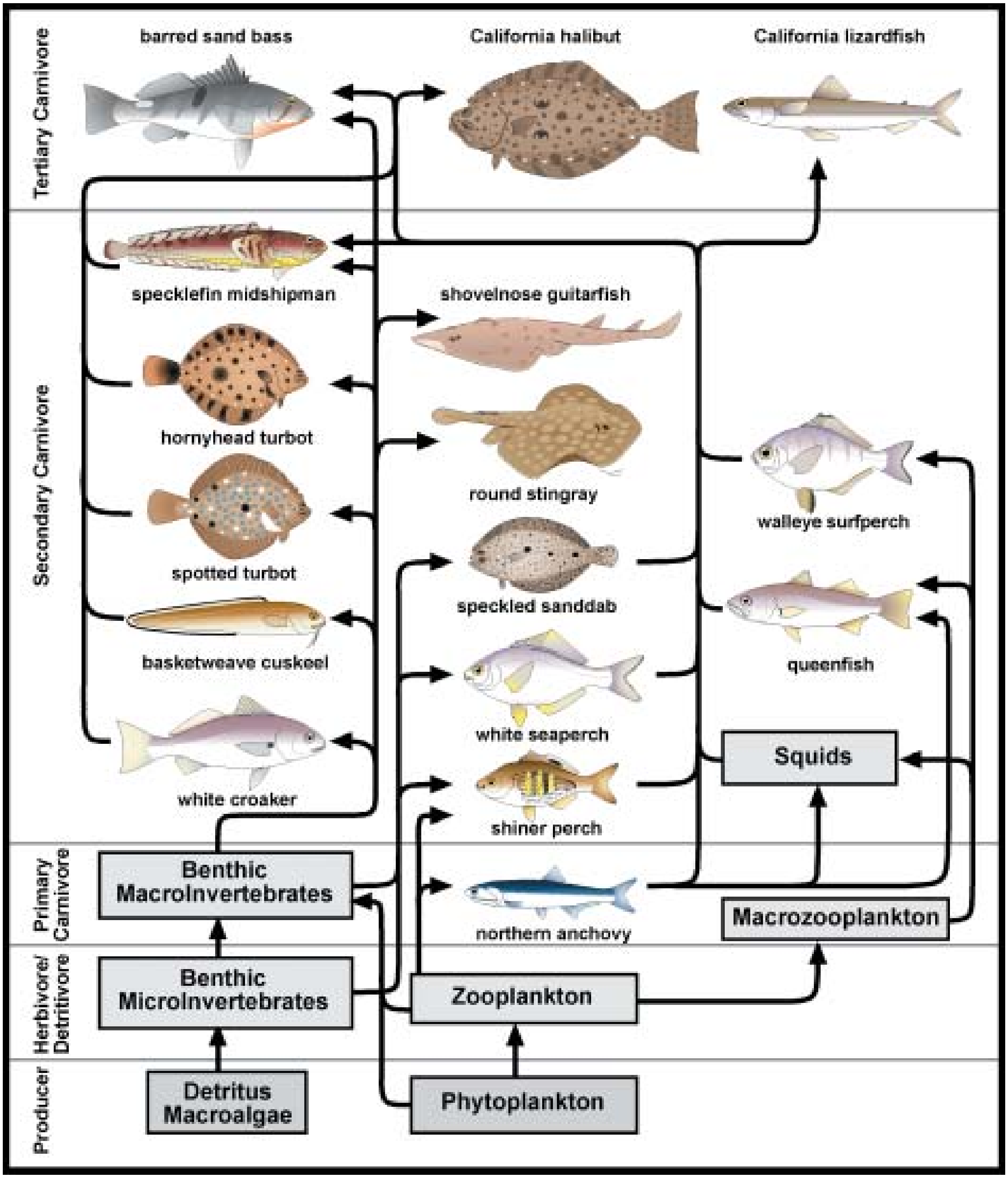

FIGURE 14-7A Trophic relationships of inner shelf fishes (after Cross and Allen, 1993).

ships, therefore, ought to be relatively simple with a food chain comprising few trophic levels. A variety of primary producers inhabit bay-estuarine systems and includes flowering plants (e.g., cordgrass, *Spartina foliosa*) from adjacent salt marshes, and submerged flowering plants (especially eelgrass, *Zostera marina*), macroalgae (e.g., *Ulva* spp.), benthic microalgae (diatoms), and phytoplankton from within the bay-estuarine system proper. Detritus derived from these and other sources provides another, more amorphous source of organic matter for higher trophic levels in the system. Based on stable isotope analysis in San Dieguito Lagoon and Tijuana Estuary, two southern California bay-estuarine systems, Kwak and Zedler

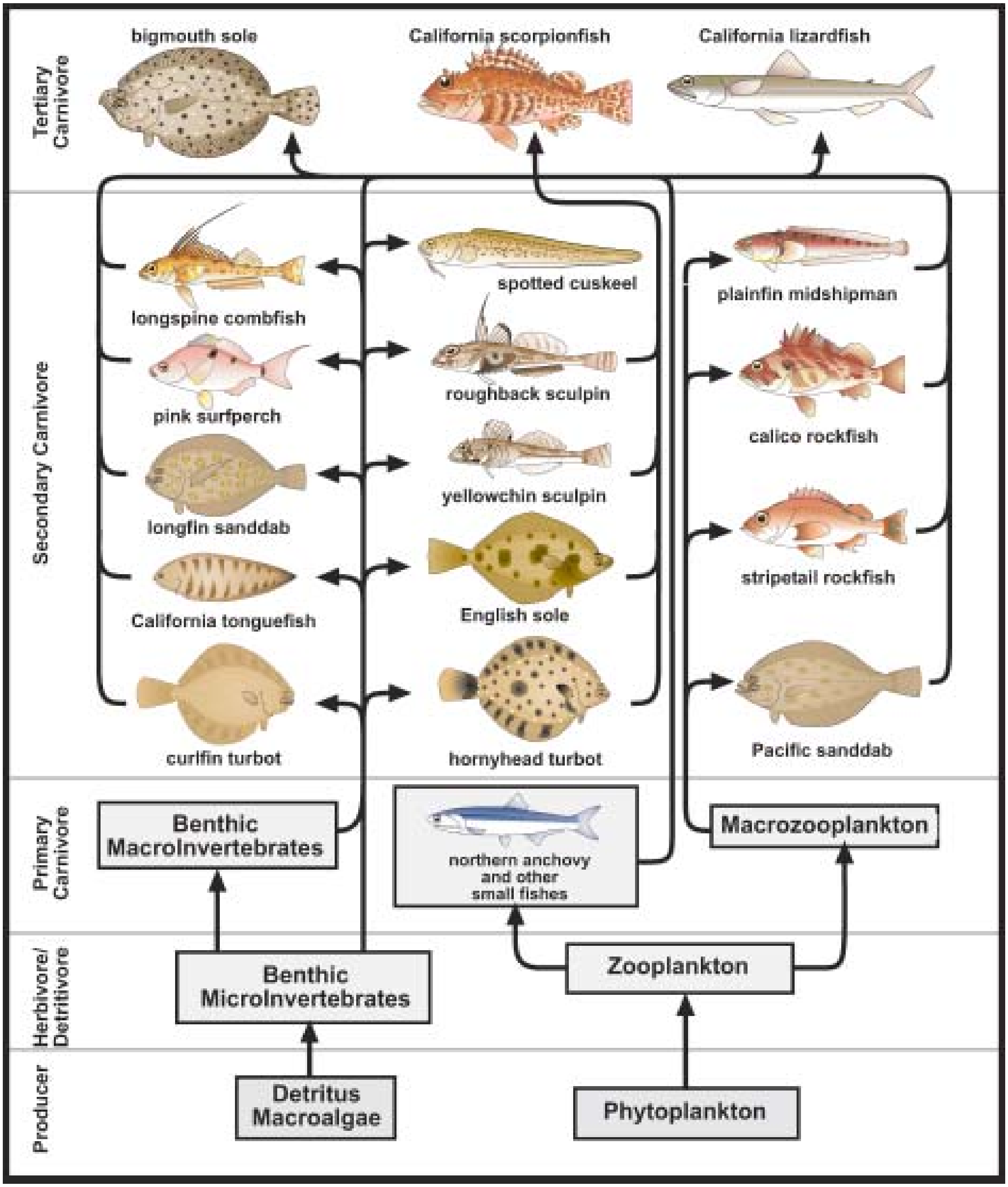

FIGURE 14-7B Trophic relationships of outer shelf fishes (after Cross and Allen, 1993).

(1997) found that intertidal macroalgae, marsh microalgae, and cordgrass provide the organic matter that supports fishes.

Trophic spectrum analysis for common fish species in the upper Newport Bay system in southern California (Horn and Allen, 1985) reveals trophic relationships composing approximately four trophic levels as shown in Cross and Allen (1993) and in fig. 14-6. Topsmelt and striped mullet, two of the most abundant fish species in the system (Allen, 1982; Horn and Allen, 1985), represent the herbivore and detritivore level and the broad base of the food web. The bulk of the diet of both species comprises macroalgae, plant detritus, and pennate diatoms in upper Newport Bay, and the proportion of plant

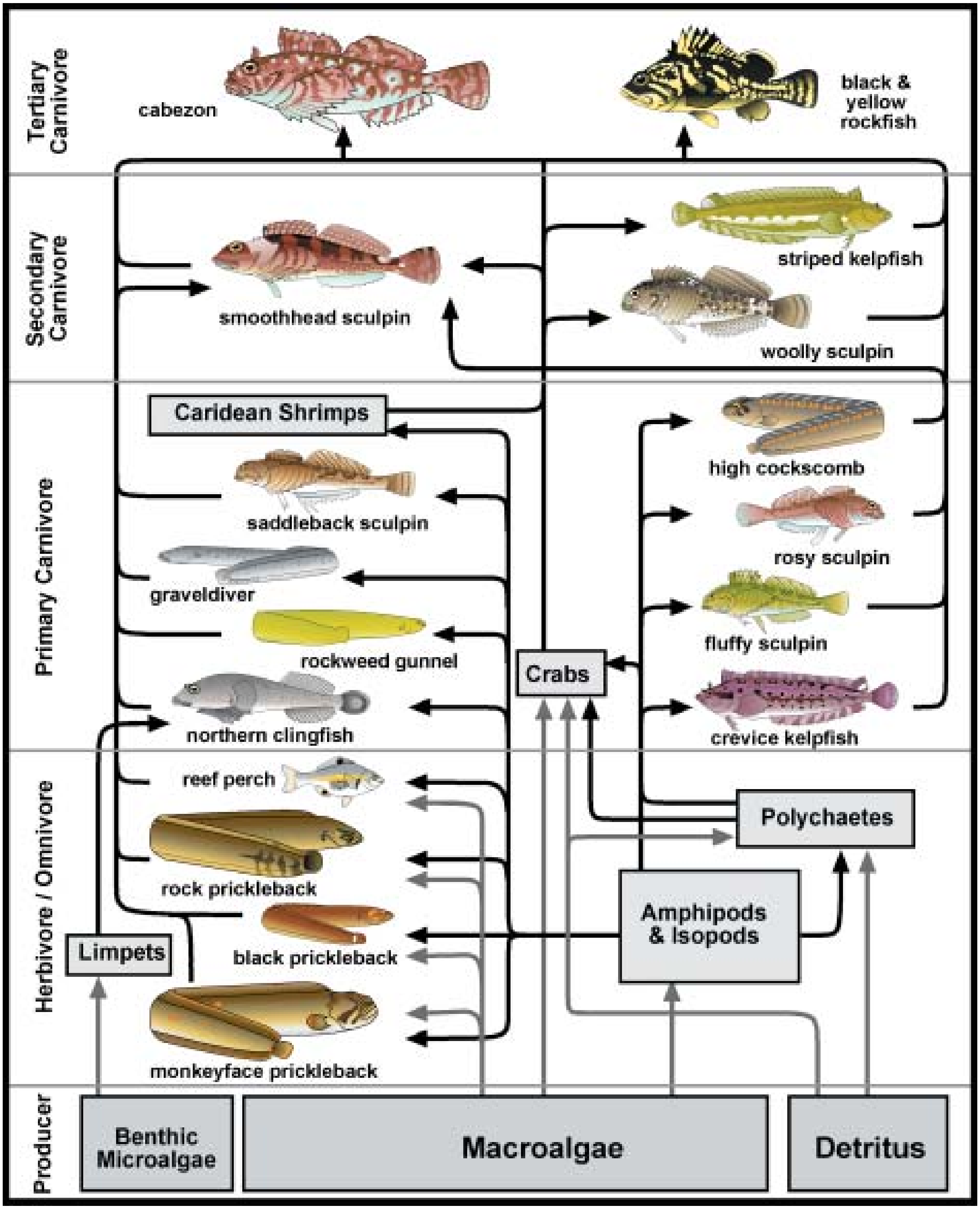

FIGURE 14-8 Trophic relationships of rocky intertidal fishes (central California coast).

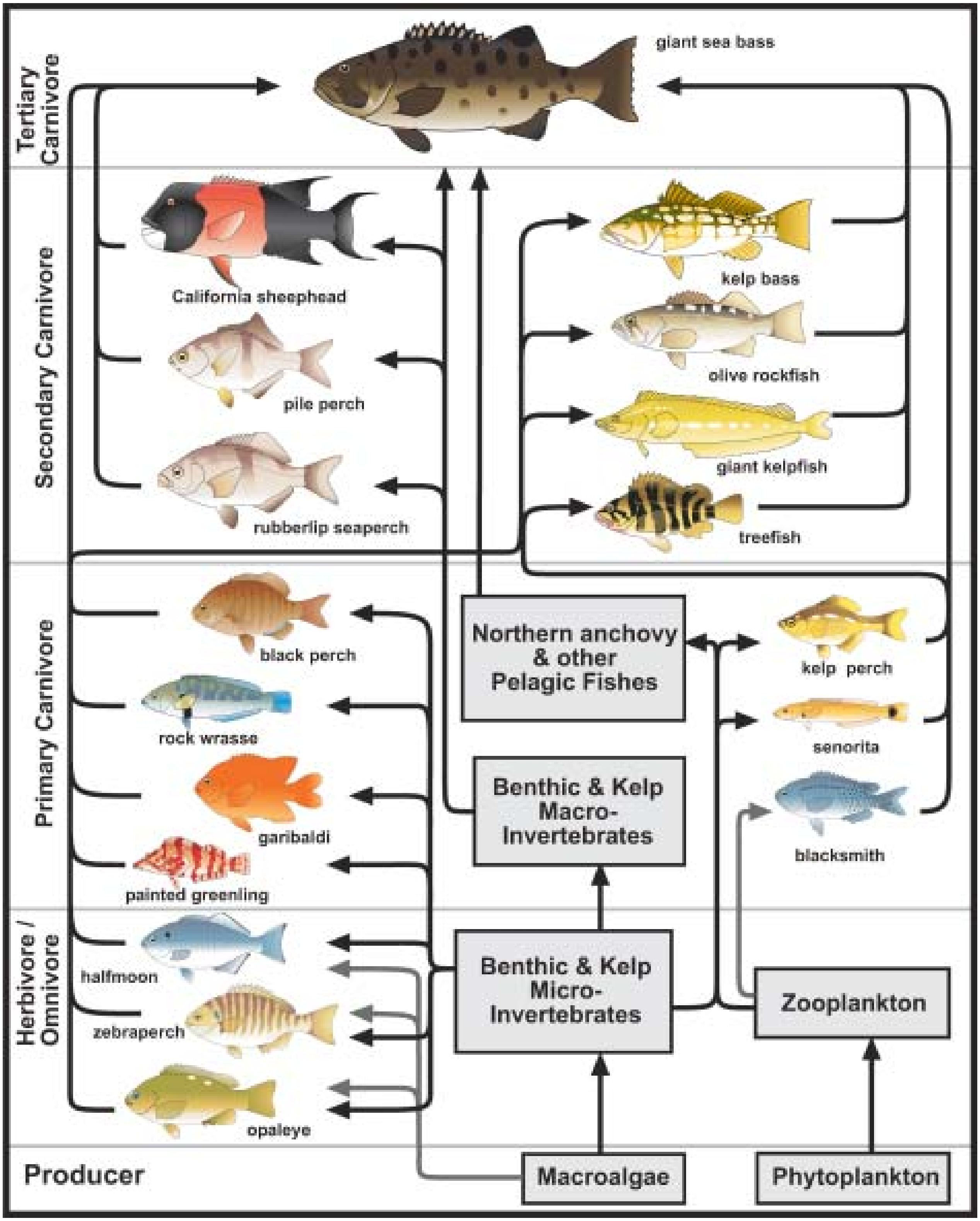

FIGURE 14-9 Trophic relationships of rocky reef and kelp bed fishes (after Cross and Allen, 1993).

material in the diet of each species increases with age (Horn and Allen, 1985). Similarly, topsmelt were placed in a trophic guild of macroalgal and zooplankton consumers in Elkhorn Slough in central California (Barry et al., 1996; chapter 5). Somewhat in contrast, topsmelt in Tijuana Estuary were positioned at a higher, secondary consumer level based on stable isotope analysis (Kwak and Zedler, 1997) and an associated gut content analysis (West et al., 2003). Moreover, Smith (2002) found that topsmelt in three southern California bays and estuaries including upper Newport Bay, where the fish consumed mainly detritus, macroalgae and zooplankton, occupied a higher trophic position than in three kelp-bed habitats

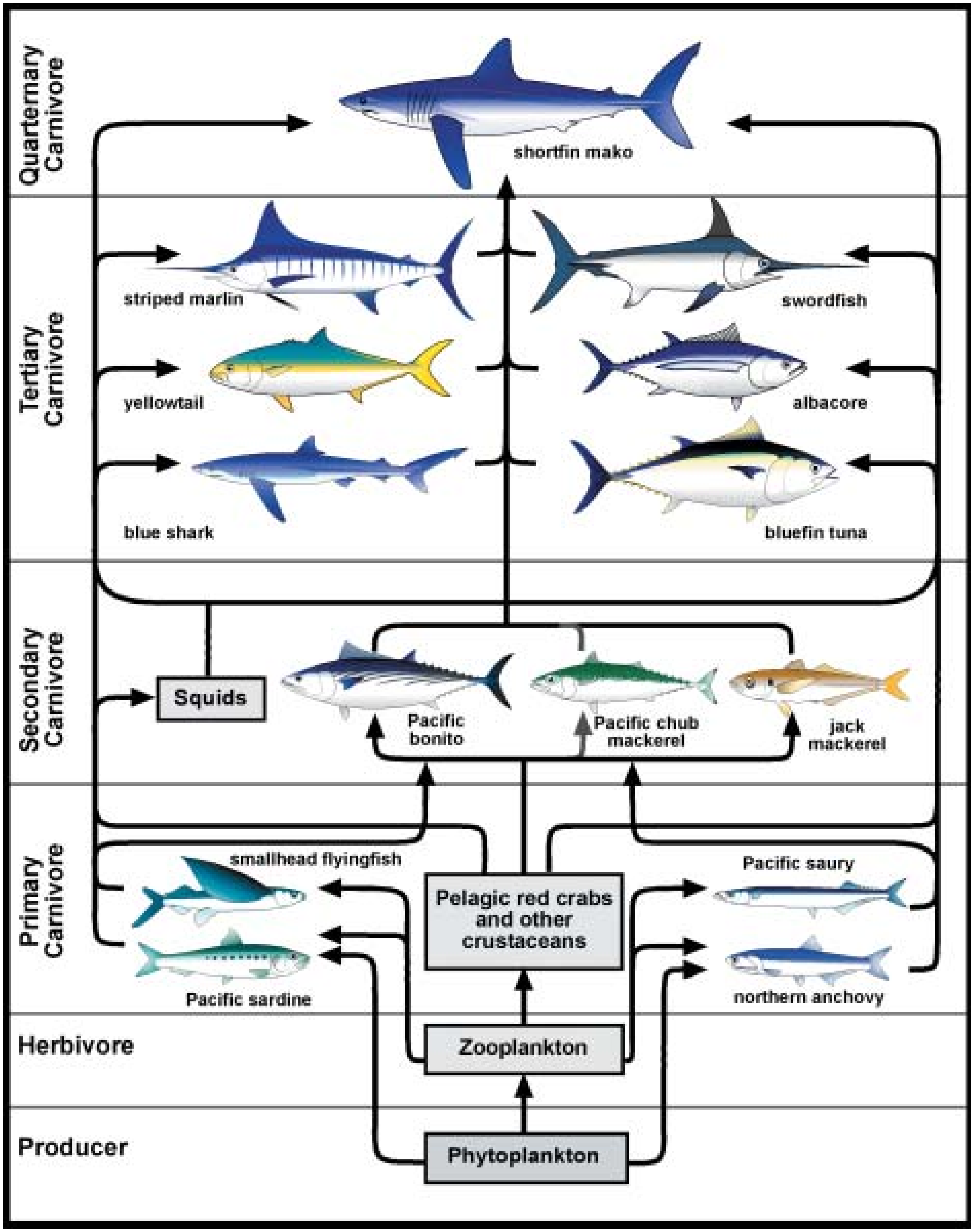

FIGURE 14-10 Trophic relationships of epipelagic fishes (after Cross and Allen, 1993).

where the fish primarily ate zooplankton. These results suggest that the topsmelt is an opportunistic omnivore involved in multiple trophic pathways in bays and estuaries and deserves further study in this regard.

The other common fish species shown in fig. 14-6 variously occupy three higher trophic levels. Primary carnivores in the upper Newport Bay system include two main groups of fishes. California killifish (*Fundulus parvipinnis*), arrow goby (*Clevelandia ios*), cheekspot goby (*Ilypnus gilberti*), and shadow goby (*Quietula y-cauda*) are benthic feeders consuming microinvertebrates, mainly crustaceans and polychaetes, whereas a second set of species, deepbody anchovy (*Anchoa compressa*), slough anchovy

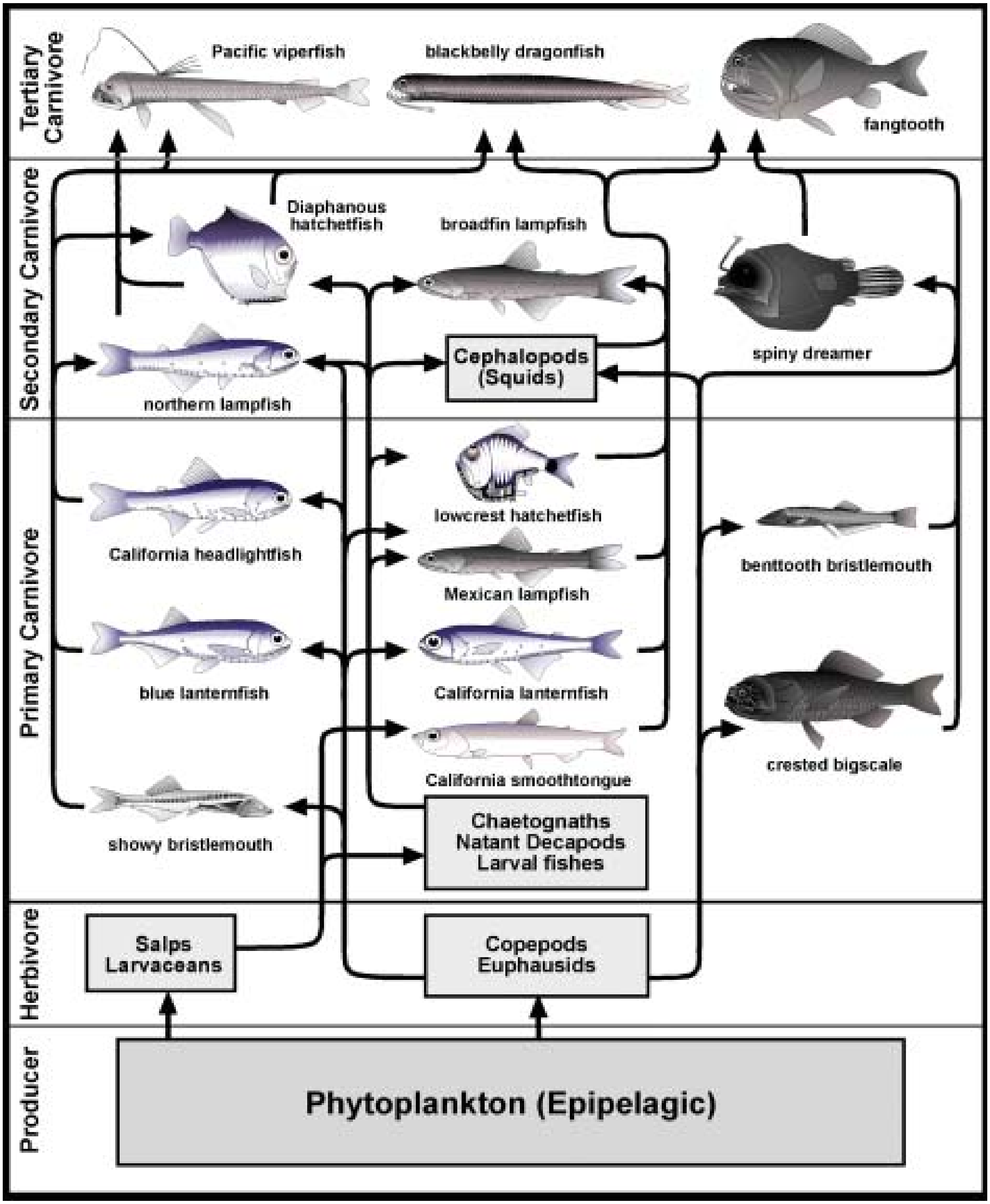

FIGURE 14-11 Trophic relationships of deep midwater fishes (after Cross and Allen, 1993).

(*A. delicatissima*), and bay pipefish (*Syngnathus leptorhynchus*) feed in the water column on zooplankton or, in the case of shiner perch (*Cymatogaster aggregata*), either on zooplankton or benthic macroinvertebrates. Secondary carnivores feed mainly on benthic macroinvertebrates and less often on fishes and include yellowfin croaker (*Umbrina roncador*), Pacific staghorn sculpin (*Leptocottus armatus*), longjaw mudsucker (*Gillichthys mirabilis*), and diamond turbot (*Hypsopsetta guttulata*). The fish species representing the tertiary carnivores, spotted sand bass, striped bass, and California halibut, are mainly piscivores and feed variously on fishes that occupy the lower trophic levels.

Inner Shelf and Outer Shelf Trophic Relationships

The fish assemblages considered here comprise those species occupying soft-bottom habitats in coastal waters extending from shallow depths out to the edge of the continental shelf at about 200 m depth (see chapter 7). Feeding patterns of these fishes predictably should reflect food webs supported by phytoplankton, detritus, and, to a lesser degree, by macroalgae. In turn, the organic matter produced is consumed either by benthic or planktonic invertebrates, mainly crustaceans. Soft-bottom fish assemblages contain no herbivorous and probably no detritivorous species; thus, the fishes occupy approximately three carnivore trophic levels as shown by Cross and Allen (1993) and fig. 14-7. Crustaceans are the most important prey type of soft-bottom fishes, as they are found in the digestive tracts of all species (Allen, 1982; chapter 7). This widespread use of crustaceans as food by fishes means that members of successively higher trophic levels feed on one to a few trophic levels below them (figs. 14-7a,14-7b). Less frequently occurring prey items in Allen's (1982) analysis included ray-finned fishes and polychaetes, but almost no gastropods or isopods were present in the diets. Hidden in the trophic relationships portrayed in figs. 14-7a and 14-7b are the ontogenetic shifts in diet that occur in numerous soft-bottom fish species. In general, neritic and benthic fishes, such as Pacific hake (*Merluccius productus*) and California halibut, feed on copepods early in life then, with growth, undergo shifts to diets of euphausiids and mysids, then to nektonic fishes or squids. Smaller neritic species that do not undergo this complete series of ontogenetic changes in diet include shiner perch and stripetail rockfish (*Sebastes saxicola*). Similarly, benthopelagic fishes, such as California scorpionfish (*Scorpaena guttata*), first consume gammaridean amphipods then change to shrimp and then to fishes and octopus as they increase in size. Smaller benthopelagic species undergo fewer ontogenetic shifts in diet and include yellowchin sculpin (*Icelinus quadriseriatus*) and white seaperch (*Phanerodon furcatus*), which continue to feed on gammaridean amphipods.

Eighteen foraging guilds are recognized by Allen (1982; chapter 7) for soft-bottom fish assemblages in southern California. These guilds consist of sets of species that displace one another with depth in southern California waters, each, according to Allen, performing a similar ecological role in its particular depth range. Several of these depth displacements can be discerned in the profiles of trophic relationships depicted in this chapter for the inner shelf and outer shelf assemblages (figs. 14-7a, 7b). As a first example, specklefin midshipman, *Porichthys myriaster* (fig. 14-7a) is replaced in deeper waters by plainfin midshipman, *P. notatus* (fig. 14-7b). These species are categorized in their foraging behavior as bottom-refuge nonvisual pelagivores. A second example illustrated is that of white seaperch (fig. 14-7a) and the deeper-dwelling pink seaperch, *Zalembius rosaceus* (fig. 14-7b),which are classified as cruising diurnal benthopelagivores. A third example is that of speckled sanddab, *Citharichthys stigmaeus* (fig. 14-7a) replaced in deeper waters by Pacific sanddab, *C. sordidus* (fig. 14-7b). These two species, along with the still deeper-living slender sole, *Eopsetta exilis* (not illustrated), are recognized by Allen (1982) as benthic pelagobenthivores.

Aside from these depth displacements of ecological counterparts, the fishes representing different trophic levels of the soft-bottom assemblages of the inner shelf and outer shelf (or inner, middle, and outer shelf regions—see chapter 7) mostly belong to the same, relatively few taxonomic groups (figs. 14-7a, 7b). Primary carnivores in both shelf zones are mainly schooling, plankton-feeding clupeoids, especially northern anchovy and, in recent decades, Pacific sardine (not illustrated). Secondary carnivores in both zones are dominated by cuskeels (Ophidiidae), croakers (Sciaenidae), surfperches (Embiotocidae), and flatfishes (Paralichthyidae, Pleuronectidae), whereas the tertiary or top-level carnivores in the two zones are mainly lizardfish (Synodontidae), sea basses (*Paralabrax* spp.), and flatfishes.

Rocky Intertidal Trophic Relationships

The feeding relationships of rocky intertidal fish assemblages are similar to those of both bay-estuarine and soft-bottom assemblages in that crustaceans are the dominant prey items for the majority of fish species (see chapter 8, fig. 14-8). Two striking, but not surprising differences, however, are that rocky intertidal assemblages are supported to a great degree by macroalgal production and contain herbivorous or omnivorous species. As is mentioned in chapter 8, the availability of an abundant and a diverse standing stock of macroalgae on rocky shores in California, especially in the central and northern regions, may have led to its use by a few fish species and several invertebrates as the assemblages evolved under competitive pressures resulting in resource partitioning and niche diversification.

Four trophic levels above the primary producers can be recognized among the feeding relationships of rocky intertidal fish assemblages, as depicted for the central California coast in fig. 14-8. The herbivore/omnivore level is represented by the monkeyface prickleback, rock prickleback, and reef perch. On northern California shores, the mosshead sculpin occurs on this level as do juvenile opaleye and bald sculpin on southern California rocky shores. Bald sculpin also occurs on the central coast, but in the compilation for fig. 14-8, this species was not sufficiently abundant for inclusion. On the primary carnivore level, gammaridean amphipods are major food items for several species of sculpin in addition to a prickleback (high cockscomb, *Anoplarchus purpurescens*), rockweed gunnel (*Xererpes fucorum*), graveldiver (*Scytalina cerdale*), and northern clingfish (*Gobiesox maeandricus*). The range of species is similar for northern California rocky shores, but in southern California the prickleback, the clingfish, and the sculpins are replaced by another species of clingfish (*G. rhessodon*), as well as the tidepool blenny (*Hypsoblennius gilberti*) and reef finspot (*Paraclinus integripinnis*). The tertiary carnivore level is represented by various subtidal predators that visit the intertidal zone during high tide periods; these species include cabezon (*Scorpaenichthys marmoratus*) and several species of rockfishes, e.g., grass rockfish (*Sebastes rastrelliger*) and black-and-yellow rockfish (*S. chrysomelas*). At low tide, wading birds (e.g., Great Blue Heron) and, during high tide, diving birds (e.g., Common Loon) also prey on intertidal fishes (pers. obs.).

In a recent quantitative analysis of feeding guilds, Boyle (2004) recognized four such guilds distributed among 14 species of rocky intertidal fish species that were collected in sufficient numbers for analysis on the central California coast. An omnivore, a microcarnivore, a carnivore, and a polychaete-feeder guild were distinguished. The omnivore guild contained the same three species as shown for the herbivore/omnivore trophic level in fig. 14-8; in addition, black prickleback (*Xiphister atropurpureus*) was determined to be a member of this guild. The microcarnivore guild consisted of northern clingfish, graveldiver, and rock prickleback, all members of the primary consumer trophic level depicted in fig. 14-8. The carnivore guild contained woolly sculpin (*Clinocottus analis*) and striped kelpfish (*Gibbonsia metzi*), the same as that of the secondary carnivore trophic level of fig. 14-8, but smoothhead sculpin was excluded from the guild because it did not meet the 71% diet similarity required for inclusion by the analysis. Boyle (2004) did not sample either of the larger predators labeled as tertiary carnivores in fig. 14-8.

Rocky Reef and Kelp Bed Trophic Relationships

The fishes associated with hard substrata and kelp in shallow subtidal waters form a diverse and abundant assemblage with densities several times greater than those estimated for soft-bottom habitats (see chapter 9). Rocky reef and kelp bed food webs appear to be largely phytoplankton-based although detrital carbon from kelps in other regions has been shown to enter near shore food webs (Duggins et al., 1989; Dunton, 2001) and to be assimilated by epibenthic consumers including fishes (Dunton, 2001). In a study of the trophic position of the topsmelt in southern California kelp beds, Smith (2002) showed from gut content analysis that the fish was feeding on zooplankton and from stable isotope analysis that the $\delta^{13}C$ signature of the fish matched those of zooplankton and, in turn, those of phytoplankton. In truth, however, the $\delta^{13}C$ signature of the kelp *Macrocystis pyrifera* overlaps that of kelp-bed topsmelt leaving open the possibility that this kelp also is a carbon source for the fish. Overall, the carbon sources for kelp-associated fishes probably are best seen as a combination of phytoplankton, kelp, and smaller macroalgae.

The potential carbon sources for bay-estuarine fishes are more diverse than those for rocky reefs and kelp beds because of land-based contributions of primary production to bays and estuaries (see above). Smith (2002) found that bay-estuarine topsmelt have more possible carbon sources and occupy a higher trophic position than kelp-bed topsmelt even though the former eat more macroalgae and the latter consume more zooplankton. Identifying the sources of organic matter (carbon) for fishes associated with kelp-beds and rocky-reefs remains a worthwhile endeavor for future research, especially given the wide variety of pelagic and benthic prey consumed (see below) and the intermingling of the water-column environment with a structured and stationary kelp-rock environment.

Food resources available to rocky reef and kelp bed fishes are varied and abundant, reflecting the structural complexity of these habitats and the closeness of water-column habitat. As a result, both pelagic and benthic organisms are variously consumed. Pelagic prey include zooplankton, micronekton, and some larger nektonic animals, whereas potential benthic dietary items include the kelps themselves, smaller macroalgae, and invertebrates variously occupying substrata such as kelp holdfasts and blades, algal turf, rock outcrops, and sandy stretches. Quast (1968) compiled a food utilization index from an extensive dietary analysis of kelp-bed fishes. In this index, gammaridean amphipods ranked first in importance followed in order by crabs, algae, certain species of shrimps, polychaetes, and perciform fishes among 38 items assessed. Thus, crustaceans emerge in still another major habitat as the most important dietary items for fishes, as they have in bay-estuarine, coastal soft-bottom, and rocky intertidal habitats (see above). Quast's (1968) analysis led him to conclude that, among kelp-bed fishes, 46% are carnivores, 46% are omnivores, and 8% are herbivores.

Trophic relationships involving rocky reef and kelp-bed fishes are complex, and four levels above the primary producer can be identified (Cross and Allen, 1993; fig. 14-9). As mentioned, these assemblages are supported fundamentally by phytoplankton and macroalgae, perhaps mostly kelps. As in the rocky intertidal zone, rock-kelp fish assemblages include species that consume macroalgae as part or almost all of their diet, enough to be classified as herbivores (e.g., Quast, 1968; Horn, 1989). Opaleye, halfmoon, and zebraperch are shown on the herbivore/detritivore trophic level in fig. 14-9. As it grows, the opaleye shifts from being an omnivorous plankton feeder to an algal browser/grazer (Mitchell, 1953; Williams and Williams, 1955), and its diet becomes a combination of red, green, and brown macroalgae and benthic invertebrates (Quast, 1968; Hobson and Chess, 2001). The diet of halfmoon is similar to that of opaleye (Quast, 1968; Hobson and Chess, 2001), and both species, often in mixed aggregations, have consumed green (Leighton, 1971), red (Foster, 1975), and brown algae, especially kelp transplants (Harris et al., 1984), in manipulated field situations directed at other purposes. The zebraperch, often treated as a species in the same family (Kyphosidae) as opaleye and halfmoon (see chapter 9), may be the most herbivorous of the three species. A species that has become increasingly abundant in southern California as ocean temperatures have warmed in recent decades (Sturm and Horn, 2001), zebraperch eat macroalgae almost exclusively, mainly red algae with much smaller amounts of brown and green algae (Sturm and Horn, 1998). Interestingly, in the same 1998 study, the fish in laboratory feeding trials assimilated constituents from nondietary brown algae as efficiently as from dietary algae, indicating that, like its tropical and subtropical relatives (*Kyphosus* spp.), it can digest a variety of macroalgae including brown algae containing defensive secondary compounds.

Although the garibaldi (*Hypsypops rubicundus*) is known to consume turf algae on a defended grazing site, this territorial species appears to be pursuing bryozoans and other encrusting animals when taking bites of these algae (Quast, 1968; Clarke, 1970; Hobson and Chess, 2001). The ingested algae shows little sign of being digested (Hobson and Chess, 2001). No studies of which we are aware have been completed on whether the garibaldi can digest and assimilate algal material.

The blue rockfish is another algae-consuming fish associated with rocky reefs and kelp beds, especially in central California kelp beds where it is one of the most abundant species (Miller and Geibel, 1973; Hallacher and Roberts, 1985). This schooling rockfish consumes macroalgae including kelp during warm, non-upwelling periods when zooplankton, its other main food, is low in abundance. The blue rockfish is the only species within the species-rich genus *Sebastes* that consumes appreciable amounts of macroalgae, and it shows herbivorous tendencies by having a somewhat longer gut than other rockfishes (Hallacher and Roberts, 1985).

At the primary carnivore level, rocky reef and kelp bed fishes consume either benthic and kelp microinvertebrates, as in black perch, rock wrasse (*Halichoeres semicinctus*), and painted greenling (*Oxylebius pictus*), or zooplankton, as in kelp perch, senorita, and blacksmith, although kelp perch and senorita feed on different types of prey (Cross and Allen, 1993; fig. 14-9). Black perch are known to browse and winnow algal turf for small invertebrates (Drucker and Jensen, 1991) and to compete for these food resources with its congener, striped seaperch (*Embiotoca lateralis*), based on extensive manipulative field studies (Hixon, 1980; chapter 17). As its name implies, the kelp perch lives in close association with *Macrocystis,* preying mainly on micro-crustaceans on the kelp's surface (Quast, 1968; Hobson and Chess, 2001) but also feeding on zooplankton before reaching 100 mm SL (Bray and Ebeling, 1975). Senorita also pluck zooplankton from the water column at sizes mainly <100 mm SL before switching to feeding from various surfaces, whether it is kelp, rock, or the bodies of animals, a habit that renders it the major cleaner fish in California kelp beds (Hobson and Chess, 2001). Predation by senorita on the isopod *Idothea resecata* apparently keeps in check the impact of this herbivore on the *Macrocystis* canopy (Bernstein and Jung, 1979).

At the secondary carnivore level, the fishes feed on benthic or kelp macroinvertebrates, as in California sheephead, pile perch, and rubberlip seaperch (*Racochilus toxotes*), or on fishes from the lower trophic levels, as in kelp bass, olive rockfish, *Sebastes serranoides*, treefish, *S. serriceps*, and giant kelpfish, *Heterostichus rostratus* (Cross and Allen, 1993; fig. 14-9). The California sheephead feeds on fixed or slow-moving bottom invertebrates such as sea urchins, mussels, crabs, and sea cucumbers (Limbaugh, 1955; Quast, 1968; Cowen, 1986), and, like labrids in general, crushes prey with well-developed pharyngeal teeth. Echinoids are major prey of this large reef fish, and the feeding activities of the sheephead have been shown to reduce sea urchin numbers and to drive them to cover on the reef (Cowan, 1983). The pile perch also crushes prey with strong pharyngeal jaws and feeds on heavy-shelled invertebrates, including molluscs, crabs, and sand dollars (Limbaugh, 1955; Quast, 1968; Brett, 1979; Hobson and Chess, 2001). Among the piscivores at this trophic level is the olive rockfish. Although this fish feeds on zooplankton as small juveniles, as they grow they shift to fishes such as juvenile rockfishes and to macroinvertebrates including squids and octopuses and smaller prey such as isopods and krill (Love et al., 2002). The treefish is another partly piscivorous rockfish that feeds on bottom-dwelling fishes and macroinvertebrates such as shrimp and crabs (Love et al., 2002). Giant kelpfish feed near kelp or on the bottom on invertebrates such as mysids, amphipods and isopods and, with increasing size, they consume more fishes including kelp clingfish (*Rimicola muscarum*), small senorita, and juvenile kelp perch (Quast, 1968). The kelp bass is a major fish predator around rocky reefs and kelp beds, with young bass feeding on small crabs, copepods, and plankton before assuming a generalized carnivore diet of small fishes, including anchovies, sardines, surfperches, and queenfish (*Seriphus politus*), and a variety of macroinvertebrates (Quast, 1968; Allen and Hovey, 2001).

At the tertiary carnivore level, the giant sea bass (*Stereolepis gigas*) is depicted in fig. 14-9 and represents the predatory species at the top of the rocky reef/kelp bed food chain. This extremely large (>2m and >250 kg), slow-growing, and late-maturing polyprionid fish has protected status in California, but its biology remains poorly known and its populations severely depressed (Domeier, 2001). The giant sea bass prefers rocky reef habitat and feeds by suction with its huge mouth to take a variety of bottom-dwelling fishes including sting rays, skates, small sharks, various flatfishes, and other species as well as macroinvertebrates such as lobsters, crabs, octopuses, and squids (Domeier, 2001). Other large predatory fishes, including Pacific electric ray, *Torpedo californica* (Bray and Hixon, 1978; Horn, 1980), at least occasionally, prey on rocky reef and kelp bed fishes, but their impact on the assemblage remains poorly known (Pondella and Allen, 2000).

Epipelagic Trophic Relationships

The feeding relationships of open ocean, surface-dwelling fishes are phytoplankton-based and are devoid of strictly herbivorous species although anchovy and sardine feed to varying small degrees on phytoplankton depending on fish age and seasonal condition. One of the greatest challenges of studying epipelagic systems is not determining the sources of carbon as it is in some other systems such as bays and estuaries, but rather it is the lack of strict spatial boundaries. Bays and estuaries end as the salinity gradient flattens out on either end, soft-bottom habitats are interrupted by rocky reefs and kelp beds and vice versa, and the rocky intertidal zone meets the land, sandy or muddy stretches of shoreline, and subtidal depths. In contrast, the epipelagic zone extends to the limits of an ocean basin or even the world ocean in the extreme sense. Only deeper, darker and colder waters provide a boundary for this system, and even this limit varies with water transparency, current patterns, and other dynamic oceanographic conditions. Moreover, vertically-migrating midwater fishes regularly penetrate the lower limits from below to feed in the warmer, richer surface waters (see chapters 11 and 13), and large, powerful, epipelagic fishes such as swordfish and some tunas visit deeper waters on feeding excursions. The fluid and changing boundaries of this large zone (see chapters 11, 12 and 13) thus create an extraordinary challenge to attempts to define the trophic relationships in a system that grades from offshore to near shore and from surface to deep waters and that includes fishes moving actively or passively in vertical and horizontal directions. In a word, it is a problem of "who" to include in any analysis or description.

The trophic relationships described here for the epipelagic fish assemblage emphasize the feeding interactions of juvenile and adult fishes, whereas Moser and Watson (see chapter 11) discuss the trophic relationships of larval fishes. The trophic network depicted in this chapter comprises five levels beyond the primary producers, resulting in this system having the longest food chain among the six portrayed and described in this chapter (fig. 14-10; see Cross and Allen, 1993). Such an outcome seems consistent with the recognition that oceanic food chains tend to be longer than those in coastal and upwelling zones (Fenchel, 1988). As shown in fig. 14-10, fishes enter the system at the primary carnivore level. These species include northern anchovy and Pacific sardine, probably the most abundant fishes in shallow coastal and offshore waters. These two filter-feeding (and biting) clupeoids primarily consume zooplankton, mainly copepods, but, as mentioned above, also take phytoplankton depending upon the size of the fishes and the size and composition of the plankton (Murphy, 1966; Loukashkin, 1970; O'Connell, 1972). These two icons of the California pelagic zone are now known to cycle out of phase in abundance with each other according to alternating warm (sardine) and cold (anchovy) climatic regimes of 25-30 years each in the northeastern Pacific (Chavez et al., 2003; chapters 12 and 25). Both species are preyed upon extensively by larger fishes of all three higher trophic levels as shown in fig. 14-10 and also by a variety of marine mammals such as sea lions, seals, porpoises, and whales, and by seabirds including pelicans, gulls, terns, and cormorants (Bergen and Jacobson, 2001; Wolf et al., 2001). Some shifts in diet by predators that feed on northern anchovy and Pacific sardine occur as these two major forage species cycle in abundance (e.g., Horn et al., 2005). Two other species, Pacific saury (*Cololabis saira*) and California flyingfish (*Cheilopogon pinnatibarbatus*), shown as primary carnivores in fig. 14-10, generally inhabit surface waters farther offshore than anchovies and sardines. The saury is the more abundant and better known of the two species and, like anchovies and sardines, forms a trophic link between zooplankton and higher level carnivores including economically important fish species (Horn, 1980).

At the secondary carnivore level, fishes of intermediate size as well as squids are important members (fig. 14-10), and these species feed on combinations of smaller fishes and planktonic crustaceans. Jack mackerel (*Trachurus symmetricus*) feeds on increasingly larger zooplankton as it grows, and squid and anchovies may form large parts of the juvenile diet, but the food habits of offshore adults are poorly known (MacGregor, 1966; Mason and Bishop, 2001). The Pacific chub mackerel (*Scomber japonicus*) shows a similar ontogenetic pattern with adult fish eating various small fish, squid, and pelagic crustaceans, and they, in turn, are consumed by an array of larger fishes, marine mammals, and seabirds (Konno et al., 2001). The Pacific bonito (*Sarda chiliensis*) is a powerful, continuous swimming, and fast-growing small scombrid that commonly eats northern anchovy, Pacific sardine, and squid (Magnuson and Prescott, 1966; Smiley et al., 2001). California market squid (*Loligo opalescens*) belongs on this trophic level because it is considered to occupy a central position in coastal food webs given that it feeds on a variety of zooplankton and other invertebrates as well as small fishes and smaller squid, and, in turn, is preyed upon by a variety of fishes, seabirds, and marine mammals (Fields, 1965; Yaremko, 2001).

At the tertiary carnivore level, tunas, billfishes, yellowtail (*Seriola lalandi*), and sharks are members of group that consumes fishes, crustaceans, and squids occupying lower trophic positions (Cross and Allen, 1993; fig. 14-10). In California, all of these species have broadly similar diets that include anchovies, sardines, and squid, and they also consume pelagic red crab (*Pleuroncodes planipes*) mostly in more southerly waters except when El Niño conditions bring this crustacean into the Southern California Bight (Pinkas et al., 1971; Tricas, 1979; Horn, 1980; Bayliff, 2001; Crone, 2001). This trophic level includes powerful swimmers, especially the tunas, that migrate over long horizontal distances and participate in different food chains along the way (e.g., Blackburn, 1969). Swordfish and striped marlin, the two billfishes depicted in fig. 14-10, also are highly migratory across ocean expanses (Holts, 2001a, b). The swordfish, however, is less limited by cool waters and occurs not only in tropical waters but temperate waters as well and dives to feed at depths >500 m in the open ocean (Holts, 2001a), thus expanding its vertical foraging range well beyond the epipelagic zone.

A quaternary carnivore level is represented by the shortfin mako in fig. 14-10. This large (to 500 kg) and fast-swimming lamnid shark is at or near the top of the oceanic food chain in warm seas around the world, and the Southern California Bight may be an important birthing and nursery area for the species (Taylor and Bedford, 2001). Its diet consists of numerous fishes, several of which are shown in fig. 14-10, but, according to Taylor and Bedford, shortfin mako also may consume several species of marine mammals.

Deep Midwater Trophic Relationships

Like other fish assemblages concentrated farther from coastal influences, deep midwater fishes are supported by a phytoplankton-based food chain (fig. 14-11; Cross and Allen, 1993). According to Neighbors and Wilson (see chapter 13), the fundamental trophic structure of fishes inhabiting California's deep-sea basins is recognized, but further investigations are needed to sort out the details of energy budgets, predatory-prey relationships, and competitive impacts. The trophic relationships depicted in fig. 14-11 are divided into four feeding levels beyond the phytoplankton producers. The trophic structure is devoid of herbivorous fishes, and thus, the fishes, as in the epipelagic zone, enter the picture as primary carnivores. Crustaceans, especially copepods and euphausiids, provide the main food source for midwater fishes although the California smoothtongue (*Leuroglossus stilbius*) feeds on salps and larvaceans during the more productive time of the year (Cailliet, 1972). Lanternfishes (Myctophidae) tend to be vertical migrators, whereas hatchetfishes (Sternoptychidae) are more likely to be nonmigrators, but both groups of species are zooplanktivores (Robison and Bailey, 1982). Other midwater fishes function as secondary and tertiary carnivores, and these include stalking and ambushing predators, such as blackbelly dragonfish (*Stomias atriventer*) and Pacific viperfish (*Chauliodus macouni*), and ambush predators, such as anglerfishes (Robison and Bailey, 1982; see fig. 14-11). Vertically migrating fishes and plankton, not only transport organic material into deeper waters from the epipelagic zone, but they also are preyed upon by epipelagic fishes and other predators in the surface layers and thus are part of a vertical transport system of energy in the open ocean (see Gartner et al., 1997).

Bathypelagic and deeper-living mesopelagic fish species have larger mouths and often larger bodies and tend to have broader diets than their shallow-living relatives (Ebeling and Cailliet, 1974). These size patterns and diets reflect the energy allocation model proposed for pelagic fishes in general (Childress et al., 1980). In this model, fishes from three depth zones are characterized based on the deeper-dwelling species being increasingly removed from the surface waters and the source of primary production and thus living in waters with a sparser food supply. Epipelagic species are portrayed as fishes of large size, firm muscles, high activity and energy density, fast growth, long life, and early, repeated reproduction. Mesopelagic species are characterized as fishes of small size, firm muscles, also high activity and energy density, slow growth, long life, and also early, repeated reproduction. For these midwater species, energy storage and high activity as shown in vertical migration leave little of the energy available for growth. Bathypelagic species are depicted in the model as fishes of large size, soft muscles, low activity and energy density, but fast growth, and late, one-time reproduction. For these deep-dwelling fishes living in a food-sparse environment, growth in body mass is favored at the expense of activity and energy storage. Growth to a large size may be of selective value to escape the large-mouthed predators at greater depths, and the associated large mouth size may to enable these fishes to capture a wide size range of prey. Although the Childress et al. (1980) model clearly is of heuristic value, some of its limitations regarding growth rates, longevity, and reproduction are pointed out by Neighbors and Wilson (see chapter 13). Further tests of the model are needed, especially among related species from different depth zones.

Fishes living in association with the deep-sea floor complete the bathymetric profile in the open ocean in terms of trophic relationships in that they participate in the vertical transfer of energy between the productive surface waters and the depth zones increasingly distant from the surface. The food supply for these species, in part, arrives from the waters above as sinking particles ranging from detritus to fecal pellets and carcasses, or as vertically migrating midwater animals occurring near the bottom, or from bottom-associated fishes undertaking upward migrations to feed in the deep pelagic realm. In addition, infaunal and epifaunal invertebrates contribute to the diet of these bottom-associated fishes. The feeding ecology of both pelagic and bottom-associated fishes has been reviewed by Gartner et al. (1997) and is discussed in detail by Neighbors and Wilson (see chapter 13).

Recommendations for Future Studies

Several types of investigations are needed if we are to broaden and deepen our understanding of feeding mechanisms and trophic relationships among the fish assemblages inhabiting California's coastal waters. Studies in both areas have been concentrated in relatively few species and habitats. Although a daunting task given the diversity and complexity of the marine fish fauna, comparative studies seem particularly important if we are to learn more about the evolution of feeding behavior and mechanics and if we are to identify the origins of carbon and track the flow of energy, and other constituents including pollutants, in the food webs of California marine ecosystems. Here are some of the types of studies that seem worthy of undertaking in the future:

1. Conduct comparative studies within related groups of species to determine the circumstances under which ram or suction feeding is used. The works by Norton (1995) and Cook (1996) on sculpins provide useful models for further investigation. Many taxonomic groups in the diverse California fish fauna are well-suited for comparative analysis including the families Cottidae (still further work), Scorpaenidae, Stichaeidae, Embiotocidae, Atherinopsidae, Paralichthyidae, Pleuronectidae, Myctophidae, and Macrouridae, the last two with the logistic challenges notwithstanding.
2. Investigate the use of the gill rakers and epibranchial organs in particle-trapping mechanisms and suspension feeding. The innovative work by Sanderson et al. (1991, 1996) on freshwater fish species offers excellent models for undertaking such studies. Appropriate candidates are fishes possessing epibranchial organs including members of the families Clupeidae, Engraulidae, Salmonidae, and Stromateidae.
3. Determine the role of detritus, compared to other carbon sources, and develop topological, energy flow, and functional food webs to track the course of carbon through the principal interactors in the near shore systems (bays and estuaries, coastal soft-bottoms, rocky intertidal zone, and rocky reefs and kelp beds) in which detritus is apparently important. Stable isotope analysis is an important technique to employ here and is widely used in such studies.
4. Develop topological, energy flow, and interaction food webs for deep-sea midwater communities so that predator-prey impacts, resource partitioning, and energy budgets can be assessed in the present state and predicted in the light of environmental change. All such research on deep-sea animals is challenging, but the studies by T. L. Hopkins and co-workers in the Gulf of Mexico (e.g., Hopkins and Sutton, 1998) serve as model approaches.
5. Investigate omnivory, including that produced by ontogenetic change in diet, as a widespread but complicating factor in understanding the trophic interactions and digestive physiology of fishes in several California marine food webs including that of the rocky intertidal zone and rocky reef and kelp bed habitat.
6. Develop and use topological and interactive food webs in altered ecosystems to assess and predict the impacts of disturbance. Humans greatly influence the structure and dynamics of food webs by removing top predators, overexploiting dominant or key species, introducing alien taxa, and contributing to global climate change. Detailed food web analyses could serve as powerful tools in assessing and predicting the magnitude of these influences. A series of papers on food webs and applied problems in Polis and Winemiller (1996) and the recent work by N. D. Martinez and co-workers (e.g., Williams and Martinez, 2000) provide stimulating background material.

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