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CHAPTER 21

Symbiotic Relationships

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Introduction

The symbiotic relationships of plants and animals have fascinated terrestrial biologists for centuries, and with the development and improvement of scuba and underwater photographic and recording equipments since the mid-20th century the symbiotic stories of aquatic creatures are now becoming appreciated as well. It is the intent of this chapter to report upon examples of symbioses involving fishes in California coastal and offshore waters extending south to Magdalena Bay, Baja California (note that throughout this text references to California fishes will comprise that region). The symbiotic activities of tropical and subtropical fishes that are transient in California waters, such as those that have arrived during recent El Niño events (Lea and Rosenblatt, 2000), are not treated. The common names of fishes used herein follow those of the American Fisheries Society (Robins et al., 1991). Selected literature concerning California examples of symbiosis as well as review articles involving extralimital symbiotic relationships are included. Opportunities for further research will be identified within this text.

Symbiosis is a word of Greek origin, meaning living together. Current usage, although not universal, arose from an address by Anton de Bary in 1878 to the German Naturalists and Physicians at Kassel and published the following year (de Bary, 1879). De Bary introduced the term "Symbiose" to include all categories of association between dissimilar organisms, ranging from mutualism to commensalism to parasitism. Later authors redirected the term to be equivalent to mutualism and the assumption that at least some benefit occurs to either or both partners, such that many 20th century authors have considered parasitism and mutualism to be nearly antithetical (discussed in: Henry, 1966; Cheng, 1967; Goff, 1982; and Lewin, 1982).

"Parasitism," of Greek origin and whose original meaning was a guest who shares the dinner table, now conveniently "implies a detrimental effect on the host, a pathological condition that is generally and typically not compensated for by the trouble caused" (Lewin, 1982: 254). Commensalism is derived from Latin *cum* (together) *mensalis* (of the table), and had at its origin much the same meaning as parasitism. Symbiotic reality is such that categories of interspecific relationships are rarely abruptly discontinuous, and more often the paired organisms might alternately or simultaneously occupy two or more categories. The categorization of symbiotic relationships is not easy, and made difficult by the fact that commensal or mutualistic associates can, between meals, transform from messmates to predators and prey. For example, cleaner shrimps are often found in the stomach of California moray eels, evidence of an evolutionary relationship in progress; cleaner fishes often cheat by consuming scales and mucus from an unsuspecting client; and how does one classify a remora, as a freeloading hitchhiker or a parasite picker, or both? Commensal partners rarely share the metabolic dependency involved with both parasitic and mutualistic relationships, thus the greatest overlap is likely to occur between mutualists and parasites (see Cheng, 1967, for an expanded discussion).

For the purposes of this discussion, I follow Hertig et al. (1937) and Starr (1975) who have established guidelines that are generally followed but continually challenged. Simply, *mutualism* benefits both partners; *commensalism* involves benefits to one partner without harming or helping the other, and *parasitism* benefits one of a pair while the other suffers a reduction in fitness. I consider *phoresis* to be a subcategory of commensalism and treat it under that section.

Mutualism

Mutualistic symbioses are among the most interesting due to the degree of fitness provided to the participants and to the evolutionary pathways along which they might have arisen. Mutualism can be obligatory or facultative, and direct or indirect. In direct mutualism, participants benefit each other through their direct contact, such as the anemonefish and the anemone, whereby the anemone provides a safe refuge from predation and the fish repels polyp-feeding fishes. Indirect mutualisms benefit species not through direct interaction between species pairs but rather by the actions taken by one participant. Cushman and Beattie (1991) assess the benefits of mutualism and cite as an example of indirect mutualism Paine's (1966) demonstration that acorn barnacles (*Balanus glandula*) benefit from the action of starfish

(*Pisaster ochraceus*) that prey on mussels (*Mytilus californianus*) that would otherwise competitively exclude barnacles from the substrate. Numerous examples of indirect mutualism might be inferred (but would be difficult to experimentally verify) from an analysis of marine food webs. Whether such associations are mutualistic requires quantitative verification of the costs and benefits to both participants (Cushman and Beattie, 1991), and undertaking those studies underwater is difficult at best.

Cleaning behavior provides ample evidence for interspecific symbiosis, however debate continues concerning its categorization. Numerous species, both above and below water, are involved in cleaning behavior, and they have doubtless arrived through a variety of evolutionary pathways. At first blush, most observers reported it to be beneficial from a mutualistic standpoint, whereby guilds of cleaner fishes and shrimps establish cleaning stations and remove ectoparasites from client fishes (Limbaugh, 1961; Feder, 1966). Such reciprocal altruism seems likely and appropriate (Trivers, 1971; Poulin and Vickery, 1995; but see Gorlich et al., 1978), however despite numerous quantitative field studies involving the removal of cleaners from reefs, the seemingly obvious benefits of cleaning has been demonstrated in but few instances (Youngbluth, 1968; Losey 1972; Grutter, 1997; the exception being that of Grutter, 1999). Losey (1972) held that "although the adaptive value of cleaning is probably ectoparasite removal, the proximate causal factors are not related to ectoparasites. Thus, in some areas, the relationship of the cleaner to the host may become commensal or even parasitic." As he aged, Losey (1987) dispassionately viewed cleaner fish as "nothing but clever behavioral parasites" that feed largely on the hosts' tissues and mucus when the production rate of ectoparasites was low. They do this by exploiting the sensory system of their clients whose benefit is one of hedonistic tactile stimulation (Losey, 1979). The exploitative consequences of such parasitism must be small (Poulin and Grutter, 1996) when one recognizes the popularity of the symbiosis. Cleaning symbiosis is further complicated by cheating by both cleaners (who consume more client tissue than ectoparasites) and clients (who eat the cleaners), a variant that was sure to evolve, and has, several times (Poulin and Vickery, 1995).

In summary, considering the various opinions and field studies mentioned above, I must categorize cleaning behavior among fishes to range gradually from mutualism, that is advantageous to clients when ectoparasite levels are critical, to parasitism, whereby cleaners feed on fish tissue and mucus when ectoparasites levels are low, but may find themselves at risk of being consumed.

Limbaugh (1955, 1961) published the first descriptions of California cleaner fish and Hobson (1971) provided its first extensive survey. Limbaugh (1961) and Feder (1966) had suggested that the presence of cleaning stations along inshore kelp beds was responsible for the aggregations of sport fishes at those localities. Hobson (1971) examined their hypothesis but concluded "There is no basis for the contention that many good fishing grounds in southern California exist because fishes have congregated in these locations for cleaning."

Eighteen species from nine fish families have been shown to provide service in cleaning symbioses in California coastal waters (fig. 21-1; table 21-1). The seven species of oceanic suckerfishes, family Echeneidae, are not considered in this discussion (see chapter 12). Their symbiotic relationships are discussed in Strasburg (1964). Hobson's (1971) research demonstrated that the señorita is the predominant cleaner fish in California waters, and it, along with the kelp perch and the sharpnose seaperch, may be the only habitual cleaners (figs. 21-2, 21-3). The other species listed above are only sporadic cleaners as an adjunct to their normal feeding behavior. It should be noted that cleaning has not been observed in shallow intertidal waters. Such high energy environments provide a low diversity of hosts and makes coordinated movements difficult between cleaner and host. Although based only on casual observation, Losey et al. (1999) suggest that this lack of intertidal cleaning activity has no apparent cost to the fishes.

Unlike their tropical counterparts, the cleaning activity of California cleaners are not centered around well-defined cleaning stations and the cleaner, rather than the client, initiates the cleaning bouts. Hobson (1971: 491) noted that "an infected fish approached by a cleaner generally drifts into an unusual attitude that advertises the temporary existence of the transient cleaning station to other fish in need of service, and these converge on the cleaner. Although señoritas, as a group, clean a number of different fishes, a given individual tends to initiate cleaning with members of just one species." Unlike the behavior of tropical cleaners, California cleaners restrict their parasite removal to the skin and do not enter the mouth and branchial cavities of clients. The majority of parasites removed are caligid copepods and gnathiid isopod larvae. Unlike señoritas, which clean as adults and juveniles, the sharpnose seaperch cleans only as a juvenile (<125 mm length). The clients most frequently cleaned are those which were most abundant and most heavily infested, and no significant preference for client species was observed. And one may assume that, unlike many of their tropical counterparts, their roles as cleaners probably does not afford California cleaners any security from being eaten during noncleaning situations. Recently, however, island kelpfish (*Alloclinus holderi*), bluebanded goby (*Lythrypnus dalli*), juvenile giant kelpfish (*Heterostichus rostratus*) and juvenile kelp bass (*Paralabrax clathratus*) have been observed at what appears to be cleaning stations for giant sea bass (*Stereolepis gigas*) at Anacapa Island (DeWet-Oleson and Love 2001). The juvenile kelpfish not only entered the mouth of the giant sea bass but also had unusual behavior of 15 to 20 individuals parasite picking at a time (DeWet-Oleson and Love 2001).

California marine cleaners, other than the fishes described above, include shrimps and birds. Limbaugh (1961) described the relationship between the California cleaner shrimp *Hippolysmata californica* (now *Lysmata californica*) and its clients, the California moray (*Gymnothorax mordax*) (fig. 21-4a), the garibaldi (*Hypsypops rubicundus*), and the spiny lobster (*Panulirus interruptus*). *Lysmata californica* is not an obligate cleaner, and continually feeds on the epibiose of the rocky substrate, which it occupies (Limbaugh et al., 1961). Limbaugh also discovered cleaner shrimp within the gut contents of California morays and observed the shrimps to occasionally feed upon tissue of their clients. Limbaugh et al. (1961: 251) summarized their observations by stating "*Hippolysmata californica* therefore exhibits a rather simple and imperfect relationship with its hosts, sometimes eating them and sometimes being eaten itself. During the cleaning process, the shrimps seem only to seek food on a new substrate. From this simple and hazardous relationship, it is easy to visualize an evolutionary path by which the more complex cleaning behavior could have developed."

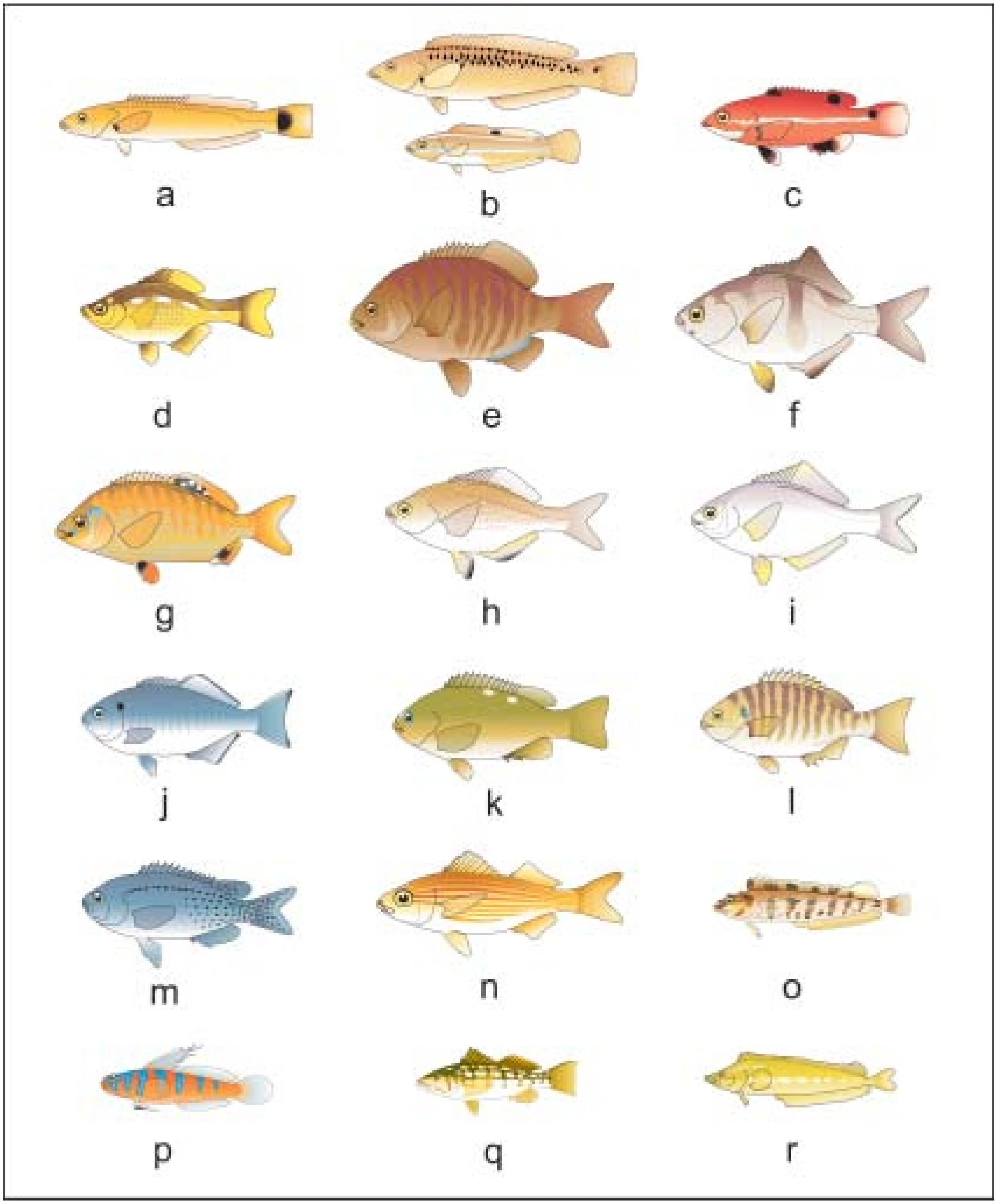

FIGURE 21-1 California cleaner fishes. Included are: wrasses, family Labridae, a) señorita, b) a juvenile and female rock wrasse, and c) juvenile California sheephead; surfperches, family Embiotocidae, d) kelp perch, e) black perch, f) pile perch, g) rainbow seaperch, h) sharpnose seaperch, and i) white seaperch; kyphosids, family Kyphosidae, j) halfmoon, k) zebra perch and l) opaleye; m) blacksmith, Pomacentridae; n) salema, Haemulidae; o) island kelpfish, Labrisomidae; p) bluebanded goby, Gobiidae; q) juvenile kelp bass, Serranidae; r) juvenile giant kelpfish, Labrisomidae (see table 21-1).

Another client commonly observed off the California coast is the ocean sunfish (*Mola mola*, family Molidae) which can be seen off the edge of kelp beds, positioned in awkward postures while being groomed by surfperches (rainbow and/or sharpnose seaperches) (Gotshall, 1967). As well, molas are occasionally observed over deep water during the summer lying on their sides at the surface with gulls picking at their skin parasites (Tibby, 1936; King, 1978; Love, 1996); these observations are complicated but not contradicted by the fact that during infrequent mola die-offs, molas may be seen floating at the surface, with gulls picking at their eyes (Gotshall, 1961).

Considerable opportunity for further research on cleaning behavior exists in California coastal waters. Greg Jensen of the University of Washington advises me that numerous undocumented fish and shrimp interactions remain unreported (and probably others still undiscovered) in the northwest Pacific, in part because much of that activity may be nocturnal. Hobson and others have noticed that cleaners are

TABLE 21-1
Fishes Known to Engage in Cleaning Behavior in California Waters

Scientific Name	*Common Name*	*Family*	*References*
Alloclinus holderi	island Kelpfish	Labrisomidae	DeWet-Oleson and Love 2001
Brachyistius frenatus	kelp perch	Embiotocidae	Limbaugh 1955, Hobson 1971
Chromis punctipinnis	blacksmith	Pomacentridae	Turner et al. 1969
Embiotoca jacksoni	black perch	Embiotocidae	Limbaugh 1955
Girella nigricans	opaleye	Kyphosidae	DeMartini and Coyer 1981, Sikkel 1986
Halichoeres semicinctus	rock wrasse	Labridae	Hobson 1971
Hermosilla azurea	zebraperch	Kyphosidae	DeMartini and Coyer 1981, Sikkel 1986
Heterostichus rostratus	giant kelpfish (juvenile)	Labrisomidae	DeWet-Oleson and Love 2001
Hypsurus caryi	rainbow seaperch	Embiotocidae	Gotshall 1967
Lythrypnus dalli	bluebanded goby	Gobiidae	DeWet-Oleson and Love 2001
Medialuna californiensis	halfmoon	Kyphosidae	Hixon 1979
Oxyjulis californica	señorita	Labridae	Limbaugh 1955, Hobson 1971
Paralabrax clathratus	kelp bass (juvenile)	Serranidae	DeWet-Oleson and Love 2001
Phanerodon atripes	sharpnose seaperch	Embiotocidae	Gotshall 1967, Hobson 1971
Phanerodon furcatus	white seaperch	Embiotocidae	Hobson 1971
Rhacochilus vacca	pile perch	Embiotocidae	Limbaugh 1955
Semicossyphus pulcher	California sheephead	Labridae	Coyer 1980
Xenistius californiensis	salema	Haemulidae	Sikkel 1986

Note: After DeWet-Oleson and Love 2001.

FIGURE 21-2 Señoritas (*Oxyjulis californica*) cleaning blacksmiths (*Chromis punctipinnis*). Note the head down posture of the blacksmiths that are soliciting cleaning. (Photo courtesy of E.S. Hobson.).

FIGURE 21-3 Sharpnose seaperches (*Phanerodon atripes*) cleaning blacksmiths (*Chromis punctipinnis*). (Photo courtesy of E.S. Hobson.).

at risk of themselves being infected by non-specific ectoparasites, but an extensive study has not been attempted. And, although much attention has been paid to the parasitized fishes, far too little is known of the biology of the parasites. The time of infestation, the mechanism of host choice, the degree of specificity, and the life history of most parasites remains to be investigated. This has value and application as has been shown in experiments with pen-cultured Atlantic salmon, which when raised in high densities become heavily parasitized, resulting in skin damage, secondary infections and impaired osmoregulation. Employing temperate wrasses as an alternative to pesticide treatment has been shown to be cost-effective and appropriate, but not without difficulties (Kvenseth, 1996; Losey et al., 1999). The introduction of exotic marine cleaner species to California waters, despite its perceived benefits, is neither legal nor appropriate, but the beneficial behaviors of native cleaner fishes and shrimps are well worth exploring.

Endosymbiotic mutualisms are probably more abundant than currently recognized and provide an area for further investigation. Two examples that I will describe briefly include the creation of light by bioluminescent bacteria and the role of microbes in assisting digestion by herbivorous fishes. Bioluminescence in marine fishes has two origins, viz. the self-luminous species such as the batrachoidid midshipmen (*Porichthys* spp.) and the myctophid lanternfishes (many genera and species) which, via specialized photophores, produce light primarily for counterillumination and intraspecific signaling, and those that employ bacterial symbionts to provide light that is used for a variety of purposes, including counter-illumination, food detection, feed attraction, intraspecific signaling, and passive predator avoidance. California fishes that participate in bioluminescent bacterial symbioses include the ceratioid anglerfishes, an anomalopid, and certain macrourids (rattails) and morids (codlings). Most are deepwater species hence little is known of the behavior of the fishes through

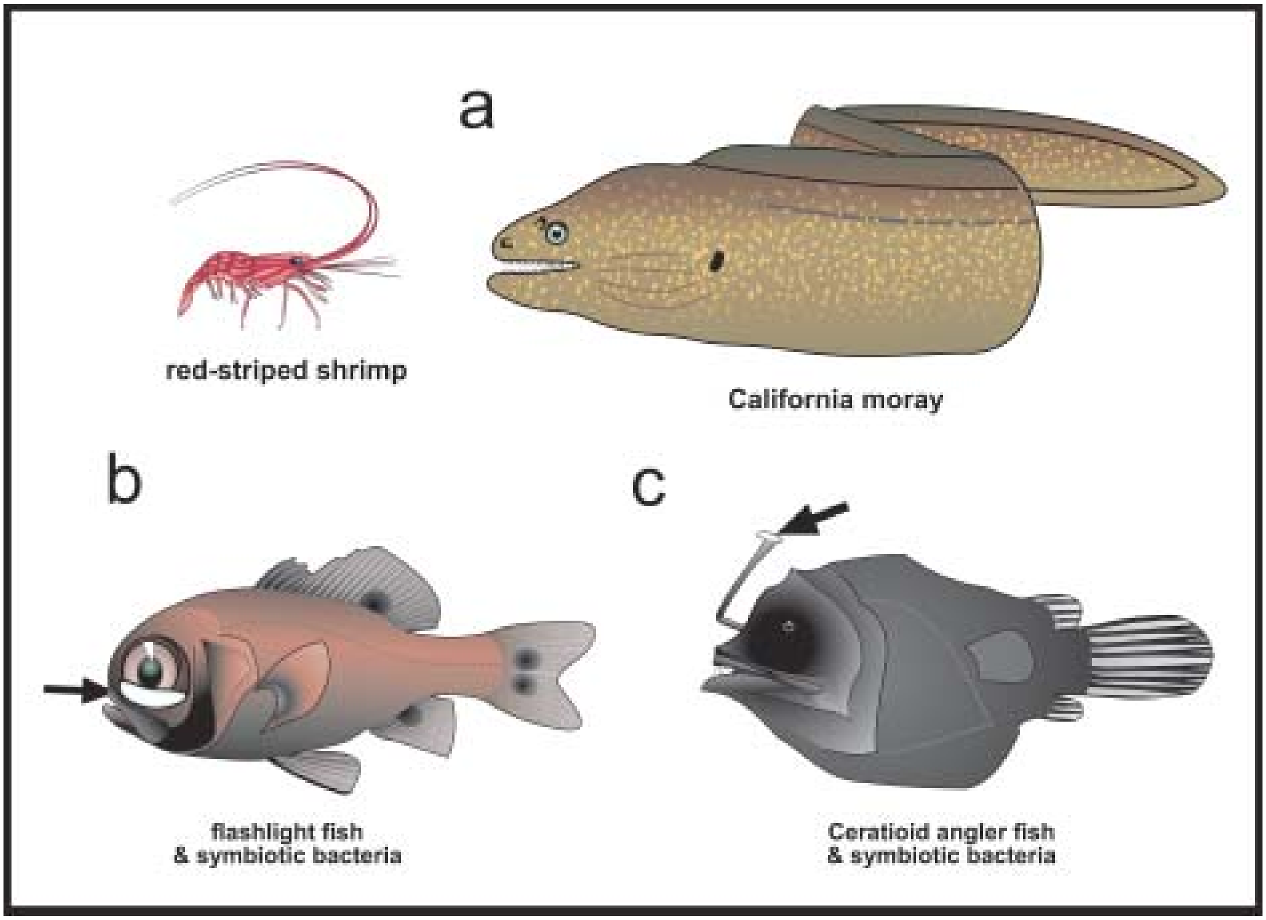

FIGURE 21-4 Examples of symbiotic relationships in fishes off the Californias: a) the California cleaner shrimp (*Lysmata californica*) and its client, the California moray (*Gymnothorax mordax*); b) the Mexican flashlight fish (*Phthanophaneron harveyi*) employ bacterial symbionts in a subocular organ (arrow) to provide light; c) luminous ceratioid anglerfishes are all obligate mutualists (worldwide, females of nine of eleven recognized ceratioid families possess escas (lures) which employ bacterial symbionts).

direct observation. It can be inferred that the symbiosis is mutualistic and obligatory to both partners in the case of those fishes that employ bacteria for the attraction and gathering of food (McCosker, 1977; Haygood, 1993), and apparently commensal or mutualistic in a number of other midwater fishes that employ bacteria within their gut as an aid to digestion (the luminescence of fecal pellets thereby provide an attractive dispersal mechanism for the bacteria) (Nealson and Hastings, 1979). Those luminous ceratioids (fig. 21-4c) that live off the continental shelf and in our coastal waters are all obligate mutualists (worldwide, females of nine of eleven recognized ceratioid families possess escas which employ bacterial symbionts). The Mexican flashlight fish (*Phthanophaneron harveyi;* fig. 21-4b), captured in shallow water in the Gulf of California and off Thetis Bank, Baja California (McCosker and Rosenblatt, 1987), is remarkable in the amount of light that it casts as well as the mechanisms that it has developed (a dark shutter and rotation of the light organ) to occlude the light. In aquarium captivity, it is possible to darken the bacteria of another anomalopid (*Anomalops katoptron*) (McCosker, unpublished data); under those conditions the fish is unable to find its crustacean prey, demonstrating the obligatory nature of that symbiosis.

Obligate bacterial endosymbionts have been shown to occur in some tropical surgeonfishes (family Acanthuridae), however other studies of fish gut endosymbionts suggest that most relationships are not obligatory and that the presence of gut microbes is often an artifact of microbial populations in the water or the food (Fishelson, et al., 1985). Horn (1992) has suggested that microbial fermentation plays a role in the digestive processes of kyphosids, including the halfmoon (*Medialuna californiensis*), the opaleye (*Girella nigricans*), and the zebraperch (*Hermosilla azurea*), but is not involved in the digestive process of another California herbivore, the monkeyface eel (*Cebidichthys violaceous*, family Cebidichthyidae).

Commensalism

The relationship between various fishes and jellyfish medusae and siphonophores is often cited as an example of commensalism (reviewed by Mansueti, 1963). Juveniles of California carangids, girellids, and most notably, stromateoids (particularly the nomeids, centrolophids, and stromateids), participate in this symbiosis (see chapter 12). The young fish gain several advantages: protection from predation; food (the small invertebrates associated with the tentacles and bell of the medusae, and ultimately the host itself); and a means of dispersal. Mansueti (1963) considers this relation to be a temporary ecological phenomenon in which the medusae are passive hosts and the juvenile fishes are active opportunists. What begins as a commensal relationship in many species

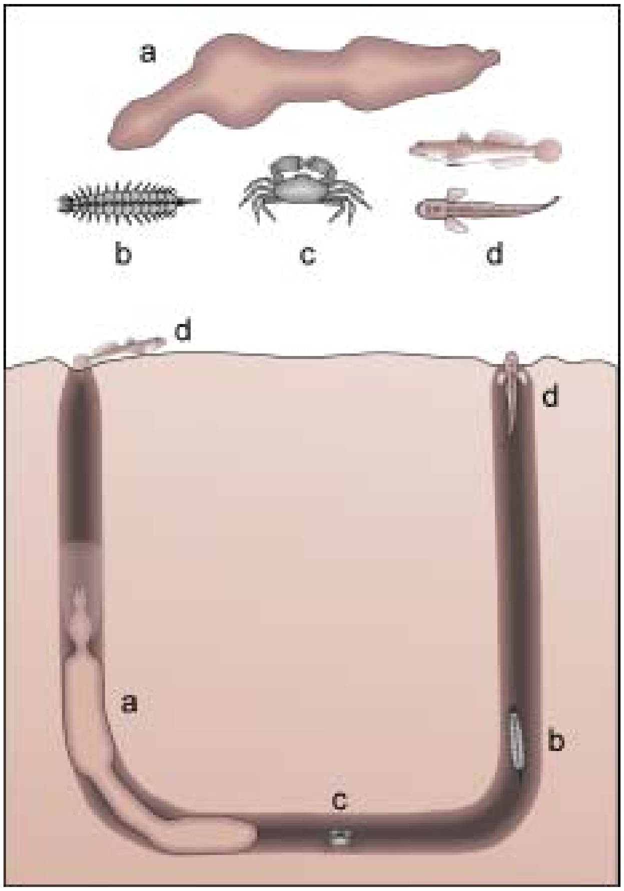

FIGURE 21-5 Depiction of the commensal relationship between the fat innkeeper worm (a) *Urechis caupo* and three mudflat organisms including: (b) the scale worm (*Hesperonoe adventor*); and (c) the pea crab, *Scleroplax granulata*); and (d) the arrow goby (*Clevelandia ios*) (after Ricketts and Calvin, 1939).

gradually becomes one of parasitism as the fish consumes the tentacles and then the entire host. In a manner not unlike that practiced by tropical pomacentrids and other reef fishes, stromateoids possess a high resistance to coelenterate toxins, however they are not entirely immune to those venoms (Lane, 1960; Totten, 1960). Haedrich (1967: 47) suggests that "besides the relatively high resistance to the toxins, simple avoidance of the tentacles and the characteristic heavy coating of slime probably are important in allowing the fishes to swim with impunity under their hosts." California stromateoids known to cohabit (at some time in their life) with scyphomedusae and siphonophores include the medusafish (*Icichthys lockingtoni*, family Centrolophidae), which when young are often found swimming in association with medusae (Jordan, 1923), and three stromateids, the bluefin driftfish (*Psenes pellucidus*), the longfin cigarfish (*Cubiceps paradoxus*), and the Pacific pompano (*Peprilus simillimus*), which as juveniles have been collected with purple-striped jellies (*Pelagia colorata*) (Horn, 1970).

Some symbiologists recognize *phoresis* as a distinct category whereas others treat it as a subcategory of commensalism. I prefer the latter, and include those loose, non-obligatory relationships in which a host provides shelter, support, or transport for one or more other species. Unlike the fishes and jellyfishes described above, metabolic dependency is not involved in phoretic associations. Phoresis defined thusly would include epizoites such as the pilotfish (*Naucrates ductor*) (see fig. 21-7; chapter 12) that accompany large sharks or the non-predatory carapids (not resident in California waters) that occupy the respiratory tract of holothurians.

Commensal associations between gobiid fishes and various invertebrates are well known. Relations between gobies and the three species of *Neotrypaea* (as *Callianassa*) ghost shrimps were the subject of classic studies by MacGinitie and MacGinitie (1949: 288–290, 429–432). Their description is worth repeating, for the charm of the verse and the fact that it reinforces the difficulty in categorizing symbioses. As concerns its digging behavior, they state "*Callianassa* is doomed to a life of almost constant digging," and the resultant local downside, "Oyster growers in the Puget Sound regions will also testify to the industry of *Callianassa*, for many oysters are buried by the soil carried to the surface by this shrimp." Alas, they exhort, "but it is an ill wind that blows no good, and if some oysters are killed by the activities of *Callianassa*, other animals are afforded living quarters and refuge, and still others are provided with a set of conditions that enable them to live where they otherwise could not live." And it is just that sort of symbiosis that the arrow goby (*Clevelandia ios*) enjoys with the pink ghost shrimp *Neotrypaea californiensis*. Arrow gobies (fig. 21-5) are not reticent to occupy other invertebrate burrows and can be found living the tubes of the fat innkeeper worm (*Urechis caupo*) or the mud shrimp (*Upogebia pugettensis*) (Fisher and MacGinitie, 1928). MacGinitie and MacGinitie (1949: 428) provided the grist for early marine symbiosis tales when they explained the relationship of arrow gobies and their co-commensals as observed in aquaria:

> It was in watching these little fish in the aquarium that we first became acquainted with a habit that is possessed by *Clevlandia* (*sic*) and other fishes. If a *Clevlandia* finds a morsel of food that is too large for it to swallow, with true Tom Sawyerish propensity it carries the piece of food to some crustacean, and, as the latter tears the food to pieces, the fish snatches particles to eat and, at intervals, even snatches the larger piece and attempts to swallow it. . . . We have tested this trait many times by giving *Clevlandia*s pieces of clam meat or fish which were too large for them to swallow. *Clevlandia*s are not at all particular as to what crustaceans they put to work. We have watched *Clevlandia*s in a burrow with *Urechis*, *Upogebia*, or *Callianassa* carry meat to a pea crab (*Scleroplax* or *Pinnixa*), and those in an open aquarium to such shrimps as *Spirotocaris* or *Crago*. The unsuspecting shrimps are only too glad to get the morsel of meat, but the *Clevlandia* watches and waits and sees that the shrimps do not get all of it. . . . Such activities as this emphasize the interrelationships of animals and how they are built up during evolutionary time.

While the symbiotic relations of most commensal gobiids are facultative, those between the blind goby (*Typhlogobius californiensis*) and the ghost shrimp (*Neotrypaea biffari*, previously *Callianassa affinis*) are obligatory (fig. 21-6). Pairs of adult blind gobies are always found in *Neotrypaea biffari* burrows (although the shrimp may be found without gobies). They are largely confined to the intertidal flats along the open coast where boulders and rocks are large enough to remain in place despite surf or tidal action. The burrows are within the sand interstices and beneath the rocks and are essentially permanent. MacGinitie (1939, summarized in MacGinitie and MacGinitie, 1949) described the natural history of the pairs and performed a series of experiments to examine the relationship. There is no apparent benefit to the partner other than shared refuge, unlike tropical shrimp/goby pairings

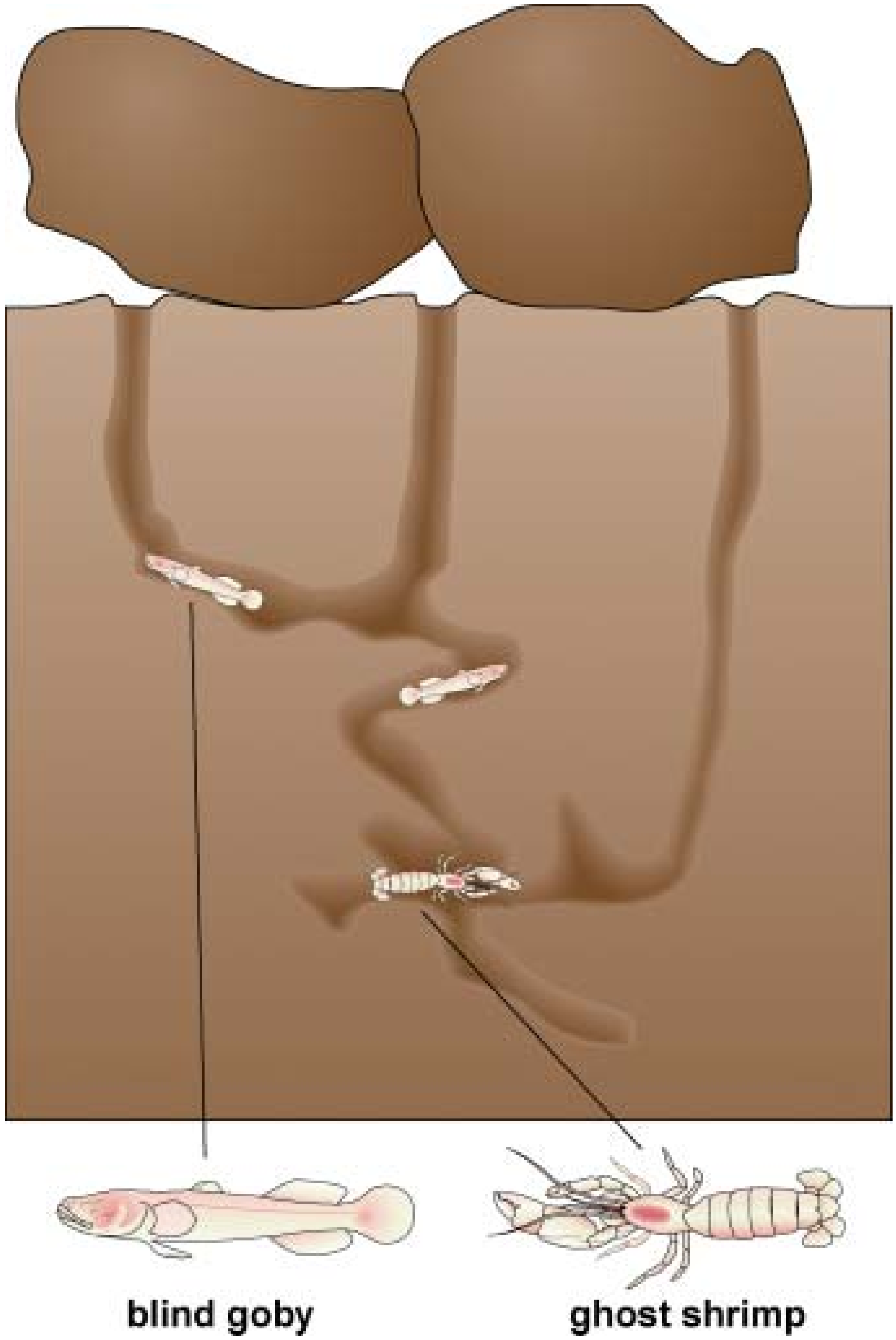

FIGURE 21-6 Depiction of the obligate commensal relationship between the California blind goby (*Typhlogobius californiensis*) and the ghost shrimp (*Neotrypaea biffari*, previously *Callianassa affinis*).

wherein the fish acts as a sentry to the industrious burrowing shrimp. The adaptations of *Typhlogobius* are extreme such that the sighted larvae soon lose their vision through the growth of tissue over their eyes and their skin is unpigmented and scaleless. The pink coloration of the goby's skin illustrates its role in aerial respiration; nearly anoxic conditions are reached at low tide and *Typhlogobius* has achieved respiratory compensation in the extreme (Congleton, 1974). Several other California gobies occupy shrimp, crab, and worm burrows, but none have evolved a commensalism as obligatory as that of the blind goby.

Although no symbiotic associations of damselfishes and anemones are known from temperate waters, an intriguing facultative commensalism has arisen involving the painted greenling (*Oxylebius pictus*, family Hexagrammidae) and two sea anemones, *Utricina lofotensis* and *U. piscivora* (family Actiniidae) (fig. 21-7). Young *Oxylebius* associate with these anemones from southern California to British Columbia, taking refuge within the anemone's tentacles in a manner much like the obligatory relationships of tropical Indo-Pacific anemonefishes and certain anemones (Fautin, 1991) or the facultative associations of various tropical Caribbean reef fishes and anemones (Hanlon et al. 1983). This symbiotic relationship was first reported by Herald (1972) and carefully described and experimentally demonstrated by Elliott (1992). Elliott found that the painted greenling of Vancouver Island could swim and rest unharmed among the tentacles of the large anemones. This occurred most often at night where fish

FIGURE 21-7 Adult painted greenling (*Oxylebius pictus*), ca. 15 cm total length, upon a white-spotted rose anemone (*Utricina lofotensis*). (Photo courtesy of Steinhart Aquarium.)

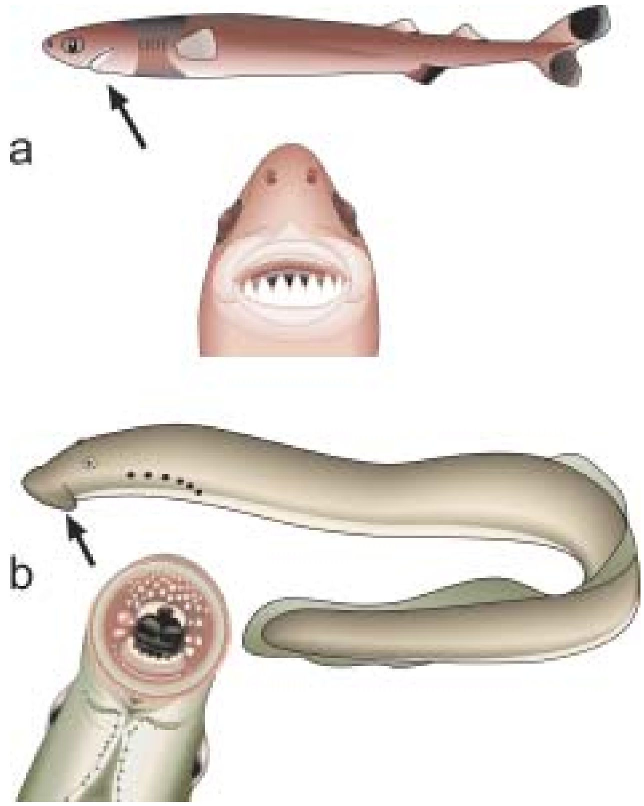

FIGURE 21-8 Examples of ectoparasitic fishes occurring off the Californias: a) the cookiecutter or cigar shark (*Isistius brasiliensis*) and b) Pacific lamprey (*Lampetra tridentata*).

and anemone densities were high. With increasing size, the fish became less dependant upon the anemone for shelter; however the abundance of copepods upon the anemone's surface provided prey for young fish and older fish fed around the anemones' bases. The fish are apparently protected from the stinging tentacles by a compound within the fish's epidermal mucous coating. Elliott was unable to demonstrate any benefit to the anemone from the fish's presence and therefore considered the symbiosis to be one of facultative commensalism.

The survival value of schooling behavior, as a means of avoiding or reducing predation is well documented (see review by Hobson, 1978). Terrestrial ethologists suggest that bird flocks are similar to fish schools and extend those benefits through special adaptations, colorations, and visual signal patterns which promote the formation of mixed species flocks. Moynihan (1968) proposed the term "social mimicry" for this activity and predicted that the study of fishes would demonstrate the same phenomenon. Randall and McCosker (1993) showed him to be correct and provided examples of tropical anthiines, a pomacentrid, and a blenniid that are remarkably similar in coloration and appearance and school together for mutual protection. Such social mimicry can be categorized as a commensal relationship and can probably be demonstrated to occur in California coastal waters. Likely candidates include mixed schools of juvenile rockfishes (*Sebastes* spp., family Scorpaenidae) and juvenile and adult surfperches (family Embiotocidae), and deserve further study.

Parasitism

As stated above, many symbionts that benefit from mutualistic or commensal relationships become predators or prey to the same partner under different circumstances. And, if one broadly defines parasitism to include the behavior of piscivorous fishes, then the vast majority of California fishes are gustatory parasites. I will not deal with that strained assumption in this chapter, but will instead describe the fascinating parasitic behavior of the cookiecutter shark and the relationship of lampreys and their salmonid prey (fig. 21-8).

The parasitic activity of the cookiecutter or cigar shark (fig. 21-8a) was first uncovered by the clever detective work of Everet Jones. Billiard ball-sized crater wounds had been observed on a variety of creatures such as beaked whales, baleen whales, sperm whales, porpoises, a variety of pelagic fishes and even a nuclear submarine (Jones, 1971; Johnson, 1978). Jones convincingly demonstrated that a small squalid shark, *Isistius brasiliensis*, inflicted the wounds. It is a facultative ectoparasite whose dentition, suctorial lips, and modified pharynx allow it to attach to the side of large prey, drive its saw-like lower jaw teeth into the skin and flesh of its victim, rotate its body and cut a conical plug of flesh, and then pull itself free with the plug cradled by its scoop-like lower jaw and held by the hook-like upper jaw teeth. LeBoeuf et al. (1987) reported on parasitic attacks by *Isistius brasiliensis* on northern elephant seals (*Mirounga angustirostris*) at Guadalupe Island, Baja California, and at Año Nuevo Island, California. I have subsequently observed recently attacked *Mirounga* at southwest Farallon Island, California, and fresh scars on a harbor porpoise (*Phocoena phocoena*) from China Beach, San Francisco Bay. *Isistius brasiliensis* is an epipelagic to bathypelagic species (and occasionally seen at the surface at night) that is known from all tropical oceans, however it is probably uncommon off the California coasts.

Lampreys, family Petromyzontidae, are well-known as parasitic fishes largely as a result of the havoc that the Atlantic sea lamprey (*Petromyzon marinus*) inflicted upon the large resident fishes once the Welland Canal allowed their entry into the Great Lakes. Many nonpredatory lampreys have evolved from predatory ancestors, and both are significant prey items for bony fishes. In California waters, their abundance has been dramatically reduced and only one of the four California species is truly predatory. The Pacific lamprey (*Lampetra tridentata;* fig. 21-8b) is the largest of California lampreys and, with the exception of landlocked populations, spends the predatory phase of its life history in the ocean. Moyle (1976: 90) states, "Little is known about their oceanic life except that they attack a wide variety of large fishes, occasionally even taking on whales. Despite far-flung ocean distribution records, it is unlikely that Pacific lampreys normally wander far from the mouths of their home spawning streams, since their prey is most abundant in estuaries and other coastal areas. The oceanic phase presumably lasts one to two years, like that of the eastern sea lamprey (*Petromyzon marinus*)."

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