CLEANING SYMBIOSIS AMONG CALIFORNIA INSHORE FISHES[1]

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ABSTRACT

Cleaning symbiosis among shore fishes was studied during 1968 and 1969 in southern California, with work centered at La Jolla. Three species are habitual cleaners: the señorita, *Oxyjulis californica*; the sharpnose seaperch, *Phanerodon atripes*; and the kelp perch, *Brachyistius frenatus*.

Because of specific differences in habitat, there is little overlap in the cleaning areas of these three species. Except for juvenile sharpnose seaperch, cleaning is of secondary significance to these species, even though it may be of major significance to certain individuals. The tendency to clean varies between individuals. Principal prey of most members of these species are free-living organisms picked from a substrate and from midwater—a mode of feeding that favors adaptations suited to cleaning.

Because it is exceedingly abundant in a variety of habitats, the señorita is the predominant inshore cleaning fish in California. Certain aspects of its cleaning relate to the fact that only a few of the many señoritas present at a given time will clean, and that this activity is not centered around well-defined cleaning stations, as has been reported for certain cleaning fishes elsewhere. Probably because cleaners are difficult to recognize among the many señoritas that do not clean, other fishes generally do not attempt to initiate cleaning; rather, the activity is consistently initiated by the cleaner itself. An infested 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.

The fishes cleaned most often are those which are most abundant and, at the same time, are most heavily infested with external parasites. The most numerous ectoparasites are caligid copepods, the most abundant and widespread of which is *Caligus hobsoni*. These particular parasites, along with gnathiid isopod larvae, are the major prey of the cleaning fishes. Cleaning is essentially limited to the external body surface; ectoparasites of the oral and branchial cavities are not ordinarily taken. Cleaning effectively reduces the number of parasites on fishes that are cleaned, and is an important activity for the organisms involved. However, 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.

It has been suggested that many of the better inshore fishing spots are, in fact, cleaning stations (Limbaugh, 1961; Feder, 1966). The contention is that fishes congregate at these locations so that ectoparasites and other deleterious material can be removed from their bodies by resident cleaning organisms. Critics of this hypothesis might well suggest instead that cleaners simply are especially active where fishes are most abundant, or that the cleaners as well as those they clean occur at these locations for reasons that have nothing to do with cleaning. Regardless of which view is correct in a given situation, one having witnessed fishes crowded around a cleaner, vigorously soliciting its services, can only conclude that this activity is indeed important to the organisms involved.

Cleaning symbiosis has been widely described in the literature (Longley and Hildebrand, 1941; Eibl-Eibesfeldt, 1955; Limbaugh, 1955, 1961; Randall, 1958, 1962; and others) and was reviewed by Feder (1966). Youngbluth (1968) studied activity of the Hawaiian cleaning labrid *Labroides phthirophagus* in some detail, and Losey (1971) analyzed the communicative signals between this same species and the fishes that it cleans. But most other reports on cleaning have been simple treatments based largely on

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Manuscript accepted March 1971.

incidental observations. In this report, I describe cleaning symbiosis among inshore fishes of southern California and attempt to relate observed activity with the incidence of specific ectoparasites.

Conrad Limbaugh, Scripps Institution of Oceanography, was among the first to report cleaning symbiosis among California fishes. In a study of fishes of the kelp beds, Limbaugh (1955) described cleaning by the señorita, *Oxyjulis californica*, a fish of the family Labridae, and also by several seaperches of the family Embiotocidae: the kelp perch, *Brachyistius frenatus;* the black perch, *Embiotoca jacksoni;* and the pile perch, *Rhacochilus vacca*. Subsequent observers have described cleaning by the rainbow seaperch, *Hypsurus caryi* (Gotshall, 1967); the sharpnose seaperch, *Phanerodon atripes* (Clarke, Flechsig, and Grigg, 1967; Gotshall, 1967; Hobson, 1969a); and the blacksmith, *Chromis punctipinnis* (Turner, Ebert, and Given, 1969).

SPECIES STUDIED

Most of the cleaning observed during this study was performed by the señorita (Figure 1), which by virtue of its great abundance in a variety of habitats is the predominant cleaner inshore. The sharpnose seaperch (Figure 2) was frequently observed cleaning, but its activity is centered in deeper water. The kelp perch (Figure 3) may be an important cleaner in the canopy region of the kelp forests, where it concen-

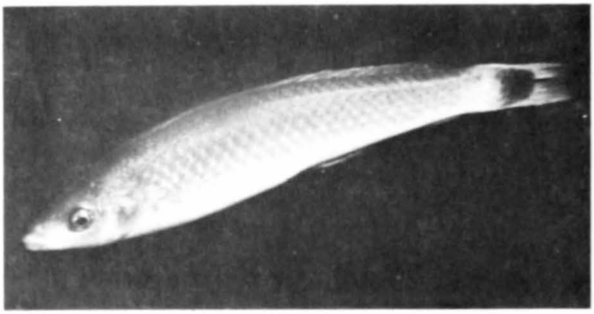

FIGURE 1.—Señorita.

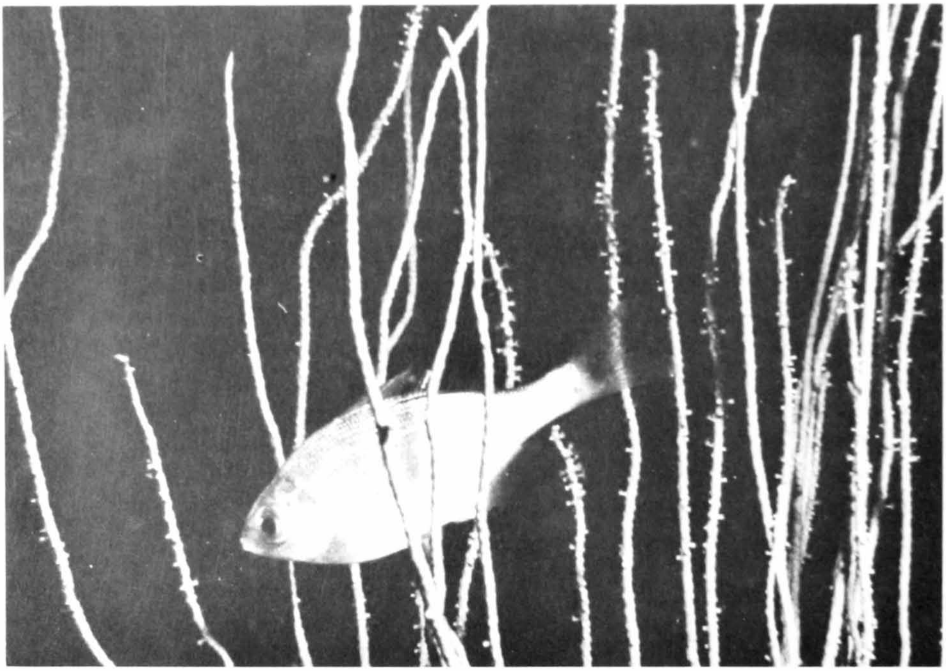

FIGURE 2.—Sharpnose seaperch among branches of a gorgonian.

trates, but this was not determined in this study because observations in the kelp-canopy habitat were infrequent. Nevertheless, observations were sufficient to recognize the kelp perch as a habitual cleaner. The only other fish seen cleaning was the white seaperch, *Phanerodon furcatus,* in which cleaning seemed to be only an occasional incidental activity.

METHODS

During 1968 and 1969, I spent more than 103 hr underwater directly observing cleaning and related activity in California inshore waters. Also contributing to the study are many incidental observations of cleaning made during other work with California fishes between 1961 and 1970.

Supplementing the observations, 421 specimens of 39 species were collected with spear. These represent most of the species common in the study area that exceed a length of 100 mm (all lengths of fishes in this report are standard length). The ectoparasites were collected from all specimens and will be reported in detail elsewhere in collaboration with R. F. Cressey, U.S. National Museum. These collections also provided the material for descriptions of 11 species of copepods formerly new to science (Cressey, 1969a, 1969b, 1970; J. Ho, California State College, Long Beach, unpublished manuscript). Additional undescribed species may occur among a number of copepods from these collections presently under study by Z. Kabata, Biological Station, Nanaimo, British Columbia.

In addition to a survey of the ectoparasites, gut contents of known cleaning species, including material from 53 señoritas, 29 sharpnose seaperch, and 3 kelp perch, were analyzed.

Many ectoparasites leave their host when it is in difficulty, and some fishes regurgitate their stomach contents under stress. To reduce this loss, all specimens were individually sealed in plastic bags immediately upon capture, and while still underwater.

To acquire detailed data on the cleaning interaction, a number of individuals of cleaning species were kept under surveillance for periods

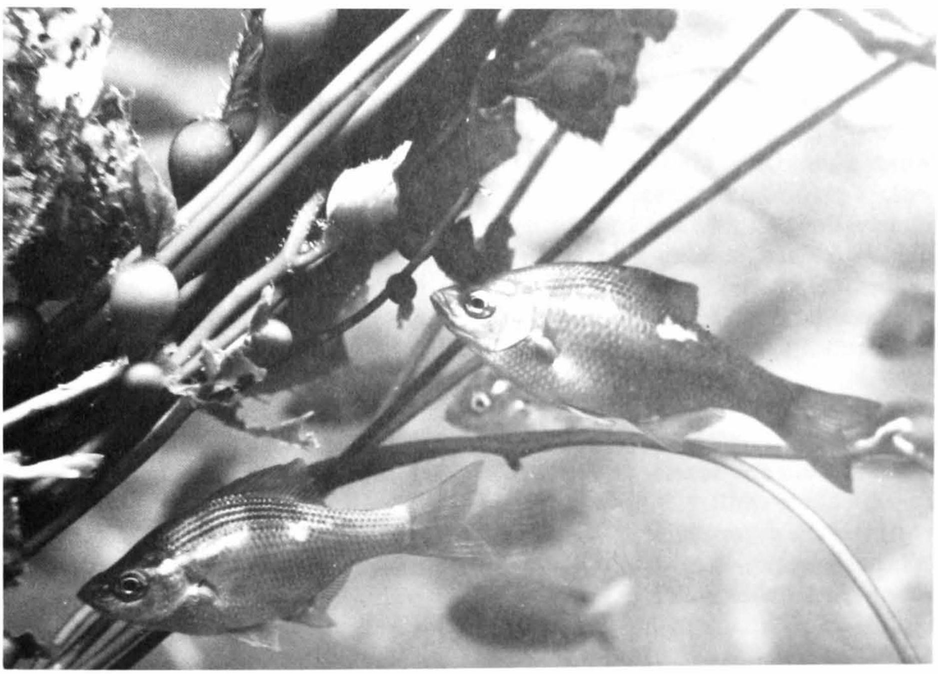

FIGURE 3.—Kelp perch next to giant kelp.

up to 15 min, and a verbal account of their activity was recorded on tape. The attempted standard of 15 min could not be maintained for all these observations because sometimes contact with the fish being watched was lost as the fish swam among vegetation or other fishes. Individuals followed included known cleaners as well as others that had not shown evidence of cleaning. In monitoring the activity of known cleaners, a record was kept of the time during which they showed an apparent cleaning interest in other fish and also the number of cleaning bouts in which they became involved. A cleaning bout is defined here as any cleaning activity involving a discrete group of fishes, whether this group includes one cleaner attending a single fish, or several cleaners attending a cluster of 40 to 50 fish. On various occasions I also recorded the number of times that the cleaner actually "picked" at the body of another fish, and precisely at what point on the body this action was directed.

Study Areas

Observations of cleaning symbiosis were made at many locations throughout southern California, including the Channel Islands, and at the Coronado Islands, Mexico. However, most of the data were collected during concentrated work at La Jolla, Calif. Here, three study sites were established, each including an area of about 100 m^2, that lie on a line running northwest offshore from La Jolla Point. Moving away from the beach along this line, the first station lies in 3 to 10 m of water about 200 m offshore, the second is in 20 to 25 m of water about 700 m offshore, and the third in 30 to 35 m of water about 1000 m offshore. The sea floor at all three stations is rocky and irregular, with many crevices and caves. Algae are not conspicuous at the two deeper stations, which are similar, but the rocks support a heavy growth of gorgonians. On the other hand, the nearshore region of the 3- to 10-m station is richly carpeted with surfgrass, *Phyllospadix,* and other parts of the inshore station are forested by large kelps, particularly giant kelp, *Macrocystis,* and feather-boa kelp, *Egregia.* However, these large kelps are sparse here in comparison to some areas nearby to the south and elsewhere in California. Other details of the principal study area will be introduced as they become pertinent.

During all observation periods at the La Jolla stations a record was kept of water temperatures from surface to bottom, horizontal visibility, and surge conditions.

OBSERVATIONS

GENERAL ECOLOGY

Señorita

The señorita, which attains a length of about 250 mm, is one of the most abundant fishes in the inshore waters of southern California, including the Channel Islands. It occurs from the shoreline to depths exceeding 40 m and is recorded from central California south to central Baja California, Mexico (Roedel, 1953). An inhabitant of water over rocky substrates and among sea weeds, the señorita sometimes swims singly, but more often in groups of from a few to many hundreds of individuals. Like other labrids, it is strictly a diurnal fish, taking shelter under cover at night.

Food habits.—The señorita feeds on a variety of benthic organisms from the surface of both algae and rocks. It also feeds heavily in the midwaters, taking small organisms in the plankton, as well as forms that are attached to or encrusted on drifting algal fragments. All this feeding is accomplished in a characteristic picking manner, a mode of feeding well suited to its pointed snout and the several long, curved canine teeth that project forward at the front of each jaw.

To determine the food habits of this fish in the study area, 26 specimens, 110 to 195 mm long, were speared randomly from the population at large. None of these were cleaning when collected. Food items in their stomachs, ranked as percentage of each item in the entire sample, were as follows: bryozoans encrusted on algae, 43%; caprellid amphipods, 32%; fish eggs, 3%; gammarid amphipods, 2.5%; unidentified crustacean fragments, 4%; and pelecypod mollusks, 2.4%. A number of items each made up less than 1% of the sample, including crab fragments, gastropod mollusks, pycnogonids, and a gnathiid isopod larva. Unidentified material constituted 16% of the sample. The gnathiid larva, a single individual from one señorita, was the only evidence of ectroparasites among this material.

Limbaugh (1955) stated that señoritas are omnivorous carnivores which feed on almost any animal material. Quast (1968) concluded that the principal foods of the señorita are small gastropods and crustaceans associated with algae. Because he found no crabs or pistal shrimps in the diet, Quast suggested that bottom feeding is infrequent; however, having seen señoritas frequently picking on the bottom, I believe there must be some other reason why these prey are not taken more often. Size may be a factor, as crabs and pistal shrimps generally are larger and more heavily shelled than most prey of the señorita.

Movements.—Although individual señoritas may range widely over the bottom in a given locality, they seem to operate within a restricted range. Individual fish, when followed, always criss-cross back and forth within a defined area. Twelve individuals, selected randomly from the population at large and kept under surveillance for 11 to 15 min each, showed no evidence of cleaning.

Señoritas are most abundant at the 3- to 10-m station and become progressively fewer with increasing depth offshore. Nevertheless, even at the 30- to 35-m station the species was among the most numerous present. Fluctuations in numbers were often apparent with changes in water temperature. Some of the movement is vertical. When a layer of colder water moved in over the bottom—a frequent phenomenon at the 20- to 25-m station—señoritas were especially abundant up in the water column above the thermal interface. Seasonal and other longer term changes may induce inshore/offshore movements in certain members of the population. The numbers present fall off noticeably when temperatures drop much below 13° C, but at least some señoritas were present no matter what the conditions. These comments on temperature effects are based entirely on casual evaluations of relative abundance under varying conditions.

Sharpnose Seaperch

The sharpnose seaperch is not regarded as a common species (e.g., Limbaugh, 1955), but was relatively abundant during this study over rocky substrates below 20 m in the La Jolla area. It grows to over 200 mm long and is recorded from Bodega Bay, central California (Miller, Gotshall, and Nitsos, 1965), south to the San Benito Islands, Mexico (Roedel, 1953). Most of those observed during this study were juveniles less than about 125 mm long that swam singly or, more often, in small groups of less than 10 individuals. Adults were seen only occasionally but sometimes swam in larger aggregations. All activity observed in these fish occurred during daylight. After dark they hover above the substrate and are alert, but their activity at this time, if any occurs, was not determined.

Food habits.—This seaperch takes a variety of benthic organisms from the surface of rocks, algae, gorgonians, and other benthic substrates. Prey are taken off the bottom in a characteristic picking manner similar to that of the señorita. However, the seaperch's dentition would seem less specialized for picking than that of the señorita; its conic teeth are relatively short and straight, and those at the front of the jaws are not notably longer than those on the sides, nor do they project forward.

To investigate the food habits of this fish in the study area, 13 individuals, 76 to 170 mm long, were speared randomly from the population at large. None of these were cleaning when collected. Food items in their stomachs, ranked as percentage of each item in the entire sample, were as follows: caprellid amphipods, 56%; chitons, 9%; planktonic copepods, 9%; isopods, 8%; limpets, 2%; pelycypod mollusks, 1%; and sponges, 1%. Unidentified material made up 14% of the sample. There was no evidence of ectroparasites in this material. One individual had fed heavily and exclusively on planktonic copepods, showing that this fish is not limited to benthic prey. I have found no references to food habits of this fish in the literature.

Movements.—On the basis of limited observations, these fish do not seem to move around in their habitat as much as señoritas do. Nevertheless, they do show marked inshore/offshore movements that may relate to changing water temperatures. Unlike the ubiquitous señorita, this fish occurred in limited numbers that allowed assessing relative abundance through actual counts. It was never seen at the 3- to 10-m station but was reasonably abundant (10-20 individuals were counted during 15-min periods) on all visits to the 30- to 35-m station. At the 20- to 25-m station its appearance was irregular and closely followed temperature fluctuations. Generally it was rare or absent at the 20- to 25-m station when bottom temperatures rose much above 13° C, and was present (a maximum of 10 was seen during a 20-min period) when the temperature dropped much below this level. As most of the individuals seen were juveniles, a seasonal factor independent of temperature was probably operating here. Nevertheless, short-term temperature changes over the critical range (approximately 12°-14° C at the 20- to 25-m station) were consistently accompanied by the presence or absence of this fish. I emphasize that these assessments of abundance are relative to the numbers of the species regularly present. The señorita was always more abundant than the seaperch at all stations and under all conditions. Thus whereas the seaperch was considered abundant during a period in which 15 individuals were seen, at no time did I find so few señoritas present at any of the three La Jolla stations.

Kelp Perch

The kelp perch was not abundant in the La Jolla study area, where it was seen only at the inshore station. Its distribution is essentially limited to the kelp beds, which were not well developed in the study area at the time of this work. Nevertheless, it is very numerous in California inshore waters that are heavily forested with kelp. Attaining a maximum length of about 150 mm, the kelp perch is recorded from Vancouver Island, Canada, south to central Baja California, Mexico (Roedel, 1953). The kelp perch occurs near the rocky bottom at the base of giant kelp, as well as adjacent to the rising kelp stipes, but is most abundant just under the kelp canopy, near the water's surface. Typically, this fish occurs in aggregations of a dozen or more, but larger individuals frequently are solitary, especially those near the rocky sea floor. Most of my observations of kelp perch were made outside the La Jolla study area, the majority around the Channel Islands.

Food habits.—This perch feeds in a picking manner, similar to that employed by the señorita and sharpnose seaperch. It preys on a variety of organisms from the surface of the surrounding kelp and also feeds extensively on material suspended in the current. Its pointed snout and small, upturned mouth, together with a number of relatively long, curved canine teeth that project forward at the front of each jaw, are well suited to its mode of feeding. The dentition of this fish is similar to that of the señorita, a fact also noted by Hubbs and Hubbs (1954). I did not sample kelp perch from the population at large for food-habit analysis; all those collected were from known cleaning stations. However, Limbaugh (1955) stated that they feed on small crustaceans, particularly those that occur on giant kelp. Quast (1968), who also reported a predominantly crustacean diet, with a preponderance of amphipods, noted that some mollusks and bryozoans are taken as well.

Movements.—Limited observations indicate that aggregations of kelp perch in the canopy, and close to large rocks, remain relatively stable. Several aggregations that were observed over 2 to 3 months did not change appreciably in location or in numbers of individuals. Data on this point are scanty, however.

At night they hover in the same areas in which they are active in daylight, but their activity at this time, if any occurs, was not determined.

CLEANING ACTIVITY OF THE SEÑORITA

Unlike some other cleaners (see Feder, 1966), señoritas do not establish well-defined stations at which they receive other fishes seeking to be cleaned. Rather, the señoritas, as they move over the local area, approach and clean fishes wherever they encounter them.

Despite their great abundance, only a small segment of the señorita population seems predisposed to clean at a given time. The cleaning habit is not limited to any particular stage in their life history: cleaning señoritas have included some of the smallest individuals seen (< 40 mm) as well as some of the largest (> 225 mm). In cleaning material from the bodies of fishes, señoritas employ the same picking technique they use to take small prey from a rock or algal substrate. This mode of feeding, along with their pointed snout and long, forward-projecting canine teeth, are well suited to the cleaning habit.

Individuals that clean are numerous where there are many resident fishes, especially of certain species (as discussed below), but I found no evidence that residents of other areas come to these locations to have parasites removed. Occasionally a migrating species, such as the California yellowtail, *Seriola dorsalis*, will pause to be cleaned while passing through areas where cleaners are active, but this is not the same as a resident of a particular area habitually swimming elsewhere to be cleaned and then returning to its home ground.

Fishes Cleaned by the Señorita

Casual observation alone show that some fish species are cleaned far more often than others, and that many species do not seem to interact with cleaners at all.

To obtain data on this point, a record was kept of the species seen being cleaned by señoritas during 62 observation periods (15 min to 2 hr long) from June 1968 to January 1969. During this period, 392 cleaning bouts were witnessed, 385 of which involved señoritas cleaning one or more individuals of a single species; in only seven instances were señoritas seen cleaning members of a mixed-species group. The tabulation of species cleaned (Table 1) does not include the mixed-species groups because in the mixed groups it was not determined whether representatives of all species present were actually cleaned. All seven mixed groups included halfmoons, *Medialuna californiensis*, and one or more fish of other species. In four of these, halfmoons were mixed with blacksmiths, in one they were mixed with opaleyes (*Girella nigricans*), in one with rubberlip perch (*Rhacochilus toxotes*), and in one with both rubberlip perch and pile perch. All of these were incidental observations. The compilation does not include data obtained on other occasions when the activity of individual cleaners was recorded for extended periods.

The data clearly indicate that blacksmiths, and to a lesser extent topsmelt (*Atherinops affinis*), predominate as recipients of the señorita's cleaning efforts in the areas where the observations were made. Table 1 is not a definitive list of species cleaned by the señorita; nevertheless, it is evident that many species which co-occur with the señorita are not cleaned. At other times, in addition to all species noted in Table 1, I have seen *Seriola dorsalis* and *Trachurus symmetricus* being cleaned. But the ratio of species listed here generally is consistent with observations made on other occasions and at many different locations.

TABLE 1.—Fishes observed being cleaned by señoritas during 62 observation periods between June 1968 and January 1969 at La Jolla, Calif. (exclusive of seven mixed-species groups).

Species	Number of cleaning bouts	Percent of total bouts observed
Blacksmith, *Chromis punctipinnis*	231	60
Topsmelt, *Atherinops affinis*	81	21
Garibaldi, *Hypsypops rubicunda*	22	6
Halfmoon, *Medialuna californiensis*	19	5
Señorita, *Oxyjulis californica*	10	3
Rubberlip perch, *Rhacochilus toxotes*	8	2
Opaleye, *Girella nigricans*	5	1
Kelpfish, *Heterostichus rostratus*	3	1
Black perch, *Embiotoca jacksoni*	1	1
Pile perch, *Rhacochilus vacca*	1	1
Sargo, *Anisotremus davidsoni*	1	1
Blue rockfish, *Sebastes mystinus*	1	1
Olive rockfish, *Sebastes serranoides*	1	1

Reports in the literature present a comparable picture. Most published accounts of cleaning by señoritas describe the way blacksmiths cluster around this cleaner to solicit its attentions (Limbaugh, 1955, 1961; Feder, 1966; and others). Limbaugh (1955) observed the following fish being cleaned by señoritas: *Myliobatis californica, Stereolepis gigas, Paralabrax clathratus, Trachurus symmetricus, Atherinops affinis, Anisotremus davidsoni, Hyperprosopon argenteum, Rhacochilus vacca, Chromis punctipinnis, Hypsypops rubicunda, Girella nigricans, Medialuna californiensis,* and *Mola mola.* Turner et al. (1969) observed the following fish being cleaned by señoritas: *Sebastes* spp., *Atherinops affinis, Atherinopsis californiensis, Trachurus symmetricus, Seriola dorsalis, Chromis punctipinnis,* and *Mola mola.* Neither of these reports gives data on the relative frequency with which these different species were cleaned, but it is significant that many of the same species consistently appear in the reports of independent observers, while at the same time many other species that frequent these waters in large numbers are not mentioned. No doubt many species not yet reported are occasionally cleaned by señoritas, but there seems little doubt that a certain few species, the blacksmith in particular, predominate in this activity.

Specific Cleaning Interactions

The fishes cleaned by the señorita vary markedly in their habits and habitat, as well as in their relative numbers. These fishes do not seek out cleaning at a "station" established by the señorita, but rather receive the señorita on their own grounds during the course of their regular activity. Cleaning interactions often proceed differently with one of these species than with another. Some of these variations in cleaning activity are characterized below.

Señorita-blacksmith interactions.—The blacksmith is one of the most abundant fish over rocky substrates in California inshore waters, where it swims in large stationary aggregations in midwater. It feeds largely on zooplankton (Quast, 1968) and attains a length of about 250 mm.

Generally the first sign of an interaction occurs when a señorita swims up alongside a blacksmith in midwater and closely inspects its body. The blacksmith may then immediately stop swimming and, holding its fins motionless and erect, drift into an awkward-appearing posture. Usually the blacksmith is head-down, but sometimes turns on its sides or is tail-down. On some occasions the blacksmith presents a particular part of its body to the inspecting señorita. The señorita swims about this fish, usually pausing briefly to pick at its body. Immediately following the first sign of this activity other blacksmiths converge on the spot, so that very quickly 10 or more crowd around the cleaner (Figure 4). The señorita soon leaves the original blacksmith and may then move on to one of the others. It may also swim slowly away, whereupon the group of blacksmiths follows along, each attempting to position itself in the señorita's path. Although the señorita shows progressively less interest in the blacksmiths, they continue to crowd in its way. Soon the señorita shows no further interest in cleaning, and all but a few blacksmiths leave the group. The remaining few doggedly continue attempting to present themselves to the now-unresponsive cleaner. Eventually, however, these last blacksmiths lose contact with the cleaner as it swims off among the kelp or the many other señoritas in the surrounding water. Once they have lost contact with the cleaner the blacksmiths do not attempt to solicit cleaning from any of the many other señoritas around them.

On only two occasions did I note blacksmiths soliciting cleaning from a señorita that did not seem to have made an initiating gesture. Once the blacksmiths were very small, about 40 mm long, and in the other observation, at a depth of 27 m, little cleaning had been seen and relatively few señoritas were present. However, in both instances the señoritas were known by me on the basis of earlier observations to be individuals that clean. It is possible that the fishes soliciting attention recognized these señoritas as cleaners through some cue not noted by me. Sometimes when a señorita incidentally passes close to a blacksmith, the blacksmith noticeably pauses in its swimming and looks as

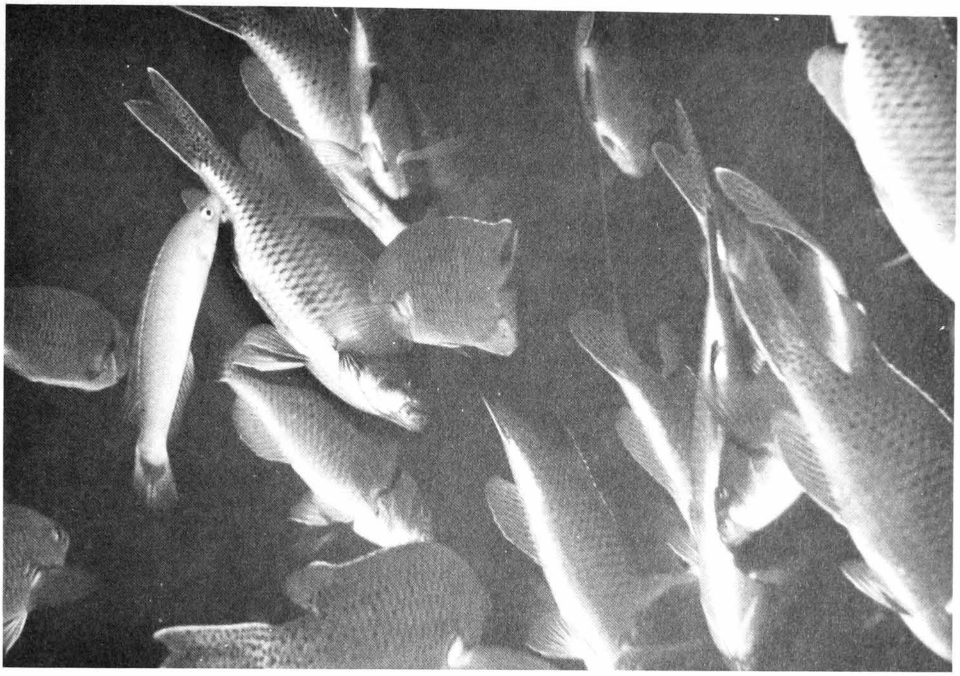

FIGURE 4.—Señorita cleaning the caudal peduncle of one of a group of blacksmiths that hover to solicit service.

though it is beginning to assume a soliciting posture; however, when the señorita swims on past, the blacksmith immediately resumes its original activity. Occasionally members of other species were seen responding similarly to passing señoritas. In most observations of cleaning, my attention was drawn to activity already in progress, so that it was not possible to determine whether cleaner or client had initiated the activity.

Individual señoritas that cleaned blacksmiths during many short-term observations were not seen cleaning any other species. This same situation held true for three individuals, known to have been cleaning blacksmiths, whose activity was monitored in detail on tape for 15 min. When observed for extended periods, señoritas were found to become involved in a succession of separate cleaning bouts. This activity was not restricted to one location but continued at various points over a relatively wide area. Periodically they joined cleaning already underway, or initiated cleaning themselves at a number of different locations—always with blacksmiths. I have no explanation for the fact that a señorita which becomes unresponsive and leaves one group of blacksmiths that still vigorously solicits its service may soon initiate activity again with another blacksmith.

The three individuals whose cleaning activity was monitored for 15 min joined in a mean of 4 separate bouts (range 2-6). For a mean of 11 min of this time (range 6.75-13.25 min) they showed an apparent cleaning interest in blacksmiths, or were accompanied by blacksmiths with which they had earlier initiated a cleaning interaction. When not thus engaged with blacksmiths, they swam in midwater showing no apparent interest in the fishes around them but occasionally picked at drifting scraps of debris, usually algal fragments. During much of the time that they swam in consort with blacksmiths, they closely inspected these fish and actually picked at their bodies a mean of 26 times (range 14-33). Of these picks, 27% were made at the base of the blacksmith's anal fin, 25% on the caudal peduncle or caudal fin, 22% at the base of the pectoral fin, 10% somewhere on the body exclusive of a fin-base or head, 8% on the head, 5% at the base of the pelvic fins, and 3% at the base of the dorsal fin.

Clearly, the bases of the fins receive most of the attention from the señoritas. These data are consistent with the many more general observations made on other occasions. At no time during this study were señoritas seen to clean within the oral or branchial cavities of blacksmiths: all cleaning was directed at the body surface.

Señorita-topsmelt interactions.—The topsmelt, which attains a length of about 200 mm, is abundant in many inshore regions of California coastal waters, but its distribution is more spotty than that of the ubiquitous blacksmith. Like the blacksmith, it feeds largely on zooplankton, which it takes while swimming in large schools at the water's surface. Quast (1968) noted the similarity in diet between topsmelt and blacksmiths, and while acknowledging that their feeding areas may overlap, he pointed out that topsmelt normally swim higher in the water column.

In the La Jolla study area, topsmelt are concentrated at the inshore station over extensive fields of surfgrass that grow in 3 to 5 m of water. They are never far from the substrate in this relatively shallow water, even though they swim in large schools at the water's surface. They are more abundant than blacksmiths in this area, and here they predominate in the señorita's cleaning activity.

The cleaning interaction proceeds in much the same way as it does with blacksmiths: the activity is initiated when a señorita swims up to an individual topsmelt and begins to inspect it closely. Immediately other topsmelt converge on this pair to place themselves in the señorita's path, thus soliciting its attention. When presenting themselves motionless before señoritas, topsmelt frequently hover tail-down, in contrast to the head-down posture most often assumed by blacksmiths. I saw señoritas clean only the external body surfaces of topsmelt. In the relatively shallow water where most of this activity was observed, señoritas break off contact with a group of topsmelt more readily than they do with blacksmiths, as they need only swim down to the substrate below, where the topsmelt seem reluctant to follow.

These shallow areas are frequently swept by surge, and the load of drifting debris in midwater is frequently heavy. In this area cleaning señoritas frequently leave the groups of topsmelt they are attending to inspect an object drifting in the water nearby. Sometimes they take the object into their mouths, sometimes not. Often when taken it is quickly rejected.

Attempts at extended observations on individual señoritas that had been cleaning topsmelt were largely unsuccessful. Too often before the observation had progressed far the señoritas disappeared among the surfgrass or other vegetation carpeting the sea floor in this area. However, two individuals were followed for 10 min each, during which time one entered into four, the other two, separate cleaning bouts. Between cleaning bouts these two swam over a wide area alone in midwater, occasionally picking at drifting debris. On several occasions they picked at benthic algae. Neither individual showed cleaning interest in species other than topsmelt, which was consistent with observations of other señoritas that cleaned topsmelt.

Señorita-garibaldi interactions.—The garibaldi, which attains a length of about 250 mm, is a solitary, highly territorial fish that lives close to the substrate. Especially during the reproductive season, when the males aggressively guard their nests among the rocks, these bright orange pomacentrids normally drive away all other fish that come near. They feed on sessile benthic invertebrates and are abundant at the 3- to 10-m station.

Garibaldis frequently are cleaned by señoritas. Most of the garibaldis seen being cleaned were swimming a meter or so above the bottom; I did not observe cleaners active around the garibaldis guarding nests among the rocks. All of the garibaldis seen being cleaned were solitary, which reflects their territorial nature. The señorita swims up to a garibaldi and closely inspects its body, thus initiating the action. Usually the garibaldi hovers motionless in a normal horizontal attitude, its fins sometimes erect. The señorita may pick at a few places on the garibaldi's body—most often around the caudal region—but usually its attentions are brief, and soon it swims away. With blacksmiths and topsmelt, each cleaning bout is prolonged by the many other individuals that join at the cleaning site to crowd in the señorita's path. Nothing of this sort happens with the solitary garibaldi, which usually makes no attempt to follow the señorita when it leaves, so that each cleaning bout is relatively brief. After leaving one garibaldi, however, often the señorita quickly approaches another. In agreement with their cleaning of blacksmiths and topsmelt, señoritas known to have cleaned garibaldis were subsequently seen cleaning only other members of that same species. This was true during several short-term observations, and also when one individual was followed for 15 min, and a record of its activity was taped; this particular señorita initiated cleaning activity with 26 different garibaldis during the observation period as it swam over an irregular course among the rocks in an area where blacksmiths, topsmelt, and other species also were present. Each cleaning bout lasted a mean of 10 sec (range 7-25 sec), totaling 4 min 15 sec of the 15-min period. In nine of these bouts, the señorita inspected the garibaldi but did not pick at its body. In the other 17 bouts, the señorita picked at the garibaldi's body a total of 42 times, or a mean of about 2.5 times per bout.

All cleaning of garibaldi that I observed was directed at the external body surface.

Señorita-halfmoon interactions.—Halfmoons, which may exceed a length of 250 mm, usually swim high in the water column, frequently in large aggregations, but just as often in small groups or as solitary individuals. They are often abundant among rising stands of giant kelp. Their omnivorous diet, which includes a variety of benthic algae, along with bryozoans, sponges, and crustaceans (Limbaugh, 1955; Quast, 1968), indicates bottom feeding; however, much of this material is taken in midwater as drifting debris.

Considering their large numbers in many southern California coastal areas, halfmoons are not particularly abundant in the principal study areas. Still, they were frequently seen being cleaned by señoritas during this study. When many halfmoons were present, cleaning by the señorita progressed much as described above for blacksmiths. Yet when just one halfmoon was present, a frequent occurrence, the cleaning bouts were brief like those described above for the garibaldi. At least one halfmoon was present in all the mixed-species groups that I recorded when collecting the data presented in Table 1. I saw señoritas clean only the external body surface of halfmoons.

One señorita, seen cleaning a halfmoon, was kept under surveillance for 12 min before contact was lost. As the observation period began, the señorita picked at the halfmoon once and then moved away, swimming slowly and alone, 2 or 3 m over the substrate. After an uneventful 3 min, the señorita approached a second halfmoon, which promptly hovered in a head-down attitude. For 15 sec the señorita closely inspected this halfmoon and picked at its body three times before swimming away. It then continued on alone for the remaining 8+ min that it was under observation, still swimming slowly over a wide semicircular course 2 or 3 m above the rocks. During this time it passed many different fish without showing interest, but it did not pass another halfmoon. It did pick at three different pieces of floating debris but rejected all three immediately.

Señorita-señorita interactions.—Señoritas themselves are cleaned by other members of their own species. Despite the large numbers of señoritas that usually are present, I saw no groups converging on cleaning individuals, as regularly occurs with blacksmiths, topsmelt, and other abundant species. In most of the señorita's intraspecific cleaning interactions, the cleaner attends just a single individual, which usually hovers motionless in a normal horizontal attitude, except that its fins are erected; sometimes the mouth is open wide and gill covers are distended, but I saw señoritas clean only the external body surface of these fish. There was no indication that señoritas which clean other señoritas also clean other species. I followed one individual for 10 min after having seen it clean another señorita. After this initial activity, the individual under surveillance swam over a wide area, showing interest only in other señoritas, even though blacksmiths, topsmelt, and other species were present. Swimming alone, 2 or 3 m over the rocks, it would assume a position alongside another señorita and follow it for a short distance. Usually these other fish showed no interest, but some stopped swimming and erected their fins, whereupon the cleaner picked at their bodies—usually once, but occasionally several times. Between cleaning encounters this señorita passed through a school of very small (< 40 mm) blacksmiths, several of which hovered head-down in its path; however, the cleaner showed no interest in these fish. On two occasions it picked at a piece of drifting debris.

Señorita-kelpfish interactions.—At least one species regularly initiates cleaning bouts with señoritas. Earlier (Hobson, 1965a) I reported observing a kelpfish, *Heterostichus rostratus*, repeatedly soliciting cleaning from unresponsive señoritas. The kelpfish was concealed among benthic algae, which is the typical habitat of this fish. But each time a señorita approached in the water overhead, the kelpfish rose up into the señorita's path, where it hovered motionless, fins erect (Figure 5). A succession of señoritas passed by without responding to the kelpfish, and each time the kelpfish returned to the cover below, where it waited until the next approach. Finally a passing señorita paused briefly and picked at the kelpfish's side before continuing on its way. After this brief encounter, the kelpfish did not rise from concealment again even though several more señoritas subsequently passed overhead.

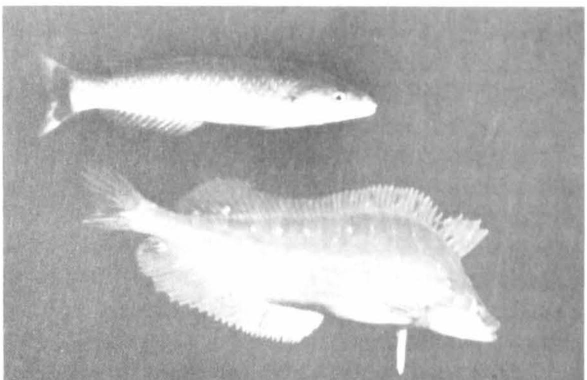

FIGURE 5.—Kelpfish hovering in midwater, fins erect, to solicit cleaning from a passing señorita.

During the present study this sequence of events involving kelpfish and señoritas was witnessed several times at a variety of locations; indeed, every instance of a kelpfish being cleaned followed this pattern—obviously it is a regular pattern in the behavior of the species.

Other interactions—Observations are too few to recognize distinctive aspects in cleaning interactions involving the many other species that occasionally are cleaned by señoritas. Usually such activity is noted simply as occasional sightings of small clusters of fish, or individual fish, hovering before a señorita. In all such encounters, however, only the external body surface was cleaned.

Notes follow regarding two other species that are cleaned by señoritas.

A single señorita was observed cleaning a pile perch, after which its activity was noted for 15 min. Pile perch are not abundant where these observations were made, and after leaving the first individual, the señorita swam alone in midwater for 14 min. It moved over a wide semicircular course during this time and showed no interest in any of the many fish that it passed, although none were pile perch. It did pick at three small items drifting in midwater. After 14 min it made an abrupt course change and, with slightly accelerated swimming, went directly to a solitary pile perch that was in midwater about 10 m away. The señorita swam about the pile perch, which now hovered head-down, but after a close inspection lasting about 10 sec it moved on without picking at the pile perch's body.

Many of the fishes cleaned by señoritas occasionally start, as if nipped too vigorously. Sometimes such fish dart away, thus terminating the cleaning. Other times they actively turn on the señorita and drive it away. The rubberlip perch was noted taking the latter course of action perhaps more often than the other species, even considering the relatively few times it was observed being cleaned.

Although the kelpfish is the only species that was observed consistently initiating cleaning from señoritas, individuals of several species do so in at least one situation. This occurs where exceptionally large concentrations of señoritas, sometimes thousands, swim above the rocks. At various times, garibaldis, pile perch, rubberlip perch, olive rockfish, and others were observed hovering in the soliciting posture amid these concentrations (Figure 6) until one of the señoritas approached and cleaned them.

Material Removed from Other Fishes by the Señorita

Food habits of cleaning señoritas.—An obvious question is: What do señoritas remove from the bodies of fishes they clean? Limbaugh (1955) stated that señoritas remove bacteria, parasitic copepods, and isopods. He was not more specific than this, nor did he present data. Various other cleaners reportedly take not only ectoparasites but also diseased and necrotic tissue (Feder, 1966, and others.)

To determine just what it is that señoritas remove from the bodies of other fishes, I examined the gut contents of 27 specimens, 111 to 175 mm long, that were speared while they were cleaning other fishes. Food items in their guts, ranked as percentage of each item in the entire sample, were as follows: caligid copepods, 39%; gnathiid isopod larvae, 12%; algae with encrusting bryozoans, 10%; caprellid amphipods, 5%; fish scales, 4%; and fragments of nonparasitic crustaceans, 4%. Unidentified material made up 26% of the sample. Of the 27 specimens, ectoparasites occurred among the gut contents of all but two. In most, the ectoparasites predominated. Even though the data are convincing, they do not fully reflect the extent to which cleaning obviously dominated the activity of these particular fish for at least several hours leading up to their capture. This is because the

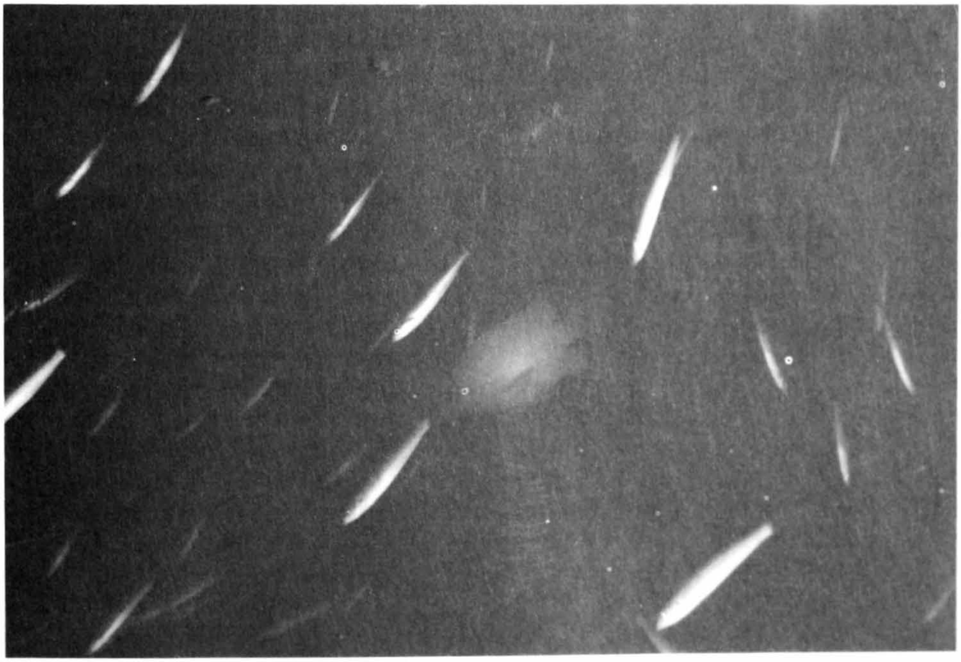

FIGURE 6.—Garibaldi hovering amid a large assemblage of señoritas.

parasites are so small (1-3 mm long) in comparison with the size of other food items. For example, 471 gnathiid isopod larvae were present in one señorita gut, but being so small they constituted only 35% of the material. On the other hand, a few algal fragments, with encrusting bryozoans, made up 40% of the material in this same specimen. However, only seven individuals contained ectoparasites alone, as compared with 17 that contained both parasites and free-living prey. In all but one of these, the two classes of material were sharply divided in the gut, usually with the free-living material posteriorly in a more advanced stage of digestion. Although most of the ectoparasites in the gut had undergone extensive damage and would not, by themselves, have been identifiable to species, this material usually graded gradually to freshly ingested specimens that were readily identified. This fact, coupled with the circumstance that individual señoritas tend to stay pretty much with a single type of food organism during a given period, greatly aided the task of analyzing this material.

Ectoparasites on the fishes.—To assess the significance of cleaning in removing ectoparasites, one must know what parasites occur on the fishes, as well as the extent of the infestation. Thus the survey of ectoparasites done in conjunction with this work included essentially every fish species exceeding 100 mm long regularly present in the La Jolla study area, as well as every species that was seen being cleaned there. Ectoparasites infesting these fishes include 33 species of copepods, one species of brachiuran, two species of isopods, one species of leech, and one species of monogenetic trematode. Following is a brief summary of the information being compiled on these parasites in collaboration with R. F. Cressey.

Copepods are the predominant ectoparasites on fishes in this area. The 33 species represent seven families: Bomolochidae (6 species), Caligidae (13 species), Dichelesthiidae (2 species), Lernaeidae (1 species), Chondracanthidae (5 species), and Lerneopodidae (6 species). The one species of the closely related brachiurans is a member of the family Argulidae. The bomolochids, which were found on 12 species of the fishes sampled, are mobile forms about 2 mm long (all lengths of parasites here and below do not include egg cases) that occurred mostly on the gills of their hosts. The caligids, which infested 29 species of the fishes, are mobile forms, 2 to 4 mm long, that occurred mostly on the external body surface of their hosts, although two species were found only in the oral cavity. The dichelesthiids are highly modified forms about 2 mm long that were attached to the gills of two species. The lernaeid is a highly modified form about 5 mm long that was attached to the fins of 12 species. The chondracanthids, which infested five species, are highly modified forms, 3 or 4 mm long, that lived attached in the branchial chamber, including the gills, of their hosts. The lerneopodids, infesting eight of the fish species, are highly modified forms, 2 to 5 mm long, mostly living attached in the branchial and oral cavities, although one individual fish carried several attached to its dorsal fin. Finally, the argulid is a mobile form about 2 mm long that was found on the outer body surface of one species of fish. The fish species hosting representatives of the different copepod and brachiuran families are listed in Table 2, and examples of the six copepod families are illustrated in Figure 7.

Thus a variety of ectoparasitic copepods occur on the fishes, but only caligids were found among the gut contents of the cleaners. Furthermore, although 13 species of caligids (five species of the genus *Caligus* and eight species of the genus *Lepeophtheirus*) occur on fishes in this area, only a relatively few of these are significant as prey of the cleaners, as noted below.

Of the two isopods, one, *Livoneca vulgaris*, a large parasite, about 20 mm long, was found in the branchial chamber of just one species of fish and was not found to be prey of the cleaners. On the other hand, the highly mobile gnathiid larvae (Figure 8), which are about 2 mm long, are a major prey of the cleaners. Only one form of gnathiid was readily recognized, but more than one species may occur among this material. Parasites of the body surface of fishes, the gnathiid larvae were taken on 11 of the fish species sampled, but I suspect that they are actually more widespread and abundant than these data

TABLE 2.—The types of ectoparasites and the fishes they infest, based on a survey of the fishes in the study area. Where more than one species of parasites is included under a heading, the number in parentheses following the name of each fish thereunder indicates how many different species of that type are represented on that fish. For all fish species listed, the number of infested individuals is shown over the number of individuals examined, followed by the range in numbers of individual parasites of that type which were taken from that species of fish.

COPEPODS

- BOMOLOCHIDAE (6 species of 3 genera)
  - Fishes infested with members of this family:
    - *Paralabrax clathratus* (1) 2/8: 1-2
    - *P. nebulifer* (2) 5/11: 1-20
    - *Phanerodon atripes* (1) 1/13: 1
    - *Rhacochilus vacca* (1) 3/15: 1
    - *Micrometrus minimus* (1) 1/7: 1
    - *Hypsypops rubicunda* (1) 1/20: 1
    - *Scorpaena guttata* (1) 6/14: 2-56
    - *Sebastes mystinus* (1) 1/9: 1
    - *S. serranoides* (1) 2/11: 1-8
    - *Oxylebius pictus* (1) 1/8: 1
    - *Atherinops affinis* (1) 2/13: 1-4
    - *Pleuronichthys coenosus* (1) 6/10: 1-11
- CALIGIDAE (13 species of 2 genera)
  - Fishes infested with members of this family:
    - *Paralabrax clathratus* (2) 4/8: 1-5
    - *P. nebulifer* (3) 4/11: 5-27
    - *Caulolatilus princeps* (1) 1/4: 2
    - *Anisotremus davidsoni* (1) 1/8: 1
    - *Cheilotrema saturnum* (1) 2/16: 1
    - *Medialuna californiensis* (2) 12/13: 1-75
    - *Girella nigricans* (3) 1/10: 1-14
    - *Embiotoca jacksoni* (2) 2/15: 1-2
    - *Phanerodon atripes* (1) 5/13: 1-5
    - *Rhacochilus toxotes* (3) 10/10: 1-10
    - *R. vacca* (2) 4/15: 1-11
    - *Chromis punctipinnis* (1) 10/10: 2-39
    - *Hypsypops rubicunda* (2) 19/20: 1-144
    - *Pimelometopon pulchrum* (3) 13/14: 1-70
    - *Oxyjulis californica* (3) 13/38: 1-59
    - *Scorpaena guttata* (1) 7/14: 1-14
    - *Sebastes atrovirens* (3) 6/16: 1
    - *S. carnatus* (2) 3/11: 1
    - *S. chrysomelas* (1) 1/7: 1
    - *S. constellatus* (1) 2/2: 1-5
    - *S. miniatus* (1) 1/5: 2
    - *S. mystinus* (3) 5/9: 1-5
    - *S. paucispinis* (1) 3/3: 1
    - *S. serranoides* (3) 8/11: 1-10
    - *S. serriceps* (2) 15/15: 1-25
    - *Scorpaenichthys marmoratus* (2) 8/10: 1-42
    - *Heterostichus rostratus* (1) 2/13: 1-2

COPEPODS—Cont.

- CALIGIDAE—Cont.
    - *Atherinops affinis* (1) 13/13: 1-23
    - *Pleuronichthys coenosus* (1) 5/10: 1-5
- DICHELESTHIIDAE (2 species of 1 genus)
  - Fishes infested with parasites of this family:
    - *Gymnothorax mordax* (1) 1/1: 9
    - *Paralabrax nebulifer* (1) 5/11: 2-70
- LERNAEIDAE (1 species)
  - Fishes infested by this parasite:
    - *Trachurus symmetricus* (1) 1/7: 1
    - *Anisotremus davidsoni* (1) 1/8: 1
    - *Cheilotrema saturnum* (1) 2/16: 1-2
    - *Medialuna californiensis* (1) 5/13: 2-7
    - *Brachyistius frenatus* (1) 1/5: 1
    - *Embiotoca jacksoni* (1) 2/15: 1-2
    - *Hypsurus caryi* (1) 2/11: 1-2
    - *Phanerodon furcatus* (1) 3/12: 1-3
    - *Rhacochilus toxotes* (1) 1/10: 1
    - *R. vacca* (1) 2/15: 1
    - *Micrometrus minimus* (1) 5/7: 1-6
    - *Atherinops affinis* (1) 2/13: 1-4
- CHONDRACANTHIDAE (5 species of 5 genera)
  - Fishes infested with parasites of this family:
    - *Oxyjulis californica* (1) 13/38: 1-4
    - *Scorpaena guttata* (1) 2/14: 1-5
    - *Scorpaenichthys marmoratus* (1) 4/10: 1-4
    - *Heterostichus rostratus* (1) 7/13: 1-7
    - *Pleuronichthys coenosus* (1) 7/10: 1-47
- LERNEOPODIDAE (6 species of 4 genera)
  - Fishes infested by parasites of this family:
    - *Cheilotrema saturnum* (1) 1/16: 1
    - *Girella nigricans* (1) 1/10: 1
    - *Phanerodon atripes* (1) 5/13: 1-4
    - *Rhacochilus vacca* (1) 1/15: 1
    - *Chromis punctipinnis* (1) 1/10: 1
    - *Sebastes atrovirens* (1) 1/16: 4
    - *S. constellatus* (1) 1/2: 1
    - *S. miniatus* (1) 5/5: 2-8
- ARGULIDAE (1 species)
  - Fish infested with this parasite:
    - *Atherinopsis californiensis* 1/1: 2

ISOPODS

- CYMOTHOIDAE (1 species)
  - Fish infested with this parasite:
    - *Sebastes mystinus* 1/9: 1
- GNATHIID LARVAE (number of species not determined)
  - Fishes infested with these parasites:
    - *Chromis punctipinnis* 1/10: 1
    - *Hypsypops rubicunda* 4/20: 1-8
    - *Pimelometopon pulchrum* 3/14: 1-4
    - *Sebastes atrovirens* 4/16: 1-20
    - *S. carnatus* 3/11: 1
    - *S. chrysomelas* 1/11: 2
    - *S. constellatus* 1/2: 1
    - *S. serranoides* 1/11: 1
    - *S. serriceps* 3/15: 1-5
    - *Oxylebius pictus* 3/8: 1-3
    - *Scorpaenichthys marmoratus* 3/10: 2-5

MONOGENETIC TREMATODE (1 species)

- Fishes infested with this parasite:
    - *Medialuna californiensis* 6/13: 2-16
    - *Girella nigricans* 4/10: 1-4
    - *Rhacochilus toxotes* 2/10: 1
    - *R. vacca* 2/15: 1-18
    - *Hypsypops rubicunda* 1/20: 1
    - *Pimelometopon pulchrum* 10/14: 1-26
    - *Scorpaena guttata* 2/14: 5-8
    - *Sebastes atrovirens* 7/16: 1
    - *S. constellatus* 1/2: 1
    - *S. miniatus* 2/5: 1-2
    - *S. serranoides* 3/11: 1-26
    - *S. serriceps* 2/15: 1-3
    - *Heterostichus rostratus* 6/13: 1-7

LEECH (1 species)

- Fishes infested with this parasite:
    - *Hypsypops rubicunda* 2/20: 1
    - *Sebastes serranoides* 1/11: 4
    - *Heterostichus rostratus* 2/13: 1-2

FISHES ON WHICH NO PARASITES WERE FOUND:

- *Xenistius californiensis* 0/1
- *Halichoeres semicinctus* 0/10
- *Coryphopterus nicholsi* 0/5

indicate. They are the most mobile of the parasites, and probably many escaped when their host fish was collected. The monogenetic trematode occurred on the outer body surface of 13 species of fishes, and the leech occurred similarly on 3 species. However, neither was found to be taken by the cleaners. The fish species hosting the various isopods and also the trematode and leech are listed in Table 2. Listed also are the three fish-species on which no ectoparasites were found.

The above summary of the survey results gives a general picture of the ectoparasites infesting the fishes that co-occur with the cleaners and might be regarded as a list of the potential prey of the cleaning fishes. The following material considers the parasites that actually are known to be prey.

Ectoparasites in the diet of cleaners relative to ectoparasites on fishes that are cleaned.—Many of the ectoparasites listed above infest parasites are so small (1-3 mm long) in comparison with the size of other food items. For example, 471 gnathiid isopod larvae were present in one señorita gut, but being so small they constituted only 35% of the material. On the other hand, a few algal fragments, with encrusting bryozoans, made up 40% of the material in this same specimen. However, only seven individuals contained ectoparasites alone, as compared with 17 that contained both parasites and free-living prey. In all but one of these, the two classes of material were sharply divided in the gut, usually with the free-living material posteriorly in a more advanced stage of digestion. Although most of the ectoparasites in the gut had undergone extensive damage and would not, by themselves, have been identifiable to species, this material usually graded gradually to freshly ingested specimens that were readily identified. This fact, coupled with the circumstance that individual señoritas tend to stay pretty much with a single type of food organism during a given period, greatly aided the task of analyzing this material.

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Fishes infested with members of this family:

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- *Phanerodon atripes* (1) 1/13: 1
- *Rhacochilus vacca* (1) 3/15: 1
- *Micrometrus minimus* (1) 1/7: 1
- *Hypsypops rubicunda* (1) 1/20: 1
- *Scorpaena guttata* (1) 6/14: 2-56
- *Sebastes mystinus* (1) 1/9: 1
- *S. serranoides* (1) 2/11: 1-8
- *Oxylebius pictus* (1) 1/8: 1
- *Atherinops affinis* (1) 2/13: 1-4
- *Pleuronichthys coenosus* (1) 6/10: 1-11

CALIGIDAE (13 species of 2 genera)

Fishes infested with members of this family:

- *Paralabrax clathratus* (2) 4/8: 1-5
- *P. nebulifer* (3) 4/11: 5-27
- *Caulolatilus princeps* (1) 1/4: 2
- *Anisotremus davidsoni* (1) 1/8: 1
- *Cheilotrema saturnum* (1) 2/16: 1
- *Medialuna californiensis* (2) 12/13: 1-75
- *Girella nigricans* (3) 1/10: 1-14
- *Embiotoca jacksoni* (2) 2/15: 1-2
- *Phanerodon atripes* (1) 5/13: 1-5
- *Rhacochilus toxotes* (3) 10/10: 1-10
- *R. vacca* (2) 4/15: 1-11
- *Chromis punctipinnis* (1) 10/10: 2-39
- *Hypsypops rubicunda* (2) 19/20: 1-144
- *Pimelometopon pulchrum* (3) 13/14: 1-70
- *Oxyjulis californica* (3) 13/38: 1-59
- *Scorpaena guttata* (1) 7/14: 1-14
- *Sebastes atrovirens* (3) 6/16: 1
- *S. carnatus* (2) 3/11: 1
- *S. chrysomelas* (1) 1/7: 1
- *S. constellatus* (1) 2/2: 1-5
- *S. miniatus* (1) 1/5: 2
- *S. mystinus* (3) 5/9: 1-5
- *S. paucispinis* (1) 3/3: 1
- *S. serranoides* (3) 8/11: 1-10
- *S. serriceps* (2) 15/15: 1-25
- *Scorpaenichthys marmoratus* (2) 8/10: 1-42
- *Heterostichus rostratus* (1) 2/13: 1-2

COPEPODS—Cont.

CALIGIDAE—Cont.

- *Atherinops affinis* (1) 13/13: 1-23
- *Pleuronichthys coenosus* (1) 5/10: 1-5

DICHELESTHIIDAE (2 species of 1 genus)

Fishes infested with parasites of this family:

- *Gymnothorax mordax* (1) 1/1: 9
- *Paralabrax nebulifer* (1) 5/11: 2-70

LERNAEIDAE (1 species)

Fishes infested by this parasite:

- *Trachurus symmetricus* (1) 1/7: 1
- *Anisotremus davidsoni* (1) 1/8: 1
- *Cheilotrema saturnum* (1) 2/16: 1-2
- *Medialuna californiensis* (1) 5/13: 2-7
- *Brachyistius frenatus* (1) 1/5: 1
- *Embiotoca jacksoni* (1) 2/15: 1-2
- *Hypsurus caryi* (1) 2/11: 1-2
- *Phanerodon furcatus* (1) 3/12: 1-3
- *Rhacochilus toxotes* (1) 1/10: 1
- *R. vacca* (1) 2/15: 1
- *Micrometrus minimus* (1) 5/7: 1-6
- *Atherinops affinis* (1) 2/13: 1-4

CHONDRACANTHIDAE (5 species of 5 genera)

Fishes infested with parasites of this family:

- *Oxyjulis californica* (1) 13/38: 1-4
- *Scorpaena guttata* (1) 2/14: 1-5
- *Scorpaenichthys marmoratus* (1) 4/10: 1-4
- *Heterostichus rostratus* (1) 7/13: 1-7
- *Pleuronichthys coenosus* (1) 7/10: 1-47

LERNEOPODIDAE (6 species of 4 genera)

Fishes infested by parasites of this family:

- *Cheilotrema saturnum* (1) 1/16: 1
- *Girella nigricans* (1) 1/10: 1
- *Phanerodon atripes* (1) 5/13: 1-4
- *Rhacochilus vacca* (1) 1/15: 1
- *Chromis punctipinnis* (1) 1/10: 1
- *Sebastes atrovirens* (1) 1/16: 4
- *S. constellatus* (1) 1/2: 1
- *S. miniatus* (1) 5/5: 2-8

ARGULIDAE (1 species)

Fish infested with this parasite:

- *Atherinopsis californiensis* 1/1: 2

ISOPODS

CYMOTHOIDAE (1 species)

Fish infested with this parasite:

- *Sebastes mystinus* 1/9: 1

GNATHIID LARVAE (number of species not determined)

Fishes infested with these parasites:

- *Chromis punctipinnis* 1/10: 1
- *Hypsypops rubicunda* 4/20: 1-8
- *Pimelometopon pulchrum* 3/14: 1-4
- *Sebastes atrovirens* 4/16: 1-20
- *S. carnatus* 3/11: 1
- *S. chrysomelas* 1/11: 2
- *S. constellatus* 1/2: 1
- *S. serranoides* 1/11: 1
- *S. serriceps* 3/15: 1-5
- *Oxylebius pictus* 3/8: 1-3
- *Scorpaenichthys marmoratus* 3/10: 2-5

MONOGENETIC TREMATODE (1 species)

Fishes infested with this parasite:

- *Medialuna californiensis* 6/13: 2-16
- *Girella nigricans* 4/10: 1-4
- *Rhacochilus toxotes* 2/10: 1
- *R. vacca* 2/15: 1-18
- *Hypsypops rubicunda* 1/20: 1
- *Pimelometopon pulchrum* 10/14: 1-26
- *Scorpaena guttata* 2/14: 5-8
- *Sebastes atrovirens* 7/16: 1
- *S. constellatus* 1/2: 1
- *S. miniatus* 2/5: 1-2
- *S. serranoides* 3/11: 1-26
- *S. serriceps* 2/15: 1-3
- *Heterostichus rostratus* 6/13: 1-7

LEECH (1 species)

Fishes infested with this parasite:

- *Hypsypops rubicunda* 2/20: 1
- *Sebastes serranoides* 1/11: 4
- *Heterostichus rostratus* 2/13: 1-2

FISHES ON WHICH NO PARASITES WERE FOUND:

- *Xenistius californiensis* 0/1
- *Halichoeres semicinctus* 0/10
- *Coryphopterus nicholsi* 0/5

indicate. They are the most mobile of the parasites, and probably many escaped when their host fish was collected. The monogenetic trematode occurred on the outer body surface of 13 species of fishes, and the leech occurred similarly on 3 species. However, neither was found to be taken by the cleaners. The fish species hosting the various isopods and also the trematode and leech are listed in Table 2. Listed also are the three fish-species on which no ectoparasites were found.

The above summary of the survey results gives a general picture of the ectoparasites infesting the fishes that co-occur with the cleaners and might be regarded as a list of the potential prey of the cleaning fishes. The following material considers the parasites that actually are known to be prey.

Ectoparasites in the diet of cleaners relative to ectoparasites on fishes that are cleaned.—Many of the ectoparasites listed above infest

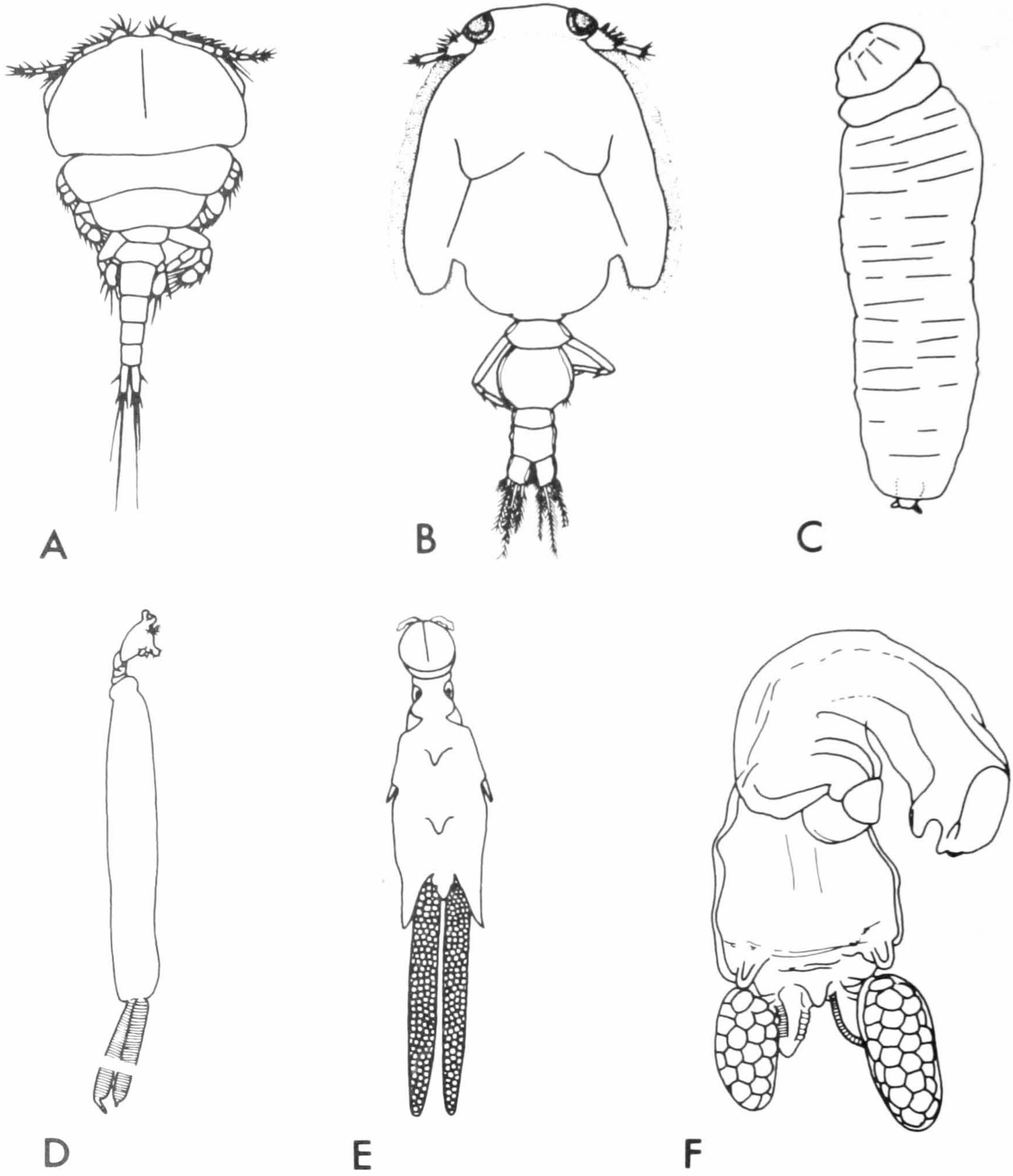

FIGURE 7.—Representatives of the families of ectoparasitic copepods found to infest fishes in the La Jolla area.
A. Bomolochidae (*Bomolochus longicaudus*, female, after Cressey, 1969b);
B. Caligidae (*Caligus hobsoni*, male, after Cressey, 1969a);
C. Dichelesthiidae (*Hatschekia pacifica*, female, after Cressey, 1970);
D. Lernaeidae (*Peniculus fissipes*, female, after Wilson, 1917);
E. Chondracanthidae (*Chondracanthus gracilis*, female, modified after Wilson, 1935);
F. Lerneopodidae (*Epibranchiella septicauda*, female, after Shiino, 1956).

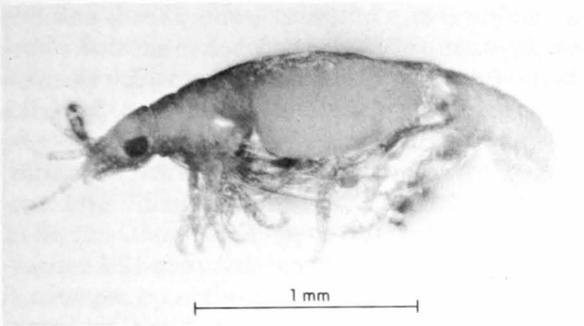

FIGURE 8.—Gnathiid larva from the body surface of the black-and-yellow rockfish, *Sebastes chrysomelas*.

fishes that rarely or never interact with cleaners. In considering the ectoparasites found in the gut of particular señoritas, it would be most meaningful to do so in regard to the ectoparasites known to be hosted by the species of fishes that these particular señoritas were cleaning when collected. Of the 27 cleaning señoritas taken for the gut-content analysis, 15 (56%) were cleaning blacksmiths, 8 (30%) were cleaning topsmelt, 2 (7%) were cleaning garibaldis, and 2 (7%) were cleaning halfmoons. Thus the selection closely parallels the relative frequency with which señoritas were observed cleaning these same species (Table 1) and is a good sample of the fishes that are cleaned by señoritas.

Three species of ectoparasites were collected from 10 blacksmiths, 141 to 199 mm long. Each of these blacksmiths carried from 2 to 39 individuals of the copepod *Caligus hobsoni* on their body surface. One specimen also carried a single gnathiid isopod larva on its body surface, and another the copepod *Clavellopsis flexicurvica* on a gill arch. All 15 señoritas that were collected as they cleaned blacksmiths contained either *Caligus hobsoni* or gnathiid larvae, but no other ectoparasites: one contained gnathiids alone, seven contained *C. hobsoni* alone, and seven contained both gnathiids and *C. hobsoni*. Up to 256 individuals of *C. hobsoni* and up to 263 gnathiid larvae were counted from among the stomach contents of individual señoritas that had been cleaning blacksmiths.

Three species of ectoparasites were collected from 13 topsmelt, 122 to 212 mm long. These topsmelt each carried from 1 to 23 specimens of the copepod *Caligus serratus* on their body surface. Two topsmelt also carried the copepod *Parabomolochus constrictus* on their gills, a single parasite on one, four on the other. Two topsmelt also carried the copepod *Peniculus fissipes* embedded in their fins. Six of the eight señoritas that had been cleaning topsmelt when collected had ectoparasites among their gut contents. Five contained only *Caligus serratus*—as many as 73 in each fish. One other contained only 10 gnathiid larvae, a parasite that was not seen on the topsmelt themselves; however, as noted above, I suspect that this parasite is more widespread than our survey data indicate.

Six species of ectoparasites were collected from 20 garibaldis, 184 to 240 mm long. Nineteen garibaldis each carried 1 to 144 *Caligus hobsoni* on their body surface. Thirteen each carried 1 to 4 individuals of an unidentified species of *Lepeophtheirus* on their body surface, and one carried a single *Bomolochus ardeole* in its branchial cavity. In addition, four carried 1 to 8 gnathiid isopod larvae, two carried a single leech, and one carried a single monogenetic trematode, all on their body surface. The two señoritas that were collected as they cleaned garibaldis had preyed mostly on gnathiid larvae, with each containing over 400 of these parasites. In addition, one had consumed six *Caligus hobsoni*, and the other had taken five *Lepeophtheirus* sp.

Four species of ectoparasites were collected from 13 halfmoons, 166 to 295 mm long. Twelve of the 13 halfmoons each carried 1 to 75 *Caligus hobsoni* on their body surface. Each of two also carried a single *Lepeophtheirus* sp. on its body surface, and each of six carried 2 to 7 *Peniculus fissipes* embedded in its fins. In addition, each of six carried from 2 to 16 monogenetic trematodes on its body surface. Of the two señoritas collected as they cleaned halfmoons, each contained only *Caligus hobsoni* in its gut contents, one a single specimen and the other eight.

Significantly, with the exception of the gnathiid larvae in a cleaner of topsmelt, as discussed above, no parasite was found in the cleaner's gut contents that did not occur on the species of fish that was being cleaned by the cleaner when it was collected. This fact further supports the contention that cleaning tends to be species-specific for a given señorita.

The data clearly show that the parasites most frequently taken by señoritas are certain mobile forms that occur on the body surface of their host. It may be that other parasites on the external body surface are not taken. No leeches or trematodes were found among gut contents, even though these forms are abundant on the garibaldi and halfmoon. Also, the gut contents did not show evidence of the lernaeid *Peniculus fissipes*, an immobile form which partially embeds itself in the skin of its hosts—mostly on the fins. This parasite occurs on topsmelt, garibaldis, and halfmoons among those known to be cleaned by señoritas. However, negative evidence based on the meager gut-content data are weak, especially as the cleaning labrid *Labroides phthirophagus* in Hawaii, which feeds mostly on caligoid copepods, frequently takes lernaeids (Randall, 1958; Youngbluth, 1968). I would expect additional study to show that cleaning señoritas at least occasionally take *P. fissipes*. Nevertheless, several abundant fishes infested by *P. fissipes*, but not found to carry caligids, gnathiids, or other mobile external forms, were not seen being cleaned. For example, the white seaperch is one of the most abundant species at the 3- to 10-m station off La Jolla and yet was never seen being cleaned. Twelve specimens of this fish were examined, and the only ectoparasites found were one to four *P. fissipes* on three individuals. Similarly, the only parasite found on 11 rainbow seaperch, an abundant species in the study areas that was not seen being cleaned, was a single *P. fissipes* on one individual and two on another.

However, not all fishes whose external body surfaces are heavily infested by mobile forms were observed being cleaned. The sheephead, *Pimelometopon pulchrum*, is a case in point. *Caligus hobsoni* occurs on this fish, but only infrequently—a single specimen of this copepod was taken from each of 2 of the 14 sheepheads that were examined. However, the sheephead is heavily infested by two species of *Lepeophtheirus*, a genus of copepods that is closely related to *Caligus*. Up to 70 *L. parvus* were taken from the body surface of a single sheephead, and this fish has not yet been seen being cleaned. Furthermore, up to 4 gnathiid larvae, which cleaners take from other fish, were found on 3 of the sheephead. Similarly, the treefish, *Sebastes serriceps*, which is heavily infested with caligids, has not yet been seen being cleaned. The treefish is not known to carry *C. hobsoni*, but 13 of 15 specimens examined carried up to 12 *Lepeophtheirus longipes* on their body surface, and 3 carried up to 5 gnathiid larvae. The significance of these exceptions to what seems a valid generalization has not been determined. Perhaps it is significant that these two species of fish are not heavily infested by copepods of the genus *Caligus*, as are the more frequently cleaned fishes.

The many parasites that infest the oral and branchial cavities might seem to be potential prey for cleaners, but I found no evidence that these parasites are taken by señoritas.

The principal ectoparasites on the body surface of the two most frequently cleaned fishes, the blacksmith and the topsmelt, are the copepods *Caligus hobsoni* and *C. serratus*, respectively, which are very similar to one another morphologically. With just one exception among the fishes surveyed (discussed below), *C. serratus* seems to be restricted to topsmelt. On the other hand, *C. hobsoni* occurs on a wide variety of species and is also the principal form on garibaldis and halfmoons. Interestingly, a list of the fishes hosting this parasite, ranked by incidence (Table 3), looks much like the ranking of fishes that were observed being cleaned by the señorita (Table 1).

The importance of cleaning in reducing the incidence of ectoparasites on fishes.—Certainly cleaners remove many ectoparasites from the bodies of certain fishes—the numbers in their diet attest to this fact. But does cleaning in fact appreciably reduce the level of infestation on these fishes, or do other parasites quickly replace those that are removed by the cleaners? Although this question is difficult to answer, some insight is provided by observations on the garibaldi. When guarding eggs on their nests during the reproductive season, male garibaldis become especially intolerant of the presence of other fish species. Clarke (1970) recorded the number of times garibaldis, in defence of their territory, attacked fish of various other species at different times of the year. He found that when males were guarding eggs their attacks on señoritas increased elevenfold. Not surprisingly, I saw no cleaning of garibaldis that were guarding eggs. At other times of the year male garibaldis do not guard their territory as vigorously against members of other species and are frequently seen being cleaned. A series of these males were collected both in and out of the reproductive season, and the numbers of ectoparasites they carried were assessed. Seven individuals (mean length 228 mm) sampled as they guarded their eggs carried a mean of 67 *Caligus hobsoni* (range 20-144), 2.5 *Lepeophtheirus* sp., 1.4 gnathiid isopod larvae, and 0.2 monogenetic trematodes. These counts contrast strikingly with those from six males (mean length 219 mm) sampled outside the reproductive season, which carried a mean of only 4.8 *C. hobsoni* (range 0-13), 1 *Lepeophtheirus* sp., 0.8 gnathiid larvae, and no monogenetic trematodes. These findings suggest that males which are guarding eggs become heavily infested with *C. hobsoni* when they do not allow cleaners to approach them, a conclusion strengthened by the fact that over this same period the relative numbers of this same parasite were not noted to change on other infested fishes. The samples included too few of the other parasites to make a meaningful comparison. It remains a question why *Lepeophtheirus* sp. and the gnathiid larvae did not show a pattern of occurrence similar to that of *C. hobsoni*, as both of these parasites are known to be prey of the cleaners. In any event, these data add to the evidence which indicates that *C. hobsoni* is the primary prey of cleaning señoritas in the study areas.

Ectoparasites on Señoritas

Señoritas that were closely observed as they cleaned other fishes often were noted to have caligid copepods on their bodies. One señorita, about 120 mm long, was host to an estimated 100 of these parasites concentrated especially along the dorsal-fin base. These observations were significant because during the survey for ectoparasites, most señoritas taken from the population at large were free of external forms, although many carried a chondracanthid copepod on their gills.

Twenty señoritas, 102 to 190 mm long, were sampled from among those giving no indication of being cleaners. Eight of these carried 1 or more of the chondracanthids on their gills, but only 2, or 10%, had parasites on their external body surfaces: one of these carried 10 specimens of *Caligus hobsoni* and 1 specimen of

TABLE 3.—Hosts of *Caligus hobsoni*.

Species	Specimens examined	Specimens hosting *C. hobsoni*	Number of *C. hobsoni* on each infested fish mean (range)	Percent occurrence
Blacksmith, *Chromis punctipinnis*	10	10	10.6(2-39)	100
Topsmelt, *Atherinops affinis*	13	[1]13	[1]10(3-23)	[1]100
Garibaldi, *Hypsypops rubicunda*	20	19	31.2(1-144)	95
Halfmoon, *Medialuna californiensis*	13	12	19.8(1-75)	92
Opaleye, *Girella nigricans*	10	8	5.4(1-14)	80
Olive rockfish, *Sebastes serranoides*	11	5	2.6(1-4)	45
Blue rockfish, *Sebastes mystinus*	9	4	1	44
Sharpnose seaperch, *Phanerodon atripes*	13	5	2(1-5)	38
Senorita, *Oxyjulis californica*	36	9	11(1-59)	24
Sheephead, *Pimelometopon pulchrum*	14	2	1	14
Rubberlip perch, *Rhacochilus toxotes*	10	1	1	10
Cabezon, *Scorpaenichthys marmoratus*	10	1	1	10
Gopher rockfish, *Sebastes carnatus*	11	1	1	9
Pile perch, *Rhacochilus vacca*	15	1	1	7
Kelp rockfish, *Sebastes atrovirens*	16	1	1	6

[1] *Atherinops affinis* does not carry *C. hobsoni*, but rather is the sole host (with one exception, see text) of the very similar *C. serratus*.

Lepeophtheirus sp.; the other señorita carried a single *Lepeophtheirus* sp. Comparative data were obtained by examining 16 senoritas, 114 to 160 mm long, that had been cleaning. Of these, 11, or nearly 70%, carried copepod parasites on their external body surfaces: 6 carried from 1 to 59 *Caligus hobsoni*, 4 carried from 1 to 9 *C. serratus*, and 1 carried 3 *Lepeophtheirus* sp.

Significantly, those señoritas carrying *Caligus hobsoni* all had been cleaning blacksmiths, those carrying *C. serratus* had been cleaning topsmelt, and the one carrying *Lepeophtheirus* sp. had been cleaning a garibaldi. Thus the ectoparasites found on cleaning señoritas were in all instances forms that also infest the species which that particular señorita had been cleaning. The occurrence of *C. serratus* is especially interesting, because these señoritas are the only fish other than topsmelt found so far to carry this parasite.

Alerted to the phenomenon, I inspected the bodies of many señoritas that incidentally passed by during various phases of the work underwater. Ectoparasites were evident on some, but only on a small minority of the population. That the vast majority are not infested by such parasites accounts for the observation, noted above, that señoritas do not crowd around cleaners that initiate activity in their midst, as do blacksmiths, topsmelt, halfmoons, and others.

On the basis of these data, and on the general cleaning picture that has developed, I believe that at least most of the señoritas infested with caligid copepods are cleaners. Presumably they acquire these parasites while intimately associated with the former hosts during cleaning. That a given cleaner is found to carry parasites similar to those on the fish it has been attending, but no others, is further evidence that cleaning by individual señoritas tends to be species-specific.

Environmental Factors That Influence Cleaning

Temperature.—As noted above, the numbers of señoritas present at the 20- to 25-m station fluctuated in an apparent response to water temperature, with the critical level at about 12° to 13° C. Less cleaning occurred at lower temperatures (Figure 9), which would be expected with fewer señoritas present. Nevertheless, even considering the smaller numbers, the señoritas present at lower temperatures seem less active than those present at higher temperatures. The effect was striking on one occasion at 25 m when, with an influx of warm water, the temperature rose suddenly from 11° to 14.5° C. No change was noted in the numbers of señoritas present over this short period of time, but where no cleaning had been seen during a 20-min survey immediately before, shortly after the temperature rise six different groups of fishes being cleaned were in view simultaneously.

Turbidity.—When the water is turbid because of plankton or suspended sediment, there is noticeably less cleaning activity than when the water is clear. The fishes are generally more wary, and remain closer to cover when visibility is reduced.

Surge.—When there is a strong surge, a frequent occurrence, especially in water less than 10 m deep, there is far less cleaning activity than when the water is still.

Day-night.—The señorita, a strictly diurnal species that takes shelter under cover at night, does not clean after dark.

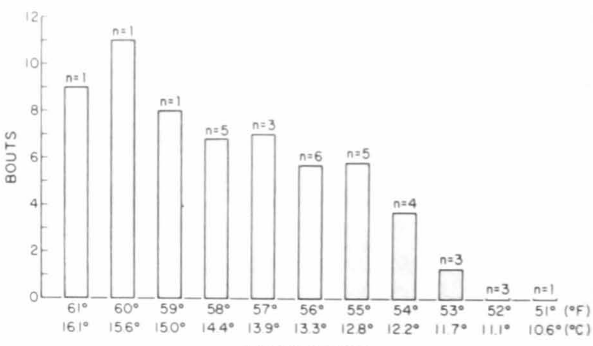

FIGURE 9.—Number of señorita cleaning bouts seen during each of 33 observation periods, 15-25 min long, at different water temperatures in an area 25 m deep at La Jolla. Periods during which temperature fluctuated were not considered. n = number of observation periods at that temperature; where $n > 1$, value given is the mean.

CLEANING ACTIVITY OF THE SHARPNOSE SEAPERCH

Unlike señoritas, which clean as adults as well as juveniles, all of the sharpnose seaperch that I observed cleaning were juveniles less than about 125 mm long. Occasionally noncleaning seaperch swim in groups of 15 or more, but those seen cleaning were always solitary, or in groups of two or three. In agreement with señoritas, cleaning seaperch do not establish well-defined cleaning stations, but instead may clean other fish at any point as they move from place to place. I found no evidence that fishes which are residents of other areas come to where seaperch are located for cleaning; rather, cleaning seaperch occur where resident fishes are numerous. As is true of señoritas, seaperch use the same picking technique to clean material from the bodies of other fish that they use to take small organisms from a benthic substrate. Clearly bottom-picking can be preadaptive to cleaning. Cleaning by seaperch, as by señoritas, usually occurs within 3 m of the substrate. However, there is little overlap in the cleaning areas of the two species: generally seaperch clean at greater depths and/or in colder water than señoritas, where limited observations indicate they may predominate as cleaners even when señoritas are more abundant. Data illustrating this distribution of cleaning activity at a point in time were obtained at the 20- to 25-m and 30- to 35-m locations off La Jolla, where the two species co-occur (Table 4). Despite the fact that señoritas were observed to be far more numerous than perch throughout the depth range of this study (3-50 m), seaperch performed almost all the cleaning observed at the 30- to 35-m location, where cleaning by the much more abundant señorita was limited to a few isolated instances.

TABLE 4.—Number of bouts in which sharpnose seaperch and señoritas, respectively, were seen cleaning other fishes during 15-min observation periods at the 20- to 25-m and 30- to 35-m locations off La Jolla. Two observation periods, one at each location, and never more than 45 min apart, were made on each of the dates indicated.

Date	Number of cleaning bouts observed			
	20- to 25-m location		30- to 35-m location	
	Seaperch	Señorita	Seaperch	Señorita
22 Nov.	2	13	17	0
27 Nov.	0	7	1	0
9 Jan.	2	5	9	0
15 Jan.	2	4	8	0
3 Feb.	2	12	9	2
Total	8	41	44	2

A measure of the incidence of cleaning individuals within the population of juvenile sharpnose seaperch was obtained during 39 observation periods at the 20- to 25-m and 30- to 35-m locations at La Jolla. These observations, totaling more than 26 hr, were made from September 1968 to February 1969. During this period, 201 juvenile seaperch were seen, of which 105, over 52%, were cleaning other fishes. Thus it appears that at least most sharpnose seaperch are cleaners when they are juveniles, whereas only a small minority of the señorita population seem to be cleaners.

Fishes Cleaned by the Sharpnose Seaperch

Because sharpnose seaperch were observed only at depths below 20 m, substantially less data are available on their cleaning activity than on that of señoritas. Of the 105 seaperch observed cleaning during the 39 observation periods reported above, all but one were cleaning blacksmiths; the lone exception was cleaning a solitary blue rockfish, *Sebastes mystinus*. On two other occasions, I saw sharpnose seaperch cleaning rubberlip perch, but otherwise the only fish seen being cleaned have been blacksmiths (Figure 10). Undoubtedly additional observations, especially in other areas, would expand this list. I observed señoritas cleaning in many different areas, but my observations of cleaning seaperch are limited to La Jolla. Clarke et al. (1967) saw a sharpnose seaperch cleaning a rockfish at 150 m off La Jolla, and Gotshall (1967) reported what he believed to be this species cleaning *Mola mola* off Monterey. Yet no matter how many different species the seaperch may in fact clean, there seems no doubt that blacksmiths are prime recipients in southern California, at least in depths shallower than 35 m.

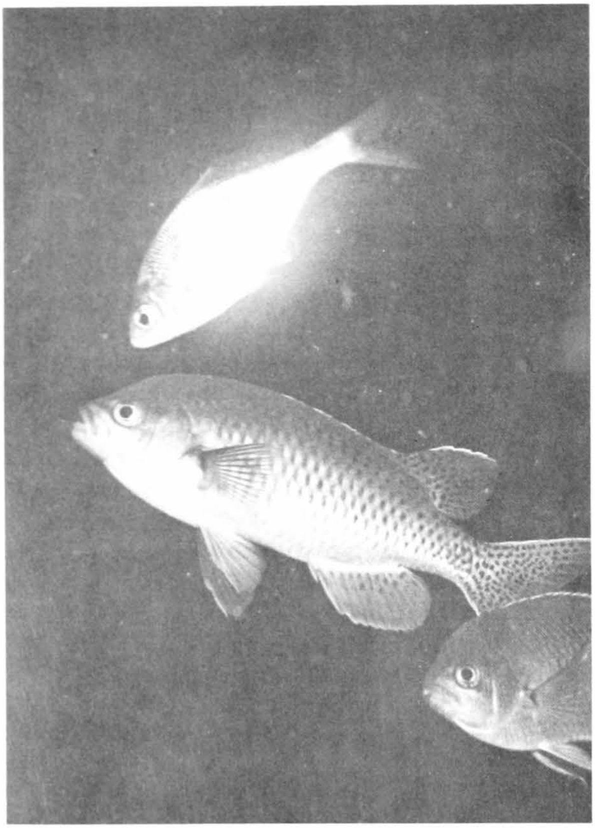

FIGURE 10.—Sharpnose seaperch inspecting a blacksmith, which hovers to solicit cleaning.

Specific Cleaning Interactions—Seaperch-Blacksmith

The limited observations on cleaning by sharpnose seaperch provide details only on interactions with blacksmiths. As nearly as could be seen, when sharpnose seaperch clean blacksmiths the activity proceeds much as it does when blacksmiths are cleaned by señoritas, as described above. However, the observations were too few to determine whether or not cleaning activity is consistently initiated by the cleaner. Several times blacksmiths hovered in their typical head-down posture before seemingly unresponsive seaperch, but perhaps the seaperch had earlier made some initial gesture. Whenever it could be determined, the seaperch initiated the cleaning.

Some details were obtained at the 20- to 25-m location at La Jolla, where two seaperch, known to have been cleaning blacksmiths, were each kept under surveillance for 15 min, while their activity was monitored on tape. Both swam on irregular courses among the rocks but remained within an area encompassing about 15 to 20 m^2. During this time one entered into 4, the other 5, separate cleaning bouts, averaging 2.6 (range 0.5-7.5) and 1.8 (range 0.75-3.5) min long, respectively, all with blacksmiths. The cleaner initiated the activity in each instance, but immediately thereafter a number of other blacksmiths converged on the spot. Most of the cleaning bouts continued after the original blacksmith had left the group, and a succession of others arrived and departed before the bout ended. Although usually they hovered head-down before the cleaners, the blacksmiths nevertheless assumed a wide variety of attitudes. During much of the time they swam with the blacksmiths, the two seaperch under surveillance closely inspected the blacksmith's bodies and actually picked at them 18 and 14 times, respectively. Most of the cleaning was directed at the fin bases, particularly the caudal. While in company with the blacksmiths, one of the seaperch broke away from the group and swam to look closely at the dorsal fin of a blue rockfish. However, no cleaning occurred: the blue rockfish swam away as though uninterested in cleaning and the seaperch returned to the blacksmiths. When not in company with the blacksmiths, the two seaperch swam alone 1 or 2 m over the substrate. One descended to the bottom twice and picked at gorgonians: five times on the first descent, once on the second.

Once a blacksmith was seen obviously attempting to present its caudal fin to a seaperch, without success in enticing the seaperch to clean. Close inspection did not reveal parasites, but part of the fin was torn away and shredded flesh was exposed. Apparently this blacksmith was presenting a point of irritation to the cleaner, which in this instance was an injury, not a parasite. Some cleaners, for example, *Abudefduf troschelii*, which picks molting skin from the Galápagos marine iguana (Hobson, 1969b), will clean dead or injured itssue, but at least on this occasion the seaperch showed no interest.

Material Removed from Other Fish by the Sharpnose Seaperch

To determine the food of cleaning seaperch, I examined the gut contents of 16 specimens, 74 to 122 mm long, that were speared as they cleaned blacksmiths. Food items in their guts, ranked as percentage of each item in the entire sample, were as follows: caligid copepods, 68%; caprellid amphipods, 16%; gnathiid isopod larvae, 9%; algae, 1%; and unidentified items, 6%. Thus ectoparasitic caligids and gnathiids made up 77% of the material. All 16 specimens contained ectoparasites; in fact, ectoparasites constituted the vast bulk of the material in all but one individual, which had fed more heavily on caprellids. As with señoritas, when an appreciable amount of free-living material was present, it was usually sharply divided from the ectoparasites and more digested to the rear in the digestive tract. All the identifiable caligid copepods among this material were *Caligus hobsoni*, which is consistent with what is known of ectoparasites on blacksmiths, the species cleaned by these seaperch, and indicates feeding habits similar to those of the cleaning señorita, presented above.

Incidental Cleaning by a Close Relative

Although sharpnose seaperch were not seen in water less than 20 m deep, the white seaperch, a very similar species, is frequently abundant there. The white seaperch was probably the most numerous of the embiotocids during most of the observations made at the 3- to 10-m location off La Jolla. Underwater the white seaperch and the sharpnose seaperch are nearly identical, but can be distinguished by the dusky bordered caudal fin of the former and the black-tipped pelvics and more pointed snout of the latter.

White seaperch are especially abundant in groups of 10 or more close to surfgrass in 3 or 4 m of water off La Jolla. Typically they hover head-down; in this attitude they are not soliciting cleaning but rather are intently regarding the surface of the vegetation, at which they pick occasionally. Tiny organisms that live on the surfgrass are prey of these fish: five white seaperch, 80 or 81 mm long, speared in this habitat, were filled with (showing percent of total volume) caprellid amphipods (80%), gammarid amphipods (5%), isopods (2%), fragments of algae with encrusting bryozoans (10%), and unidentified crustacean parts (3%). Quast (1968) found that specimens from a kelp bed had fed mostly on small bottom-dwelling crustaceans, polychaetes and bivalves, as well as kelp fragments, some of which were heavily encrusted with bryozoans. Thus the bottom-picking feeding habits of the white seaperch are very similar to the noncleaning habits of the sharpnose seaperch.

On one occasion, I saw a white seaperch swim 1 or 2 m above the surfgrass in company with a lone blacksmith, which hovered head-down in the manner typical of one that desired to be cleaned. The white perch picked at the blacksmith's body several times, but the bout was brief, and the perch soon joined a group of 8 to 10 others of its own kind near the surfgrass below. This seaperch, which proved to be 79 mm long, was speared, and its gut contents included 58 caprellid amphipods, a single gammarid amphipod, one small isopod, plant fragments with encrusted bryozoans, and some unidentified nonparasitic crustacean remains. No ectoparasites were found; its food was similar to that of the other white seaperch reported above. On another occasion I saw a white seaperch cleaning several blacksmiths over a sandy bottom in 12 m of water, but this individual was not collected. Probably the observed cleaning was no more than a brief incidental activity for these fish. At no other time did I see any indication of cleaning by this species, but perhaps the activity is more frequent under appropriate conditions.

CLEANING ACTIVITY OF THE KELP PERCH

Because the kelp perch is not abundant in the La Jolla study area, where larger kelps are sparse, most observations of cleaning by this fish were made incidentally during other projects in areas heavily forested with kelp. However, these other projects generally were centered on the sea floor, whereas kelp perch concentrate above in the midwater and canopy regions. Nevertheless, observations of cleaning were sufficiently frequent to recognize this species as a habitual cleaner, though probably less so than either the señoritas or the juvenile sharpnose seaperch. In taking material from the bodies of other fishes, the kelp perch uses the same picking technique that it employs to pick items from an algal substrate, or that are adrift in midwater. Its pointed snout and dentition, which is similar to that of the señorita, as described above, are well suited to cleaning.

Insofar as an aggregation of kelp perch tends to remain in one location, these fish can perhaps be regarded as maintaining a station at which other fishes are cleaned. But I saw no indication that more than one or a few members of a given aggregation clean, or that other fishes come to these locations from any distance for cleaning. In fact, I saw only blacksmiths and other kelp perch being cleaned by this fish. In the one observation of intraspecific cleaning, a single kelp perch swam among others of its aggregation, intently inspecting their bodies. Usually the subject of this attention moved away, whereupon the cleaner moved to another fish. A few responded to the cleaner by erecting their fins and hovering immobile in a head-down posture, and these were cleaned. Occasionally a fish being cleaned suddenly darted away as if the cleaner had been too vigorous in its attentions. All blacksmiths being cleaned were solitary individuals that hovered in head-down soliciting fashion close to an aggregation of kelp perch. Whether or not one of the perch had earlier made an initiating overture was never determined. Never more than one or two of the perch in the aggregations were seen cleaning these blacksmiths. Occasionally a cleaner would closely follow a halfmoon or kelp bass that incidentally passed close by, but I saw no evidence that these fish were interested in the perch, and no cleaning occurred.

Three kelp perch, 94 to 99 mm long, one of which had been cleaning a blacksmith, were collected from an aggregation hovering near a stand of feather-boa kelp. The gut contents of the individual known to have cleaned the blacksmiths contained (showing the percent of total volume): gnathiid isopod larvae (50%), nonparasitic isopods (5%), gammarid amphipods (5%), caprellid amphipods (20%), and unidentified material (20%). Neither of the two that were not known to have cleaned contained evidence of ectoparasites: one was full of caprellid amphipods (90%) and unidentified material (10%), whereas the other had nothing in its digestive tract except a few unidentified fragments posteriorly.

Limbaugh (1955) reported kelp perch cleaning kelp bass, opaleyes, garibaldis, blacksmiths, and walleye surfperch (*Hyperprosopon argenteum*).

DISCUSSION

Various cleaning fishes remove a wide variety of deleterious material from the bodies of the animals they service. In addition to ectoparasites, this material includes diseased, injured, or necrotic tissue, fungi, and unwanted food particles (Feder, 1966; Hobson, 1968, 1969b; and others). However, the discussion below considers cleaning only as the removal of ectoparasites, because my data indicate that these are the only items taken in significant amounts from California fishes by the cleaners considered in this report.

INCIDENTAL VS. HABITUAL CLEANING

Cleaning is widespread among small-mouthed marine fishes that characteristically pick minute organisms from the substrate (Hobson, 1968). Included are species of the families Chaetodontidae, Pomacentridae, Labridae, Embiotocidae, Blenniidae, and others. Morphological and behavioral characteristics suited to their way of life have preadapted many species of these families for the cleaning habit. Probably some such fishes pick ectoparasites only incidentally during routine foraging when under certain conditions the body of an adjacent fish, infested with ectoparasites, becomes accessible as just another feeding substrate. The relative tendency of a given species to clean likely is influenced by both short-term and long-term environmental changes. Such changes may be expected to alter interspecific relations, by affecting not only the relative availability of various prey organisms and the incidence of various ectoparasites, but also the species composition of the interacting fishes themselves.

In California the white seaperch likely is one of those species that cleans only occasionally as an incidental adjunct to regular foraging. Several other California species reported by Limbaugh (1955) and Gotshall (1967) clean, including black perch, pile perch, and rainbow seaperch, but they have not been seen doing so by me. The report of cleaning by the blacksmith (Turner et al. 1969) remains an anamoly, as this fish does not fit the pattern of a bottom-picking predator described above. However, it may be significant that many of those substrate-picking predators which clean most frequently are species that also feed on material adrift in midwater, as do the señorita, sharpnose seaperch, and kelp perch. Thus this mode of feeding too, including the taking of plankton, may, in some species, favor adaptations that are suited to cleaning. Fishes that are adapted to both substrate-picking and plankton-picking may possess adaptations especially well suited to cleaning.

Probably many species of fishes clean incidentally on isolated occasions, but relatively few are habitual cleaners. And even the habitual cleaners vary greatly in the degree to which they are specialized for this habit. Species of the Indo-Pacific labrid genus *Labroides* are highly specialized cleaners that feed almost exclusively on ectoparasitic crustaceans (Randall, 1958; Youngbluth, 1968). These fishes possess many specific morphological and behavioral specializations that are adapted to this way of life (Feder, 1966; Losey, 1971). However, only a small minority of cleaners are so highly specialized; most are but part-time practitioners of the cleaning habit, with much of their food being derived from other sources.

That some cleaners depend on ectoparasites for prey, whereas others can subsist equally well on food from other sources, has led to classifying various species as either obligate or facultative cleaners (e.g., Youngbluth, 1968). The señorita, sharpnose seaperch, and kelp perch may well resist being so classified because their cleaning seems to be characteristic not so much of a species as of just certain individuals. At least at a given time, most señoritas do not clean, whereas some seem to be facultative cleaners, and a few might even be obligate cleaners. Juvenile sharpnose seaperch follow a similar pattern, but with a relatively higher incidence of individuals that clean. Limited data can only suggest that the status of the kelp perch may be similar.

CLEANING INITIATED BY THE SEÑORITA

Usually there seem to be fishes present that need cleaning, as shown when a señorita identifies itself as a cleaner by initiating action with, say, a blacksmith or a topsmelt, and immediately is converged upon by many other fish that crowd in its way seeking attention. That such fishes generally wait for a señorita to begin the cleaning, rather than attempting to initiate activity themselves with one of the many señoritas present, likely reflects a low probability of success if they make the first move. If, as it seems, the vast majority of señoritas are not cleaners, or at least not currently predisposed to clean, then random efforts to solicit service would not seem adaptive.

This situation contrasts with that of the Hawaiian wrasse *Labroides phthirophagus*, of which all individuals seem to be obligate cleaners (Youngbluth, 1968), and which is not nearly as abundant on Hawaiian reefs as the señorita is in California. In centering their activity around well-defined stations, the distinctive *L. phthirophagus* can be recognized readily by others that need cleaning. Thus, not surprisingly, cleaning encounters that involve *L. phthirophagus* are regularly initiated by fishes seeking cleaning (Losey, 1971).

We have seen that under certain circumstances various fishes initiate cleaning encounters with señoritas. Some fishes successfully do so by hovering amid unusually dense concentrations of señoritas, but the overtures of such fish are not directed at individuals; rather, they are broadcast to the assemblage at large. The success of this tactic presumably follows the probability that an individual predisposed to clean occurs among such a large number of señoritas.

Kelpfish regularly solicit cleaning from individual señoritas, but the situation is exceptional. Because kelpfish rise into midwater for cleaning, it appears that they do not receive satisfactory service in their regular habitat amid benthic vegetation. In their usual surroundings, where they are extremely difficult to discern, the cryptic kelpfish may be relatively inaccessible to cleaning señoritas. One can see why a fish thus handicapped might be required to initiate needed cleaning itself. The number of unsuccessful attempts experienced by kelpfish before a señorita was finally induced to clean them underscores the existing problem of locating a cleaning individual.

SPECIES-SPECIFIC CLEANING

Because the cleaning señorita initiates most of its activity, it has the opportunity to select its clients, and the data indicate that a species-specific choice is exercised. That individual cleaners tend to limit their selection to members of only one species may be related to the fact that they initiate cleaning on the home ground of the fishes they serve, when these fishes are engaged in some of their regular activity. As each of these clients has distinctive habits, a señorita approaching to clean a fish of one species faces a somewhat different situation than a señorita approaching to clean a fish of another species. The distinctions often are subtle, but may be significant enough to account for a given señorita's tendency to seek out members of only one species.

Again we can draw a contrast with the cleaning behavior of *Labroides phthirophagus*, individuals of which receive members of many different species at well-defined cleaning stations (Randall, 1958; Youngbluth, 1968). Probably such nonspecific cleaning is characteristic of cleaners whose activity is confined to these established locations. Fishes that visit such cleaning stations enter the cleaner's own territory, and frequently join a mixed-species group that hovers in wait for service. In tending these fishes on its home ground, the cleaner is receiving them on its own terms, so to speak, so that the situations surrounding cleaning bouts with all of the different species are essentially the same.

Cleaning by the señorita may not be species-specific on those few occasions when the cleaning activity is initiated by the fish in need of such service, for example by the kelpfish, as described above. Although they show some difficulty locating a receptive señorita, kelpfish nevertheless seem far more successful at doing so than one would expect if indeed they are required to find one that will clean only kelpfish. Thus, although individual señoritas seem to be species-specific when they themselves initiate cleaning, they may be considerably less so, and perhaps even nonspecific, when the other fish makes the initial overture. There are no data on this point, however.

The extent to which these considerations apply to juvenile sharpnose seaperch and kelp perch cannot be ascertained because data are lacking.

SIGNIFICANCE OF POSTURES ASSUMED BY FISHES THAT SOLICIT CLEANING

When members of an assemblage of fishes like blacksmiths or topsmelt converge on a cleaning site that has developed in their midst, probably their attention was initially alerted by the unnatural-appearing posture assumed by the individual first approached by the cleaner. Usually this posture does not seem to be assumed purposefully, but rather results when the fish, having ceased swimming and immobilizing its fins, passively drifts out of its regular attitude (Hobson, 1965b). The posture thus assumed varies, especially between species, where perhaps differing centers of gravity are determining factors. Thus the blacksmith usually hovers head-down, whereas the topsmelt is more often tail-down. Sometimes an unnatural-appearing posture is actively assumed when the fish attempts to present to the cleaner a certain part of its body, presumably that part carrying an irritation. By virtue of their unusual appearance, these postures in cleaning interactions serve to draw attention to the fish that is cleaned. It does not seem necessary that any particular posture be assumed, only that it look out of the ordinary. Reports are widespread (see Feder, 1966) of cleaning recipients assuming these unnatural-appearing postures.

Attention-getting postures assumed by fishes being cleaned probably occurred incidentally during the early development of cleaning symbiosis, when fishes hovering to be cleaned quite naturally stopped moving and passively drifted out of their regular attitudes. As the various cleaning relations evolved, apparently this obvious cue subsequently assumed a different role as a signal in different situations. Generally these postures are suggested to be signals between the recipient of cleaning and the cleaner, indicating a readiness to be cleaned. Quite likely this is the primary signal-function in activity involving such cleaners as *Labroides phthirophagus,* where all members of the species are cleaners and where activity is centered around cleaning stations that are well known to other fishes in the area. In this situation a fish in need of cleaning should be reasonably successful in advertising its condition by assuming the characteristic soliciting posture before a fish recognizable as a cleaner. Losey (1971) showed that various fishes regularly employ this tactic to induce *L. phthirophagus* to clean them. Observations in the Gulf of California demonstrated that the cleaning station itself has played a role in establishing the soliciting posture as a cue. There I have seen the goatfish *Mulloidichthys dentatus* hovering head-down at cleaning stations of the butterflyfish *Heniochus nigrirostris,* when the resident cleaner was itself temporarily absent. Losey (1971) observed similar behavior among Hawaiian fishes. In such a situation the hovering posture probably alerts the cleaner to fishes that have arrived for cleaning.

However, in cleaning activity involving the señorita, the soliciting posture usually is assumed only after cleaning has been initiated by the cleaner. The problem of recognizing an individual that will clean among the vast majority of señoritas that do not clean, coupled with the absence of well-defined cleaning stations, would reduce the adaptiveness of the client's soliciting posture as a cue to initiate cleaning. Probably the most effective way for a fish to obtain needed cleaning in this situation is to wait until a cleaner has identified itself by initiating activity with some fish in the area. Once this has occurred, one can see the value of the posture, when assumed by the first fish to be approached, as a cue in alerting other fish that need cleaning to the presence of a cleaner. In effect, then, the fish assuming the soliciting posture advertises the temporary existence of the transient cleaning "station" to other potential recipients of cleaning. Well-defined cleaning stations like those of *Labroides phthirophagus* do not need this sort of advertisement, as their locations are well known to the fishes that visit them. Nor is it necessary that cleaning individuals of *L. phthirophagus* be pointed out, as all members of that distinctive species are cleaners. Despite this, it is probable that fishes hovering to be cleaned at a *Labroides* station themselves create a visual cue that tends to attract other fishes.

There may also be a maladaptive aspect to the postures assumed by fishes that solicit cleaning. In hovering at an unnatural angle, fins immobile and erect, a fish may enhance its chances of being cleaned, but it would also seem likely to draw the attention of predators and to handicap itself in evading attack. Perhaps such an increased vulnerability accounts at least in part for the sharp decline in cleaning that occurs with reduced visibility, when predators can approach closer undetected. Increased vulnerability may also account for the observation reported earlier (Hobson, 1965c), where pomadasyids in the Gulf of California abruptly broke away from cleaners when a predator approached.

THE POSSIBILITY THAT FISHES BEING CLEANED EXPERIENCE STRESS

Being prodded and picked over by an animal of another species would seem to require a difficult adjustment for a fish. It may well be that fishes experience stress under this circumstance, even when the behavior is well established. Certainly observations have shown that this experience can be uncomfortable, judging from how often fishes being cleaned suddenly bolt forward, and swim away, apparently having been nipped too vigorously by the attending cleaner. Sometimes too, a fish approached by a cleaner clearly experiences conflicting responses, one moment tolerating or even soliciting the cleaner's attentions, and the next moment chasing it away on each approach. Such ambivalent behavior was especially evident in rubberlip perch. Losey (1971) noted that *Labroides phthirophagus* in Hawaii is sometimes attacked by fishes that it attempts to clean, and suggested that this may occur when the cleaning is painful to the host fish.

The color changes shown by many fishes being cleaned (Randall, 1958; and others) may in fact be manifestations of stress. It is well known that many fishes experience color changes in response to stress. Earlier (Hobson, 1965a) I discussed the striking color change of the goatfish *Mulloidichthys dentatus* when it solicits cleaning in the Gulf of California, and pointed out that this fish shows the same color change in other situations that are obviously stressful. Such color changes have been regarded as signals between the fishes being cleaned and the cleaners, (e.g., Feder, 1966), functioning in the cleaning interaction much like the soliciting attitudes discussed above. As with the attitudes, any role such color changes may now have assumed as a signal probably evolved from an incidental byproduct of early cleaning. I have no data on this point relating to the California species, as such color changes are not especially evident in fishes that were observed being cleaned there.

ARE CLEANERS IMMUNE FROM PREDATION?

Reportedly some cleaners are immune from predation because of the service they provide the predators (Feder, 1966; and others). Limbaugh's (1961) belief that the señorita enjoys such immunity is based on observations of this labrid entering the open mouth of kelp bass to clean and on not finding it among the stomach contents of predators during a food-habit study. However, Quast (1968) found señoritas in the stomachs of kelp bass, and H. Geoffrey Moser, U.S. National Marine Fisheries Service (unpublished data), found señoritas in stomachs of the bocaccio, *Sebastes paucispinis*, and the starry rockfish, *S. constellatus*.

I doubt that cleaners enjoy immunity in the sense that predators, recognizing them as benefactors, actively avoid preying on them. Cleaners may recognize those predators which are not at that time intent on feeding and may restrict their cleaning to such individuals. A predator that assumes a soliciting posture may effectively advertise this situation, and no doubt other cues exist. Such mechanisms would reduce the chance of cleaners placing themselves in vulnerable situations while cleaning. In addition, cleaners probably are not as vulnerable while cleaning large predators as might be expected simply because cues characteristic of feeding situations are not present. In associating themselves so intimately with predators, cleaning fishes show behavior that is so unlike that of prey that predators probably do not regard them as food. However, even if such factors do reduce the danger that might seem inherent in the cleaning act, I doubt that their cleaning role affords these fishes any security from being eaten in noncleaning situations.

PARASITES AS PREY OF THE CALIFORNIA CLEANERS

It is hardly surprising that the fishes which are cleaned most frequently in California are those which are the most abundant and at the same time carry the most ectoparasites. Thus the blacksmith, topsmelt, halfmoon, and garibaldi are the fishes cleaned most frequently, and the survey of ectoparasites showed them to be among the most heavily parasitized. The vast majority of ectoparasites on these particular fishes are mobile forms, mostly caligid copepods and gnathiid isopod larvae, that occur on the body surface of their hosts. That these same parasites were found to make up the diet of the cleaners attending these fishes is consistent with the observation that only the exteriors of fishes were seen being cleaned during this study.

Although the forms infesting the external body surface are the most numerous ectoparasites on the fishes available to the California cleaners, many other types were found to infest the oral and branchial cavities. One might question why these other parasites do not seem to be taken, especially as Limbaugh (1955, 1961) reported señoritas entering the mouth of the kelp bass and cleaning beneath the gill covers of the garibaldi. Furthermore, such behavior has been widely reported for some other cleaners, such as species of *Labroides* (Eibl-Eibesfeldt, 1955; Randall, 1958; and others), and some echeneids are known to habitually feed on copepods from the branchial cavities of sharks (Cressey and Lachner, 1970). Nevertheless, any such activity by señoritas must be relatively rare. In discussing this situation I limit my remarks to the señorita, because data are presently insufficient to determine whether the same may apply to the sharpnose seaperch and kelp perch.

Señoritas would not be expected to take parasites from the oral or branchial cavities as often as species of *Labroides* or echeneids if for no other reason than they simply are too large relative to most of the fishes they clean. Whereas species of *Labroides* or the echeneids are small enough to enter the oral and branchial cavities of most of the fishes they service, the señorita is nearly as large, and sometimes even larger, than most of its clients. Significantly, Limbaugh observed señoritas cleaning within the oral and branchial cavities of kelp bass and garibaldis, both of which are relatively large species. Most of the señorita's cleaning is directed toward smaller species, like the blacksmith and the topsmelt.

The specialized techniques that would be required to prey on the parasites of the oral and branchial cavities would probably pose another problem to the señorita. In its regular habit of taking parasites from the external surfaces of fishes, the cleaning señorita concentrates on just a few forms that not only are numerous on many of the most abundant fishes, but also are not too dissimilar from free-living prey of the species. Sometimes these external forms also occur in the branchial cavity, and some similar forms, e.g., bomolochids (Figure 7), habitually occur there and in the oral cavity. But the majority of parasites characteristic of the branchial and oral cavities are aberrant forms, e.g., dichelesthiids, chondracanthids, and lerneopodids (Figure 7), and these are unlike anything else encountered by the señorita. No one type predominates; rather, they occur in a wide variety of forms, none widespread among the different species of fishes, and none especially abundant (except on an occasional individual fish). Thus a cleaner probably could not subsist on one type alone but would have to master a repertoire of specialized techniques in order to exploit enough of these varied forms to make it worthwhile. And before access is gained to the site of infestation, a much more refined cleaner-host interaction must have evolved than is necessary when parasites are simply cleaned from the external body surface. No such relation would evolve unless the cleaner acquired the precise manipulations necessary to pick attached parasites off the gills without damaging the delicate gill membranes. Obviously the cleaning relation would not be adaptive if such damage occurred. In short, to feed habitually on parasites from the oral and branchial cavities would seem to require a higher degree of specialization than has been demonstrated by the señorita. It seems unlikely that such specialization would develop as long as the more abundant and readily available forms on the body surfaces continue to satisfy the cleaning needs of the species. Certainly judging from the way blacksmiths, topsmelt, and other fishes vigorously compete to have their external parasites removed, it would seem that there is little immediate chance of these parasites falling into short supply.

CLEANING SYMBIOSIS AND THE DISTRIBUTION OF SHORE FISHES

In his often-cited report on cleaning symbiosis, Limbaugh (1961: 48) stated:

> In my opinion it is the presence of the señorita and kelp perch that brings the deep-water coastal and pelagic fishes inshore to the edge of the kelp beds on the California coast. Most concentrations of reef fishes may similarly be understood to be cleaning stations. Cleaning stations would therefore account for the existence of such well-known California sportfishing grounds as the rocky points of Santa Catalina Island, the area around the sunken ship *Valiant* off the shore of Catalina, the La Jolla kelp beds and submarine canyon and the Coronado Islands.

Presumably this conclusion was intuitive, as no data were presented. In his review of cleaning symbiosis, Feder (1966: 368), basing his conclusion on Limbaugh's work, similarly stated: "In all probability, many good fishing grounds are such primarily because they are cleaning stations." I believe that this contention is unfounded. Señoritas are the major cleaners in California inshore waters, so that if cleaning symbiosis does account for most concentrations of reef fishes in this region, as Limbaugh suggested, then señoritas would be the cleaner largely responsible. Cleaning occurs wherever señoritas are concentrated but clearly is not a major activity of the population, even though it may be so for a relatively few individuals. In any event, it seems safe to conclude that cleaning is not among the major factors determining the distribution of señoritas. And if cleaning does not determine the distribution of señoritas themselves, it seems unlikely that it would determine the distribution of other species.

Undoubtedly many factors contribute to creating situations that draw concentrations of fishes to certain locations. Where a number of different species have similar requirements, assemblages will develop where conditions satisfying these requirements are optimum. The presence of these fishes increases the complexity of the environment, thus creating situations that support still other species, and so on. Often it is apparent that certain features are especially significant as a basis for these concentrations. Consider, for example, the rocky points that Limbaugh included in his list of "well-known California sport-fishing grounds." The flora and fauna of these locations are generally rich, a fact probably related to such local features as converging currents that frequently produce upwelling and nutrient-rich waters. Plankton is commonly abundant here, along with plankton-feeding fishes like the blacksmith. Señoritas and other species frequently are numerous here too, but the main attraction seems to be a generally rich food supply rather than available cleaning. Similarly it is unrealistic to attribute concentrations of fishes around sunken ships to cleaning activity. Where a wreck has settled on an open expanse it becomes a haven for fishes that require a nearby structure for cover or a spatial reference point. Obviously such fishes will center themselves here, because the surrounding featureless substrate does not meet their requirements. I am describing a well-known phenomenon, one that is the rationale behind constructing artificial fishing reefs. Thus food and a suitable substrate often appear to be key features in a habitat that supports large numbers of fishes. Of course to cite just one or the other would be an oversimplification, as requirements in both must be satisfied, along with many other perhaps more subtle needs. The various species assembled at such locations interact in a variety of ways; cleaning symbiosis is one such interaction, and undoubtedly an important one, but hardly the prime reason for them being there.

CHANGES IN HABITS WITH TIME

Uncertainty remains regarding changes in habits with time. The picture of activity developed in this report was derived directly by observing activity and also indirectly by examining both digestive-tract contents and the specific ectoparasites that infest the various fishes. But these methods only define situations that exist over a relatively brief span of time. Data on individual activity over longer periods are needed. Certainly habits of individuals change with time, but how much change and over how much time? The fact that material in the digestive tracts frequently occurs in sharply delimited homologous blocks indicates that these fishes often feed heavily or even exclusively on one particular type of prey, and then abruptly shift to something else. Are habits such as a relative tendency to clean and to clean members of just one species immutable characteristics of individuals, or have the observations described in this report simply defined temporary situations that the various individuals just happened to be experiencing at the time they were singled out for study? It is possible that all señoritas clean at one time or another, though not all at once, and only a few at a time. It is also possible that a señorita, which tends to clean members of just one species during a given period of cleaning, may select members of another species during a subsequent period of cleaning. Despite these questions, the conclusions drawn in this report are dependent only on an accurate assessment of the immediate situation, so that their validity is not affected by whether or not the habits of individuals under study remain basically unchanged over time.

A NOTE ON INDIVIDUAL VS. SPECIES HABITS

Information on variations in feeding behavior among individual fish under natural conditions is difficult to acquire. Typically a given behavior is described as a species characteristic, and the extent to which this behavior varies among the different members of the species is unknown. Observations of cleaning by the señorita demonstrate that different individuals in a population may react differently to a given situation. Unquestionably this phenomenon extends beyond cleaning behavior to other facets of the animal's activity. If, as is probable, some of the characteristics of individual fish result from early imprinting, then different members of the same population could be expected to react differently in certain situations throughout life. In any event, it seems unquestionable that the behavior of an individual is considerably more limited than that descriptive of its species, or even its own population.

CONCLUSIONS

1. Three inshore species of fishes in southern California are habitual cleaners: the señorita, the sharpnose seaperch, and the kelp perch. A number of other species clean occasionally as an incidental adjunct to their regular feeding.

2. The señorita may clean throughout its postlarval life, whereas cleaning by the sharpnose seaperch is an activity largely of juveniles. The life-history period during which kelp perch clean has not been defined.

3. Cleaning is of secondary significance to these species, although it may be of major significance to certain individuals. Only a few of the many señoritas present at a given time clean, and the same seems to be true of the kelp perch. The incidence of cleaners is much higher among juvenile sharpnose seaperch, but the adults of this species do not seem to clean regularly. The major food of all three species is free-living organisms which they pick from a substrate and midwater.

4. There is little overlap between the cleaning areas of the three species. The señorita is the major cleaner in southern California inshore waters by virtue of its great abundance in a variety of rocky habitats. However, the kelp perch may be the predominant cleaner in the canopy region of the kelp beds, where the species concentrates, and the sharpnose seaperch is the predominant cleaner where it occurs at depths below about 20 to 30 m and/or water under 12° or 13° C, even though the señorita may be more abundant.

5. The señorita and sharpnose seaperch do not establish well-defined stations at which they receive other fishes seeking to be cleaned—a situation frequently described for other cleaner fishes. Rather, as they move from place to place, individuals of these species approach and clean other fishes in various different locations.

6. Cleaning activity by these species is essentially limited to removing ectoparasites from the external body surfaces of fishes. They do not ordinarily take parasites of the oral and branchial cavities. The dentition of the señorita and kelp perch, which is similar and which includes a number of long, curved canines that project forward at the front of each jaw, seems especially suited to pick ectoparasites.

7. The major prey taken by these fishes through cleaning are caligid copepods and gnathiid isopod larvae. The species of parasite taken most often by the señorita and sharpnose seaperch is *Caligus hobsoni*.

8. Some species of fishes are cleaned far more often than others, and many species that co-occur with these cleaners are not cleaned at all. The fishes most frequently cleaned are those which at the same time are most abundant and most heavily infested with ectoparasites. The most numerous ectoparasites on these fishes are caligid copepods, the most abundant of which is *C. hobsoni*.

9. Cleaning effectively reduces the number of ectoparasites that infest the external body surfaces of fishes that interact with the cleaners.

10. At any given time, many individuals of the more frequently cleaned species are in need of cleaning. Nevertheless, in activity involving the señorita, infested fishes do not ordinarily attempt to initiate cleaning but instead wait for cleaning to be initiated by the cleaner. Because the vast majority of señoritas are not cleaners, or at least are not currently predisposed to clean, random efforts to solicit cleaning from señoritas in the population at large would not be adaptive.

11. When initiating its cleaning activity, a given individual señorita tends to approach and clean members of only a single species of fish.

12. Because the vast majority of señoritas are not currently predisposed to clean and because there are no well-defined cleaning stations, the unnatural-appearing posture assumed by a fish approached by a cleaner is an important cue in advertising the location of available cleaning to other fish in need of this service.

13. Fishes being cleaned probably experience some degree of stress. The color changes exhibited by some fishes when being cleaned are essentially manifestations of this stress; secondarily, they may have assumed a signal-function in certain cleaning interactions.

14. While intimately associated with the fishes they clean, señoritas frequently become infested themselves by the same parasites they are attempting to remove from these other fishes.

15. Cleaning activity is sharply curtailed when visibility is reduced by turbid water or when there is strong water movement, such as a heavy surge.

16. Cleaning activity among these fishes is a diurnal phenomenon. There is no evidence that it continues after dark.

17. Any so-called "immunity" from predation that a cleaner may enjoy probably relates (1) to an ability to recognize predators that are not intent on feeding and to limit cleaning to such individuals, and (2) to the fact that behavior exhibited by a cleaner servicing a predator is so unlike that of prey that the predator does not regard the cleaner as food. However, their role as cleaners probably does not afford these fish any security from being eaten during noncleaning situations.

18. Cleaners are widespread among small-mouthed marine fishes that characteristically pick tiny organisms from a substrate. This mode of feeding, especially when combined with the capacity to pick tiny prey that are adrift in midwater, preadapts fishes to the cleaning habit.

19. There is no basis for the contention that many of the good fishing grounds in southern California are such because fishes have congregated to be cleaned by resident cleaners.

20. Feeding behavior varies significantly among individuals of at least some species. Thus the habits of an individual can be more limited than those descriptive of its species or even its own population.

ACKNOWLEDGMENTS

Lloyd D. Richards assisted me in collecting the data for this study. I thank Roger F. Cressey and Thomas Bowman, U.S. National Museum, who identified the parasitic copepods and isopods, respectively, around which much of this study is centered. I thank, too, Carl L. Hubbs and Richard H. Rosenblatt, Scripps Institution of Oceanography, and John R. Hunter, U.S. National Marine Fisheries Service, for helpful comments on a draft of the manuscript.

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