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Resource partitioning of two fish ectoparasites, Lironeca vulgaris and Lironeca californica (class isopoda, family cymothoidae)

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RESOURCE PARTITIONING OF TWO FISH ECTOPARASITES, LIRONECA VULGARIS AND LIRONECA CALIFORNICA (CLASS ISOPODA, FAMILY CYMOTHOIDAE)

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ABSTRACT

RESOURCE PARTITIONING OF TWO FISH ECTOPARASITES,
LIRONECA VULGARIS AND LIRONECA CALIFORNICA
(CLASS ISOPODA, FAMILY CYMOTHOIDAE)

by Tony Bennett

The gill cavities of over 6000 fishes (comprising 98 species) were inspected for isopod parasites. In general, host resources were partitioned between two isopod species. In California, L. californica infested 11 of 14 pelagic fish species, whereas, L. vulgaris infested 14 of 16 benthic fish species. In laboratory choice experiments, L. californica adult males and juveniles chose a pelagic host (shiner surfperch, Cymatogaster aggregata) significantly more frequently than a benthic host (staghorn sculpin, Leptocottus armatus), whereas Lironeca vulgaris adult males chose a benthic host more frequently than a pelagic host. Wild, free-swimming, juvenile L. californica were found only in surface water, whereas L. vulgaris only near the bottom, suggesting a difference in vertical distribution of the juveniles. Laboratory experiments on juveniles suggested that L. californica was more photopositive than geopositive and conversely that L. vulgaris was more geopositive than photopositive, helping explain the difference in vertical distribution. The two parasites partitioned resources in the general, but not the strict sense, because it was not shown whether this distribution resulted from competition.

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INTRODUCTION

The isopod crustacean family Cymothoidae contains approximately 37 known genera, including Lironeca, which are ectoparasites on marine, freshwater, and estuarine fishes (Noble and Noble 1976, Brusca 1981). They are often very conspicuous to anglers or fish consumers, but are harmless to humans (Moser et al. 1983, Love 1991). Cymothoid isopods are morphologically adapted for a parasitic lifestyle. They attach to host fishes with hooked pereopods. Host's blood is obtained using mouth appendages (maxillae) that hold the buccal region to the host's flesh and cut through the epidermis (Caullery 1952, Brusca 1981).

All cymothoid isopods are protandrous hermaphrodites (Noble and Noble 1976, Brusca 1981). They are good swimmers only during manca (juvenile recently released from marsupium) and male life stages, when they are able to find and attach to a host fish (Brusca 1978). Females are obligate symbionts, and lack a directed swimming ability (Brusca 1978, Robinson 1982b). Cymothoids (Lironeca vulgaris) find a host using cues of color, light, and mucus (Moser and Sakanari 1985).

Although most cymothoids consume blood of their host, at least two other modes of feeding are possible. They may ingest food particles taken in by the fish (Lincoln 1971) or directly eat the host's flesh. Gills of host fish often are eroded, apparently by the isopods (Kroger and Guthrie 1972, Lindsay and Moran 1976, Waugh et al. 1989 and personal observation), but it is not likely that parasites rely on a host's flesh as a primary food source, though this never has been tested.

Lironeca vulgaris inhabits tropical to temperate latitudes from Puget Sound, Washington to Colombia at depths from 1 to 311 m (Calman 1898, Richardson 1905, Hatch 1947, Brusca 1978). Lironeca californica is found at temperate latitudes from Alaska to Punta Eugenio, Baja California, Mexico, in depths of 0 to 90 m, and is particularly common in bays and estuaries (Brusca 1981; Fig. 1).

Although both isopods are similar morphologically, L. vulgaris (max. 43 mm length) grows larger than L. californica (max. 20 mm length; Brusca 1981 and this study). Generally, L. vulgaris has a greater interorbital distance than L. californica, and L. californica has darker pigmentation than L. vulgaris.

Some cymothoid isopods are highly host specific, whereas others are less so. Isopods with broad geographic distributions are associated with more host fish species than isopods with restricted distributions (Brusca 1981). Most Lironeca possess low host specificity. Lironeca californica has infested shiner perch (Cymatogaster aggregata), northern anchovy (Engraulis mordax), California killifish (Fundulus parvipinnis), topsmelt (Atherinops affinis), arrow goby (Clevelandia ios), and other fishes (Appendix 1b). Lironeca vulgaris has infested numerous scorpaeniform fishes, embiotocids, serranids, and flatfishes (Appendix 1a).

Parasites that infest hosts with wide geographic ranges usually exhibit "ecological host specificity" rather than taxonomic preference (Rohde 1982). They occur on fishes found in similar habitats or with similar behaviors or habits (Noble 1960). Brusca (1978) found that L. vulgaris infested demersal fishes such as flatfishes and rockfishes. Alternatively, L. californica usually occur on pelagic, schooling fishes such as topsmelt, anchovies, and surfperches (Embiotocidae), often in bays and estuaries (Brusca 1981, Waugh et al. 1989).

Two species cannot occupy the same ecological niche (Gause 1934), defined as the role an organism plays in a community (Elton 1927, Whittaker et al. 1973). Possibly these two isopod species, when they occur sympatrically, partition host resources (Hutchinson 1959, Noble 1960, Schoener 1974) by occupying different host niches.

In the first phase of this study, I examined whether L. californica and L. vulgaris partition host resources between pelagic and benthic fishes. Resource partitioning has historically been a controversial ecological term (Norton 1991). In the broad or general sense (the definition used in this paper), resource partitioning is simply the segregation of resources between two species (Kraft and Kitchell 1986, Larson 1980, Norton 1991). In the strict sense, it is a process by which resources are divided between organisms and is the result of interspecific competition, which permits the coexistence of similar species (Ebeling and Laur 1986, Pulliam 1985, Schoener 1974, Strong 1983).

The first objective was accomplished by testing the null hypothesis that L. californica and L. vulgaris infested benthic fishes and pelagic fishes with equal prevalence in the wild. If the null hypothesis was falsified (i.e., that one isopod species parasitized benthic species and the other infested pelagic fishes) it would raise many questions. These include whether the segregation was due to interspecific competition for common resources (hosts), to environmental tolerances, or to the morphology or size of the fish host (i.e. the size of the gill cavity). Then one could evaluate whether such a separation could be the product of evolutionary divergence resulting from competition in the past (Connell 1980, Stanley and Newman 1980).

I attempted to determine whether L. californica and L. vulgaris were competing. Two organisms are competing when they inhibit each others' access to limited resources, such as food and space (Birch 1957, Hixon 1980). The methods used in determining whether competition plays a role in the structure of the community are matters of considerable controversy (Schoener 1982, Connell 1983). Most reports of competition are based on observations of organisms that exhibit overlap in some resource or observations of niche shifts via "natural experiments" (Diamond 1978). In "natural experiments" two species segregate resources in locations where they are sympatric, but use a broader range of resources when allopatric (Brooks and Dodson 1965, Zaret and Rand 1971, Rees 1975, Mittlebach 1984). I sampled, therefore, in locations where the two isopod's geographical ranges overlap in addition to areas outside the overlap.

Some researchers believe that the best method for demonstrating the existence of competition is to form and test null hypotheses, using well designed and controlled field experiments (Connell 1980, 1983, Heck 1980, Schoener 1982, Ebeling and Laur 1986). This has been accomplished in few studies (e.g., Harger 1972, Menge 1972, Hixon 1980, Larson 1980). I attempted this by using live fishes as "bait" for parasites. Benthic and pelagic fishes were placed in traps near the surface and bottom.

The second phase of this study involved laboratory experiments and field sampling to record behavioral mechanisms (geotaxis or phototaxis) or other factors that facilitate resource partitioning (Larson 1980). One question is whether the two species are found in different locatic , in the water column because of differences in geotaxis or phototaxis (Moser and Sakanari 1985). In addition, live isopods were used in host-choice experiments to corroborate field observations.

METHODS

Field Work

Fishes were collected at 10 sites on the California coast, two sites in the Padilla Bay National Estuarine Research Reserve, Washington, and two sites in Baja California Sur, Mexico. California sites occurred within the ranges of both isopods, Washington sites were just north of the reported range of L. vulgaris, and Baja sites were south of the reported range of L. californica (Fig. 1).

Fishes were collected using an otter trawl (8 m length, 6 m head rope length, 20 mm mesh with 6 mm mesh cod end liner), a beach seine (8m x 1m, 6mm mesh), spearfishing, and hook and line. Spearfishing was accomplished using a pole spear while SCUBA diving. Fishes were attracted by breaking apart urchins or clams and then speared. After capture, each fish was placed in a 3.8 L plastic ziplock bag and examined later at the surface. Small fishes, such as topsmelt, were collected in King Harbor and Marina del Rey using 2 kilogram (kg) test monofilament, and a number 16 treble hook baited with Velveeta cheese. Larger serranids in Baja were caught using small plastic "scrounger" and feathered crappie jigs on 4 kg test monofilament.

Live fishes were placed into 18 liter (L) plastic buckets containing seawater, and identified to species (Miller and Lea 1972, Gotshall 1987, Thomson et al. 1987). Standard length of each fish was measured in millimeters (mm), and gill cavities were inspected for Lironeca. Any isopods were removed and placed into labeled vials of 70% isopropyl alcohol. Because isopods abandon their host during trawling and seining (Robinson 1982a), short trawl sets less than 15 min duration were performed, when possible. In addition, net and buckets were examined for isopods that had abandoned their host.

Species of isopod was determined in the laboratory using a dissecting microscope, when necessary. The two Lironeca were distinguished using three criteria: 1) interocular distance was less than 1.5 times the eye diameter in L. californica and greater than 1.5 times eye diameter in L. vulgaris (Kozloff 1974), 2) L. californica has 8-9 segments on its second antennae, L. vulgaris has 10-11 (Kozloff 1974, Smith and Carlton 1975), and 3) L. vulgaris has distinct pereopodal carinae but L. california does not (Brusca 1981).

Eighty-three specimens of Lironeca were examined from the Los Angeles County Museum. Species identification was confirmed and host species was noted if available. These records were compared to my field results.

Prevalence (percent of hosts infested) and intensity (number of parasites per infested host) were calculated for all species collected in the field (Rohde 1982).

Fishes examined in this study were categorized as benthic or pelagic. Benthic species were those that spend most of their adult lives on the bottom. Pelagic fishes were those that spend most of their lives swimming in the water column (although they may feed near the bottom). Fish life history information was obtained from Fitch and Lavenberg (1971, 1975), Emmett et al. (1991), and Love (1991).

I used contingency tables to test whether L. californica and L. vulgaris infested benthic and pelagic fishes with equal frequency (Zar 1974). The contingency table rows were L. vulgaris and L. californica, the 2 columns were pelagic fish species and benthic fish species, and the cells were numbers of fish species infested by L. vulgaris or L. californica.

Free-swimming isopods were captured at the water's surface in south San Francisco Bay using a 80 um plankton net (30 cm diameter, 1 m length) from June 1990 to March 1992, excluding January, July, and August. Surface plankton tows (approximately 0.2 to 0.5 m/s) were made from the 85 foot INLAND SEAS, Marine Science Institute, Redwood City, California. Tows were approximately 5 min duration, performed 4 times per week. Samples were examined visually for free-swimming isopods, which were placed in labeled vials of 70% isopropyl alcohol.

Benthic samples of free living parasites were collected in funnel traps deployed 0.5 m off the bottom at 30 m depth in Monterey Bay. Traps were constructed from plastic cylindrical waste baskets (50 cm height by 25 cm diameter) with a plastic funnel glued into the mouth of the waste basket. A 3-cm hole in the bottom of the wastebasket was plugged with a rubber stopper. Funnel traps were deployed funnel side down by SCUBA divers. Three steel rods (0.5 cm diameter, 1 m length), attached to the cylinder, were forced into the sediment until the mouth of the wastebasket was approximately 0.5 m from the bottom. The traps were attached to a fence anchor which was loosely set into the sediment. A buoy attached to the fence anchor by a line was easily located and retrieved from the surface 48 hours later. After the traps were returned the laboratory, rubber stoppers were removed and contents poured into a 0.5 mm sieve and placed in labeled jars of 70% isopropyl alcohol. Isopods were later identified to species.

Minnow traps (50 cm length, 20 cm diameter, 0.5 mm mesh) were baited with sentinel hosts (live fish; Sonstegard 1977, Stepien and Brusca 1985) and deployed in south San Francisco Bay. A trap was attached to a line 0.5 m below the buoy and another 0.5 m above the anchor. Before setting the traps, either two live staghorn sculpin or two shiner surfperch were examined for isopod parasites (any found were removed) and placed into traps. The traps were secured with plastic lock-ties and deployed for 24 to 120 hours. After traps were retrieved, fishes and traps were carefully examined for isopods.

Laboratory Work

Post marsupial mancas of Lironeca can be obtained from fish gills (Brusca 1978, Waugh et al. 1989), marsupia of gravid females found in fish gills (Moser and Sakanari 1985, Sandifer and Kerby 1983, Robinson 1982b), or in surface plankton tows (Lindsay and Moran 1976).

Live isopods used for laboratory study were obtained from trawl-caught fishes in south San Francisco Bay. Between October 1991 and May 1992 six 15-min trawls per week were performed to obtain fishes. The gill cavites of nearly all fishes collected were examined for Lironeca.

Others have performed laboratory studies on Lironeca, providing useful data on longevity of isopods maintained in aquaria. Isopods (L. vulgaris), placed on sanddab (Citharichthys sp.) hosts, have been kept alive in the laboratory for up to 752 days (Robinson 1982b). Female isopods (L. vulgaris) have survived without a host from 10 (Moser and Sakanari 1985) to 40 days (Brusca 1978). Manca stage L. ovalis survived for up to 15 days without a host; however, their swimming activity noticeably decreased after 2-4 days (Sandifer and Kirby 1983).

Manca stage Lironeca vulgaris were obtained from a gravid isopod (18.5 mm long, 11.0 mm wide) collected from the gill cavity of a staghorn sculpin on 7 November 1991. The female isopod had eyed mancas in its marsupium so it was placed in the gill chamber of another sculpin. A staghorn sculpin was used because it was the natural host and is a hearty species (Fitch and Lavenberg 1975). The sculpin was kept in a 80-L aquarium, and fed live grass shrimp (Crangon sp). On 18 December, hundreds of mancas (2-4 mm long) were observed swimming in the aquarium. The fish host and female isopod were then removed. A pipette was used to catch mancas, which were used in phototaxis, geotaxis, and host-choice experiments.

Young Lironeca californica (2-4 mm long) were obtained from two gravid isopods collected from the gill cavities of two gravid shiner surfperch on 30 April 1992. The gravid isopods were removed from the fish and placed in a small aquarium with flowing seawater until all live mancas were released from the marsupium (4 hr). The mancas were used in phototaxis, geotaxis, and host-choice experiments. In another attempt to obtain mancas, a gravid L. californica was removed from a shiner surfperch and placed in the gill cavity of a live staghorn sculpin. After 60 days, since no live mancas were ever seen, the isopod was removed from the sculpin. Its marsupium contained a new brood of yellowish eggs and its digestive tract was filled with blood.

Larger adult male L. californica (> 9 mm length) and L. vulgaris (> 10 mm length) were collected opportunistically from shiner surfperch and staghorn sculpin caught in otter trawls conducted in south San Francisco Bay. Isopods that swam actively were placed in a small aquarium until host-choice experiments were conducted. To avoid using weak or starving isopods, those not on a host for more than 3 days were placed on the gills of a staghorn sculpin for 24 hours to feed or were not used.

Phototaxis and Geotaxis

Phototaxis and geotaxis of the two isopod species were compared using techniques adapted from Moser and Sakanari (1985). Thirty juveniles were placed in a rectangular glass aquarium (50 cm x 25 cm, 15 cm water depth) in a darkened room with a flourescent white light (20 watts) placed against one end. Isopods were dark adapted for ten minutes before each experiment. The light was turned on, and after two minutes the number of isopods in each half of the aquarium was counted. Ten minutes were allowed between each trial and the light was alternated from end to end after each trial. The water was mixed after each trial to randomly distribute the isopods. Five trials were conducted with L. vulgaris and nine with L. californica. Isopods were replaced after every other trial for L. vulgaris and after every third trial for L. californica. To determine whether the frequency of isopods in either half of the aquarium was equal, chi-square tests were performed on results from each trial. Heteogeneity chi-square analyses determined whether results could be pooled for each isopod species.

For the geotaxis experiments, 20 isopods (mancas) were placed in a clear glass 1 L graduated cylinder (10 cm diameter, 60 cm long), filled with seawater, and the numbers in the top half and the bottom half counted. Different isopods were used in each trial. Three treatments were used: a darkened room, sunlight, and another in sunlight with the top and bottom of the cylinder alternately covered. Before beginning dark experiments, isopods were placed in the cylinder and dark adapted for 10 minutes. The numbers in the top and bottom were then counted, using a flashlight. Then the flashlight was turned off and the next trial started (after dark adaption). Sunlight experiments were conducted in full sunlight. After ten minutes of acclimation, number of isopods in the top and bottom half were counted every thirty seconds for five minutes, resulting in a mean number of isopods in each half of the cylinder for each trial. The other treatment was performed just as the sunlight trials except either the top half or bottom half was blocked with black cardboard. To determine whether the frequency of isopods in either half of the cylinder was equal, chi-square tests were performed on results from each trial.

Host-choice Tests

The shiner surfperch was chosen as the pelagic host (Fitch and Lavenberg 1971, 1975, Emmett et al. 1991, Love 1991), and the staghorn sculpin as the benthic host (Fitch and Lavenberg 1975, Tasto 1975). These species were used because they were natural hosts for Lironeca, and relatively easy to collect.

For each replicate, approximately 10 live staghorn sculpin and 10 shiner surfperch were each placed in an aquarium (122 cm x 61 cm, 43 cm depth) with running seawater. After an acclimation period of at least 0.5 hour, from 3 to 10 adult male or 20 to 26 manca isopods were released into the aquarium. Only one isopod species was used in each experiment, and individual isopods were used only once. After 3 to 14 hours, each fish was captured with a small aquarium net and the outside of the body, gill cavity, and mouth examined for isopods. After all fishes were removed, the water in the aquarium was visually examined for free-swimming isopods and sampled with a net until five successive attempts yielded no isopods. The aquarium was drained and refilled before each trial. Prevalence and intensity of infestation for each host species, and percentage success of isopod (number of isopods on any fish divided by total number of isopods at start of experimental run) were calculated for each experiment. Because these numbers are percentages and potentially not normal, I performed arcsine transformations before calculating means (Zar 1974).

One of the problems encountered in these experiments was that optimal numbers of host fishes and isopods were not always simultaneously available. Therefore, these experiments were performed opportunistically, with whichever fish hosts and isopods were available.

RESULTS

Field Work

Both species of isopod were found on many fish species in California (Table 1 and 2). Of 5099 fishes and 82 species examined from 10 California locations, 548 Lironeca were found on 30 host species. Lironeca californica was most often found attached to the gills of their host, whereas L. vulgaris was usually attached to the inside of the gill cover.

The prevalence of Lironeca varied among host types (Table 1). Lironeca occurred on 8.0% (N = 408 isopods) of all fishes, but was more prevalent on pelagic (13.9%, N = 327) than benthic fishes (2.9%, N = 81; $X^2 = 190.6$, $p < 0.001$). Lironeca californica (6.5%, N = 334) occurred more frequently than L. vulgaris (1.5%, N = 74; $X^2 = 165.6$, $p < 0.001$).

Most infested fishes had either one or two (intensity = 1.34), and never more than three isopods (Table 1 and 2). Fishes with two isopods had one in each side of the gill cavity, often a male and female. Infestation intensity was about equal for both isopod species.

Fourteen pelagic and sixteen benthic fish species from California were hosts for both species of Lironeca. A significantly greater number of pelagic species were infested by L. californica than L. vulgaris and conversely, a significantly greater number of benthic species were infested by L. vulgaris than L. californica (Fig. 2; $X^2 = 9.2$, $0.005 < P < 0.01$). Eight pelagic and five benthic fishes had not been reported as hosts for L. californica. Five benthic fishes and one pelagic fish had not been reported as a host for L. vulgaris (Table 2).

Few isopods were found where the isopod species were allopatric. In Padilla Bay, Washington, only two L. californica were found on shiner surfperch after examining 761 fishes (10 species; Table 1 and 3). No Lironeca were found on 225 fishes, (12 species) from the Gulf of California (Table 4). Thus, prevalence of Lironeca on all host fishes, specifically on shiner surfperch, was significantly less in Washington and the Gulf of California than in California.

Host records of Lironeca in the Los Angeles County Museum collection were consistent with field results. In general, benthic hosts were infested by L. vulgaris and pelagic hosts by L. californica or L. vulgaris (Table 5). The cases where L. vulgaris infested pelagic fishes (black surfperch and salmon) and where L. californica infested a benthic fish (arrow goby) agreed with California field results (Table 2).

Although relatively few free-swimming isopods were captured, the two species appeared to have different vertical disturbutions. Eleven L. californica mancas (2.6-5.2 mm long) were found only in surface samples (N= 300), whereas four L. vulgaris mancas (3.5-4.5 mm long) were found only in bottom samples (N = 17).

The sentinel hosts failed to attract any isopods. Neither minnow traps nor the fish hosts harbored any isopods. The traps attracted other invertebrates such as grass shimp (Crangon sp.), shore crabs (Hemigrapsus oregonensis), and anemones (Diadumene leucolena).

Laboratory Work

Mancas of both species exhibited a positive photataxis (Table 6). Significantly more L. vulgaris mancas were observed in the lighted half of the aquarium than in the dark half in all 5 experiments ($P < 0.001$). More L. californica mancas were observed in the lighted half of the aquarium than in the dark half in 8 of 9 experiments. This was statistically significant in 5 experiments .

In the dark treatments of the geotaxis experiments, L. vulgaris and L. californica behaved differently (Table 7). All L. californica were found in the upper half of the cylinder, either swimming near or floating on the surface of the water. However, there was no pattern in the distribution of L. vulgaris in dark experiments.

In the sunlight treatments, virtually all mancas of both species were observed in the lower half of the cylinder. Lironeca californica, however, occurred with equal frequency in the upper and lower halves of the cylinder, when the lower half was darkened (Table 8).

Host Choice Experiments

Adults of the two isopod species behaved differently and, in general, infested fish species similar to those infested in the wild. After adult L. vulgaris were released into an aquarium, most swam along the bottom. An average of 30.1% of staghorn sculpin were infested with L. vulgaris, whereas none were found on shiner surfperch (Fig. 3). Adult L. californica, however, actively swam in the water column. Some attached to shiner surfperch, causing the surfperch to shake vigorously. They had a significantly greater average prevalence on shiner surfperch (35.2%, S.D.= 9.1, N = 5) than staghorn sculpin (13.8%, S.D.= 13.8, N = 5; $t = 2.89$, $p < 0.02$; Fig. 3).

Mancas of L. vulgaris were more successful at finding a host than L. californica mancas (Fig. 3). Only one L. californica manca of 80 was found on a fish (shiner surfperch). Lironeca vulgaris had a greater prevalence on staghorn sculpin (32.1%, S.D.= 13.3, N = 5) than shiner surfperch (16.6%, S.D. = 24.1, N = 5), but this was not statistically significant ($t = 1.26$, $p > 0.05$). Lironeca vulgaris mancas infested staghorn sculpin in all five runs of the experiment and infested shiner surfperch in only 2 of 5 runs.

Average percent success varied between the two isopod species and between life stages (Fig 4). Adult L. californica were more successful infesting a fish (61.3%, S.D. = 18.8, N = 5) than adult L. vulgaris (49.9%, S.D.= 5.6, N = 4), but this was not statistically significant ($t = 1.16$, $p > 0.05$). Adults of both isopod species were significantly more successful than mancas of the same species ($t = 5.84$, $p < 0.01$ for L. californica; $t = 2.76$, $p < 0.05$ for L. vulgaris).

Average intensity of parasitism was never greater than 2 isopods per fish for any choice experiment. However, some individual fishes were infested by 3 or 4 isopods.

There was no correlation between success of isopods and length of time experiments were run.

DISCUSSION

Because Lironeca has low host specificity (Brusca 1981), many host species were expected. Thirty fish species, including 15 that were not previously known to be hosts, were identified as hosts.

Prevalence of Lironeca probably was underestimated because isopods, especially males, abandon host fishes when removed from water (Lindsay and Moran 1976, Keusink 1979, Robinson 1982a). This tendency may indicate that males use certain sizes or species of fishes (where space is limited) as intermediate hosts and then, after successfully breeding with a female isopod, leave the host in search of another host (where space is not limited) (Robinson 1982b). In a laboratory study, Robinson (1982b) reported that male isopods can locate a new host after abandoning a previous host.

Lironeca was more prevalent on pelagic than benthic fishes. One would expect more benthic than pelagic fishes to be parasitized because they may be easier targets for parasites in the two dimensional space of the bottom rather than the three dimensional space of the water column. Pelagic fishes, however, such as shiner surfperch, form schools (Fitch and Lavenberg 1975, Emmet et al. 1991) which may facilitate parasite infestation (Brusca 1978). It was assumed that sampling was not biased towards collecting certain species of fish. For example, if methods used in this study tended to overcatch shiner surfperch (a pelagic species), which has a high prevalence value (63.4%), prevalence of the pelagic fishes category would be overestimated.

The high prevalence of L. californica on shiner surfperch may be related to behaviors and life histories of both animals. Hobson and Chess (1986) reported shiner surfperch fed actively at night and were less active during the day. Geotaxis experiments indicated that L. californica were more active at night, which may increase its chances of contacting shiner surfperch. Shiner surfperch form schools, providing a greater concentration of potential hosts for newly released mancas. In addition, shiner surfperch release live young rather than planktonic eggs, increasing a mancas chance of finding a host, especially because the reproductive period of isopods and shiner surfperch may coincide. Observations of gravid L. californica (containing well developed young) in the gills of gravid shiner surfperch suggest that L. californica released mancas at nearly the same time surfperch gave birth (this study).

L. californica was a more prevalent (successful) parasite than L. vulgaris. Out of 5,099 potential hosts, 337 (6.5%) were infested with L. californica but only 74 (1.5%)

were infested with L. vulgaris. Even if L. californica was assumed to have only 2,345 (number of pelagic fishes examined) and L. vulgaris only 2,754 (number of benthic fishes examined) potential hosts, the same trend is evident.

Isopod recruitment to a fish host depends on many factors, including: 1) morphology and physical capabilities of isopods, 2) morphology and habits of potential hosts, and 3) parasite avoidance. Lironeca californica may be a superior swimmer or have better eyesight than L. vulgaris, but this has not been tested. Benthic fishes may be more difficult for isopods to find than pelagic schooling species, especially if they bury in the substrate like certain gobies (arrow goby, Clevelandia ios, longjaw mudsucker, Gillichthys mirabilis) and flatfishes (California halibut, sanddabs, starry flounder; Fitch and Lavenberg 1971). Furthermore, free-swimming L. vulgaris may be more susceptible to predation near the bottom, since the benthic community probably contains more predators than the water column.

The two parasites L. californica and L. vulgaris partitioned host resources according to host type, but there were exceptions, which are supported by previous host records (Brusca 1981, Love and Moser 1983) and museum isopod/host records (Table 5)). Habits of the host, individual variation among isopods, and movement from one host to another during capture could help explain exceptions. For example, pelagic fishes, such as black and pile surfperches, spend time feeding near the bottom (Ebeling and Laur 1986, Hixon 1980) which may account for infestation by L. vulgaris. Lironeca vulgaris also infests salmon (Onhcorhyncus sp.) (Jennings and Hendricksons 1982). A salmon would most likely become infested in an estuary as a juvenile, where they feed on benthic crustaceans (Emmett et al. 1991). Jennings and Hendricksons (1982) reported that isopods dropped off salmon after they migrated into fresh water. Benthic fishes which harbored L. californica were gobies and small sculpins. These species were collected with a small beach seine in shallow water (less than 1.5 m depth) where L. californica would most likely be found near the bottom.

The segregation of these two parasites is an example of resource partitioning in the general sense but not necessarily the strict sense. It was not shown whether resource partitioning was the outcome of competition for hosts. Controlled field manipulations, important in determining the existence of competition, should be performed. I was not successful in attracting any isopod parasites to the "sentinel hosts" placed in minnow traps. This may be because the traps were not in the water long enough, the mesh on the traps was too fine, or it may have been the wrong season to trap free-swimming isopods.

"Natural experiments" (i.e., sampling outside the geographic ranges of both parasites) did not yield information useful in assessing past or present existence of competition. This was because few isopods were found on fishes collected in Padilla Bay, Washington or the Gulf of California. This probably reflects a low abundance of isopod parasites in these locations relative to California, but also may be related to the brief sampling period, size composition of fishes, and environmental conditions. It was particularly surprising to find the prevalence of L. californica on shiner surfperch was only 0.4 % in Padilla Bay compared to 63.4% in California. Padilla Bay samples consisted mostly of juvenile surfperch (less than 50 mm SL, Emmett et al. 1991), which had less time to accumulate parasites than adults

Some possible causes or mechanisms that led to the observed separation of host resources were: 1) a preference for host size of parasites, 2) morphological preferences of the isopod species, 3) physiological restrictions, 4) differences in the distribution of the two isopods with respect to distance from bays and estuaries, 5) differences in avoidance behavior between host types, and 6) location in the water column of free swimming isopods.

A preference for host size of the isopods was not observed; L. californica and L. vulgaris infested a large size range of hosts (Fig. 5). If there were a size preference, L. vulgaris, the larger parasite, would have been restricted to the larger hosts and the smaller isopod, L. californica could have infested any size host, but this was not observed.

It was unlikely that the segregation was due to morphological preferences of the isopod species. Host morphology, including gill chamber structure, was highly variable among fishes infested by both parasites. For example, L. vulgaris infested fishes as morphologically different as staghorn sculpin (Scorpaeniformes), lizardfish (Aulopiformes), and sanddabs (Pleuronectiformes)..

Isopods were not physiologically restricted to certain host types because there were instances where L. californica infested benthic fishes and L. vulgaris infested pelagic fishes. Furthermore, L californica survived on a staghorn sculpin for 60 days in the laboratory. However, physiological tolerances may have affected the distribution of L. californica because it was never found on a fish outside of an enclosed bay or estuary, whereas L. vulgaris was found inside and outside of bays. Possible physical factors which may relate to this observation were salinity, temperature, and pressure. It also may be the result of the greater sampling effort inside of bays than outside.

The resource partitioning of L. californica and L. vulgaris likely is due to differences in vertical distribution of free-swimming isopods. In the field, planktonic L. californica were found on the surface, whereas L. vulgaris were found near the bottom. The apparent rarity of free-swimmers may reflect their actual abundance, but they are relatively fast swimmers (Robinson 1982b, Moser and Sakanari 1985) and probably avoided plankton nets to some extent. There are few reports of capturing free-swimming Lironeca (Lindsay and Moran 1976).

All mancas in the present study were obtained from only three females, therefore it is risky to extrapolate results to the entire population of isopods. In addition, aquaria did not mimic natural conditions well. One problems worth considering was that aquaria and cylinders were shallow compared to natural depths.

Zooplankton often exhibit phototaxis, a response toward or away from light (Forward 1986a). For example, some crab larvae are photopositive (Shanks 1985, Shirley and Shirley 1988) and others photonegative (Forward 1986a). Although the angular light distribution of natural underwater light (Forward 1986b) was not simulated in the present study, both isopod species were photopositive. In addition, Sandifer and Kerby (1983) and Moser and Sakanari (1985) reported that Lironeca ovalis and L. vulgaris were photopositive. It is unclear how a positive phototaxis could aid an isopod in finding a host, unless fish were near a light source or the surface.

Moser and Sakanari (1985) found L. vulgaris geopositive in sunlight and in dark. My results agreed with their data on sunlight but not dark. Both isopod species were geopositive in sunlight but not in dark. Moser and Sakanari (1985), however, illuminated aquaria with red light for dark experiments, which they assumed was invisible to isopods. Shirley and Shirley (1988) found that crab larvae were photopositive to some intensities of red light. The geonegative response at night may reflect a greater activity of both species at night, when fishes may be easier prey because it may be more difficult for them to see parasites; however, isopod activity was not quantified.

Moser and Sakanari (1985) also found L. vulgaris was more geopositive than photopositive, which was supported by the present study. These results and the determination that L. californica was more photopositive than geopositive suggests that L. californica is attracted to the surface and L. vulgaris to the bottom. This is consistent with the observed vertical distribution of the two isopods and is a possible mechanism for resource partitioning.

Others making laboratory observations of Lironeca found them unselective in their host choice, usually infesting any fish species in an aquarium (Lindsay and Moran 1976, Sandifer and Kerby 1983, Waugh et al. 1989). This was supported by Robinson's (1982b) observation that contact between isopods and fishes was a "random process." In the present study, both isopod species swam around the aquarium in a random manner; however, they actually occupied different zones in the aquarium. Lironeca vulgaris swam close to the bottom, whereas L. californica usually swam above the bottom, which may have facilitated the resource partitioning observed in the host-choice tests and the wild.

The greater success rate for adult male isopods versus mancas was due to a number of factors. First, larger isopods can swim faster, giving them more opportunities for attachment. In addition, adults probably were less susceptible to avoidance responses from the host. Attempts of hosts to dislodge isopod parasites were described as "leaping and thrashing motions" by striped bass (Sandifer and Kerby 1983), rubbing on objects (Waugh et al. 1989), "yawning motions" of sanddabs (Robinson 1982b), and vigorous shaking in the present study. Robinson (1982b) found adult L. vulgaris took a more direct route to the gill cavity than mancas, which made a zig-zag pattern.

There is practical use for the knowledge that the two isopods partition host resources between benthic and pelagic fishes. Undigested isopods have been found in feces of harbor seals (Dion Oxman, pers. comm.). Since the isopods most likely came from fishes eaten by the seal, this provides preliminary evidence that the seal was piscivorous. Furthermore, if the species of isopod can be determined, one can get an idea of whether the seal was feeding on benthic or pelagic fishes. This may be useful for studies on any piscivorous animal lacking enzymes that digest chiton.

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Table 1. Summary of field data from California, Washington, and Gulf of California collection sites: numbers of fish species (sp) infested (inf) by Lironeca californica (LC) and Lironeca vulgaris (LV) and numbers of fishes infested by the two parasite species. prev = prevalence (%), N = number.

		FISH SPECIES				NUMBER OF FISHES				
	host type	observed	inf by LC	inf by LV	inf by either	observed	inf by LC N(PREV)	inf by LV N(PREV)	inf by either N(PREV)	total parasites N(intensity)
CALIFORNIA	benthic	26	10	3	14	2345	323(13.8)	4(0.17)	327(13.9)	438(1.34)
	pelagic	56	5	14	16	2754	11(0.4)	70(2.5)	81(2.9)	102(1.26)
	total	82	15	17	30	5099	334(6.6)	74(1.5)	408(8.0)	548(1.34)
WASHINGTON	pelagic	4	1	0	1	493	0.4(2)	0	0.4(2)	2(1)
	benthic	6	0	0	0	268	0	0	0	0
	total	10	1	0		761	0.26(2)	0	0.26(2)	2(1)
GULF OF CALIFORNIA	pelagic	8	0	0	0	72	0	0	0	0
	benthic	4	0	0	0	153	0	0	0	0
	total	12	0	0	0	225	0	0	0	0

Table 2. Fishes collected in California infested with Lironeca. HAB = habitat, pelagic (P) or benthic (B), N = number of fishes examined, PREV = prevalence (% infested), INT = intensity (avg. number of parasites per infested host), LC = number infested by L. californica, LV = number infested by L. vulgaris. * indicates new host record.

HOST	SCIENTIFIC NAME	HAB	N	PREV	INT	LC	LV
topsmelt	Atherinops affinis	P	1463	8.4	1.01	122	0
shiner surfperch	Cymatogaster aggregata	P	276	63.4	1.47	167	0
CA killifish*	Fundulus parvipinnis	P	151	6.0	1.50	10	0
mullet*	Mugil cephalus	P	92	4.3	1.00	4	0
tubesnout*	Aulorhynchus flavidus	P	58	8.6	1.00	5	0
barred surfperch	Amphistichus argenteus	P	51	11.8	1.67	6	0
black surfperch*	Embiotoca jacksoni	P	47	4.2	1.00	0	2
white surfperch	Phanerodon furcatus	P	32	6.2	1.00	2	0
striped bass*	Morone saxatilis	P	15	33.3	1.6	7	1
pile surfperch	Damalichthys vacca	P	12	8.3	1.00	0	1
American shad*	Alosa sapidissima	P	13	15.4	1.00	2	0
blue rockfish	Sebastes mystinus	P	8	12.5	1.00	?	?
kelp surfperch*	Brachyistius frenatus	P	4	25.0	1.00	1	0
PELAGIC TOTAL			2225	14.7	1.2	326	4
staghorn sculpin	Leptocottus armatus	B	444	5.9	1.23	7	14
English sole	Parophrys vetulus	B	205	1.0	1.00	0	2
speckled sanddab	Citharichthys stigmaeus	B	161	8.7	1.29	1	13
CA tonguefish*	Symphurus atricauda	B	159	1.3	1.00	0	2
Pacific sanddab	Citharichthys sordidus	B	116	6.0	1.57	0	7
cabezon	Scorpaenichthys marm.	B	54	7.4	1.00	0	4
lizardfish	Synodus lucioceps	B	54	18.5	1.3	0	10
CA halibut*	Paralichthys californicus	B	33	3.0	1.00	0	1
arrow goby	Clevelandia ios	B	27	7.4	1.00	1	1
diamond turbot*	Hypsopsetta guttulata	B	13	7.7	1.0	0	1
sand sole*	Psettichthys melanostict.	B	10	100	2.0	0	10
buffalo sculpin*	Enophrys bison	B	10	10	1.00	1	0
starry flounder	Platichthys stellatus	B	5	20	2.00	0	1
shadow goby*	Quietula y-cauda	B	3	33.3	1.00	1	0
lingcod	Ophiodon elongatus	B	2	100	1.5	0	2
painted greenling*	Oxylebius pictus	B	2	100	2.00	0	2
BENTHIC TOTAL			1298	6.2	1.41	11	70

Table 3. Padilla Bay, Washington fishes examined for Lironeca. Shiner surfperch was the only species infested, with a prevalence of 0.4 % by L. californica. N = number of fishes examined, P = pelagic, B = benthic.

COMMON NAME	SCIENTIFIC NAME	HABITAT	N
shiner surfperch	Cymatogaster aggregata	P	455
threespine stickleback	Gasterosteus aculeatus	P	25
pipefish	Syngnathus leptorhynchus	P	12
tubesnout	Aulorhynchus flavidus	P	1
staghorn sculpin	Leptocottus armatus	B	98
tidepool sculpin	Oligocottus maculosus	B	79
saddleback gunnel	Pholis ornata	B	54
starry flounder	Platichthys stellatus	B	19
snake prickleback	Lumpenus sagitta	B	17
penpoint gunnel	Apodichthys flavidus	B	1
TOTAL			761

Table 4. Gulf of California fishes examined for Lironeca, April 1992. None were infested. N = number of fish examined, P = pelagic, B = benthic.

COMMON NAME	SCIENTIFIC NAME	HABITAT	N
unknown grunt	Haemulidae	P	59
Pacific porgy	*Calamus brachysomus*	P	5
mojarra	Gerreidae	P	3
mullet	*Mugil* sp.	P	1
Mexican hogfish	*Bodianus diplotaenia*	P	1
barracuda	*Sphyraena lucasana*	P	1
graybar grunt	*Haemulon sexfasciatum*	P	1
zebra perch	*Hermosilla azurea*	P	1
leopard grouper	*Mycteroperca rosacea*	P	1
Panama graysby	*Epinephalus panamensis*	B	108
spotted sand bass	*Paralabrax maculatofasciatus*	B	43
unknown blenny	Blennidae	B	1
TOTAL			225

Table 5. Isopods in the Los Angeles County Museum collection with host records. N = number examined, HAB = habitat, P = pelagic, B = benthic.

COMMON NAME	SCIENTIFIC NAME	HAB	N	ISOPOD SPECIES
shiner surfperch	Cymatogaster aggregata	P	2	L. californica
salmon	Onchorhyncus sp.	P	1	L. vulgaris
black surfperch	Embiotoca jacksoni	P	1	L. vulgaris
mullet	Mugil sp.	P	1	L. californica
Pacific sanddab	Citharichthys sordidus	B	8	L. vulgaris
lingcod	Ophiodon elongatus	B	7	L. vulgaris
speckled sanddab	Citharichthys stigmaeus	B	3	L. vulgaris
lizardfish	Ophiodon elongatus	B	2	L. vulgaris
rockfish	Sebastes sp.	B	1	L. vulgaris
arrow goby	Clevelandia ios	B	1	L. californica
TOTAL			27	

Table 6. Average number (and one standard deviation) of isopods in dark and light half of aquarium two minutes after release. * = statistically significant.

LIRONECA VULGARIS

EXPERIMENT	LIGHT	DARK	SIGNIF. LEVEL	X^2
1	30 (0)	0 (0)	*P < 0.001	30.0
2	29 (0)	1 (0)	*P < 0.001	26.1
3	28	2	*P < 0.001	22.5

LIRONECA CALIFORNICA

EXPERIMENT	LIGHT	DARK	SIGNIF. LEVEL	X^2
1	18.3(6.5)	11.7(6.5)	0.10 < P < 0.25	1.4
2	24(1)	6(1)	*0.001 < P < 0.005	10.8
3	22.3(5.1)	7.7(5.1)	0.005 < P < 01	7.1

Table 7. Average number of Lironeca found in each half of the cylinder after ten minute acclimation in darkness.

DARK TREATMENT

EXPERIMENT	AVG NO.(SD) OF L. VULGARIS IN EACH HALF OF THE CYLINDER UPPER	LOWER	X^2
1	4.67(0.58)	15.33(0.58)	$0.01 < P < 0.025$
2	13.67(4.9)	6.33(4.9)	$0.10 < P < 0.25$
3	11.67(2.3)	8.33(2.3)	$0.25 < P < 0.50$

EXPERIMENT	AVG. NO.(SD) OF L. CALIFORNICA IN EACH HALF OF THE CYLINDER UPPER	LOWER	X^2
1	20(0)	0(0)	*$P < 0.001$
2	20(0)	0(0)	*$P < 0.001$
3	60	0	*$P < 0.001$

Table 8. Average number of Lironeca in each half of the cylinder during experiment (EXP) in sunlight. Counts were made every thirty seconds for five minutes. Three treatments were used: cylinder fully exposed to sunlight, lower half darkened, upper half darkened.

SUNLIGHT

LIRONECA VULGARIS

TREATMENT	EXP	AVG NUMBER (SD) IN EACH HALF OF CYLINDER UPPER	LOWER	X^2
both halves	1	0(0)	20(0)	*P < 0.001
exposed	2	0.45(0.52)	19.55(0.52)	*P < 0.001
lower half	1	0(0)	20(0)	*P < 0.001
darkened	2	1.8(0.75)	18.2(0.75)	*P < 0.001
upper half	1	0(0)	20(0)	*P < 0.001
darkened	2	0.27(0.47)	19.73(0.47)	*P < 0.001

LIRONECA CALIFORNICA

TREATMENT	EXP	AVG NUMBER (SD) IN EACH HALF OF CYLINDER UPPER	LOWER	X^2
both halves	1	1.64(0.67)	18.36(0.67)	*P < 0.001
exposed	2	1.91(0.70)	18.09(0.70)	*P < 0.001
	3	1.64(0.92)	18.36(0.92)	*P < 0.001
lower half	1	10.36(2.33)	9.64(2.33)	0.75 < P < 0.90
darkened	2	9.73(2.94)	10.27(2.94)	0.90 < P < 0.95
	3	12.9(1.22)	7.09(1.22)	0.10 < P < 0.25
upper half	1	0(0)	20(0)	*P < 0.001
darkened	2	0(0)	20(0)	*P < 0.001
	3	1.54(0.52)	18.45(0.52)	*P < 0.001

Figure 1. Geographic ranges of Lironeca californica and Lironeca vulgaris. Collection sites of fishes examined for isopod parasites of the genus Lironeca. Method of capture at each site is shown: BS = beach seine, OT = otter trawl, HL = hook and line, PS = pole spear.

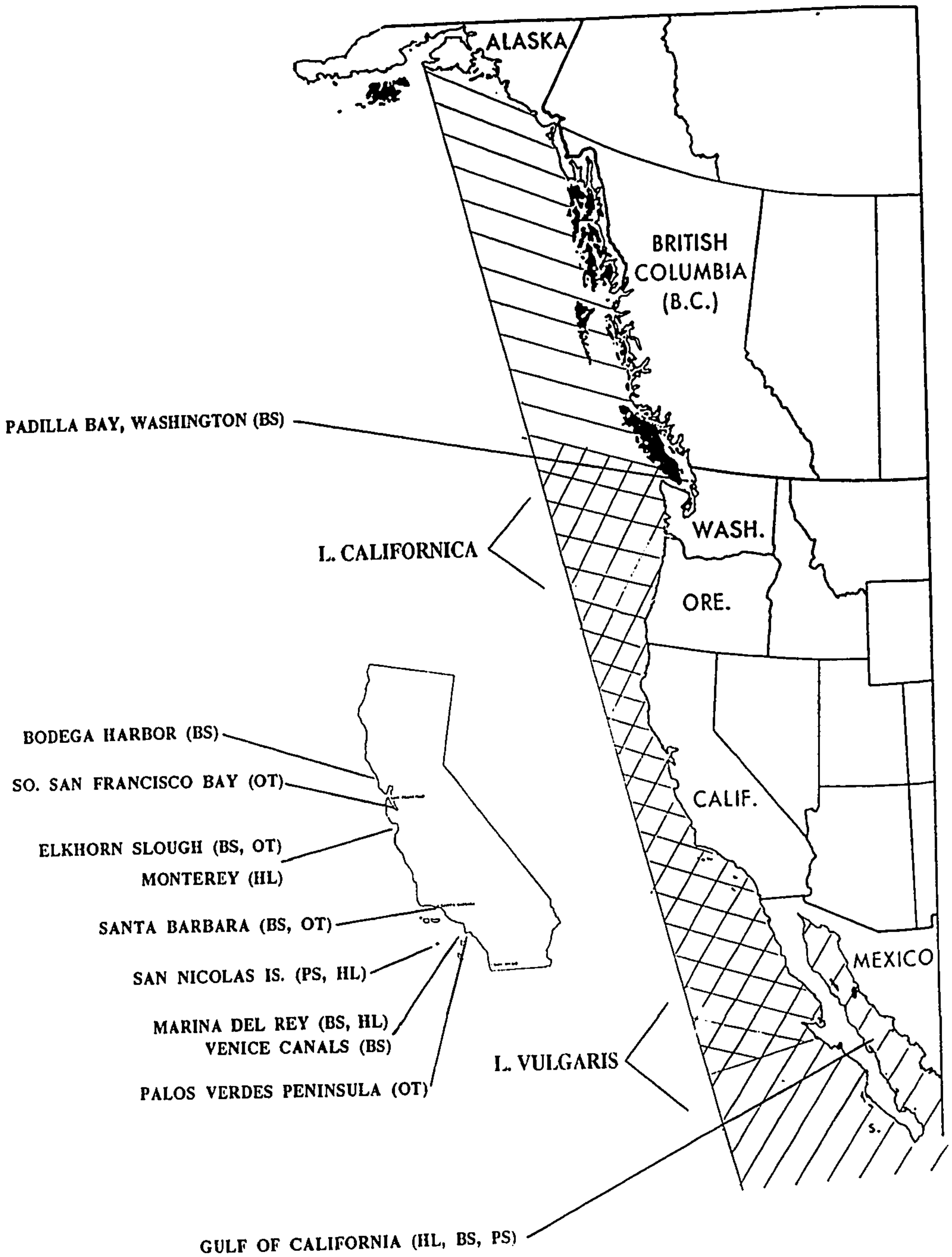

ALASKA
BRITISH COLUMBIA (B.C.)
PADILLA BAY, WASHINGTON (BS)
WASH.
L. CALIFORNICA
ORE.
BODEGA HARBOR (BS)
SO. SAN FRANCISCO BAY (OT)
ELKHORN SLOUGH (BS, OT)
MONTEREY (HL)
CALIF.
SANTA BARBARA (BS, OT)
SAN NICOLAS IS. (PS, HL)
MEXICO
MARINA DEL REY (BS, HL)
VENICE CANALS (BS)
L. VULGARIS
PALOS VERDES PENINSULA (OT)
GULF OF CALIFORNIA (HL, BS, PS)

Figure 2A. Prevalence of isopod parasites on pelagic host fishes collected in California (numbers of fishes examined at tops of bars). CY = shiner surfperch, SB = striped bass, LS = kelp surfperch, AS = american shad, BR = blue rockfish, BA = barred surfperch, WE = walleye surfperch, TU = tubesnout, TS = topsmelt, PP = pile surfperch, W = white surfperch, CK = California killifish, M = mullet, BL = black surfperch, TOT = total.

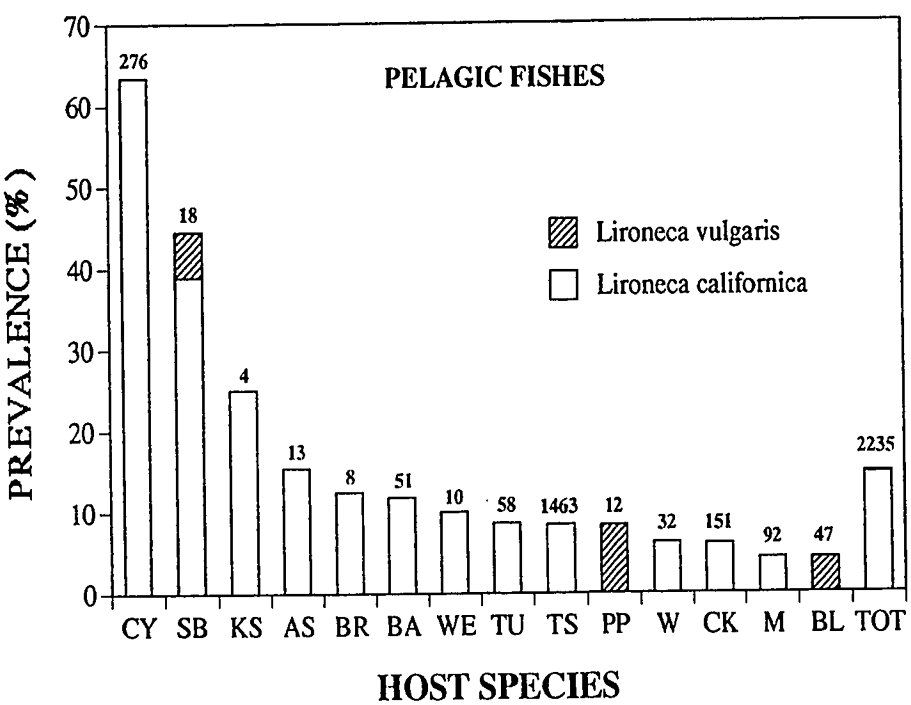

PELAGIC FISHES
PREVALENCE (%)
HOST SPECIES
Lironeca vulgaris
Lironeca californica
0
10
20
30
40
50
60
70
276
18
4
13
8
51
10
58
1463
12
32
151
92
47
2235
CY SB KS AS BR BA WE TU TS PP W CK M BL TOT

Figure 2B. Prevalence of isopod parasites on benthic host fishes collected in California (numbers of fishes examined at tops of bars). SS = sand sole, LI = lingcod, PG = painted greenling, SG = shadow goby, SF = starry flounder, LZ = lizardfish, BS = buffalo sculpin, SD = speckled sanddab, DT = diamond turbot, CZ = cabezon, AG = arrow goby, PS = pacific sanddab, LA = staghorn sculpin, CH = California halibut, TF = tonguefish, ES = English sole, TOT = total.

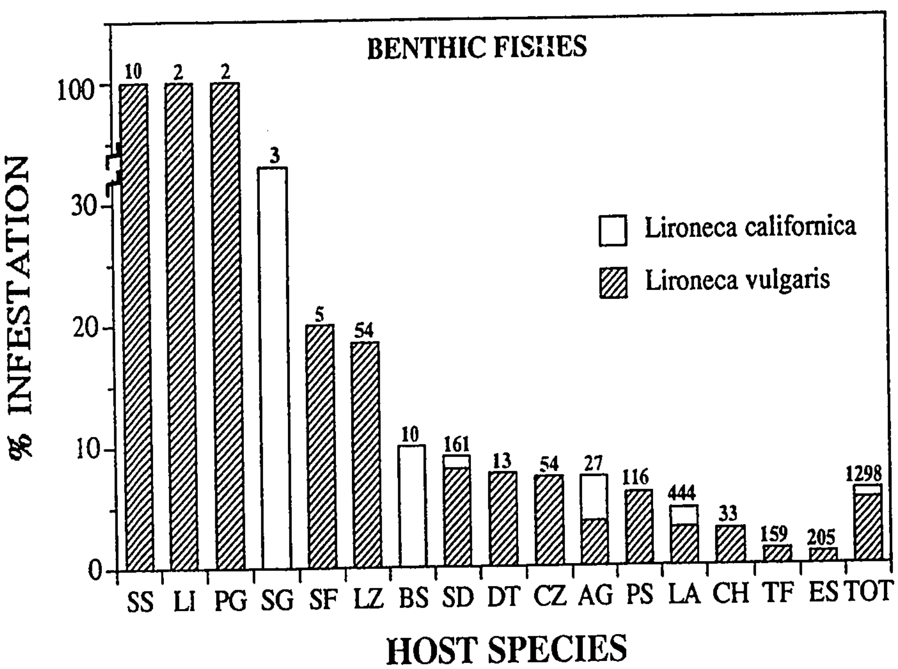

BENTHIC FISHES
Lironeca californica
Lironeca vulgaris
% INFESTATION
HOST SPECIES
SS LI PG SG SF LZ BS SD DT CZ AG PS LA CH TF ES TOT
10 2 2 3 5 54 10 161 13 54 27 116 444 33 159 205 1298
0 10 20 30 100

Figure 3. Average prevalence of Lironeca californica and L. vulgaris (adult male and manca stage) on fishes (shiner surfperch, staghorn sculpin) in an aquarium. Note: an arcsine transformation was performed on the data. Error bars are one standard deviation. Numbers of fish used are shown at the top of the bars. LV = Lironeca vulgaris, LC = Lironeca californica, N = number of isopods.

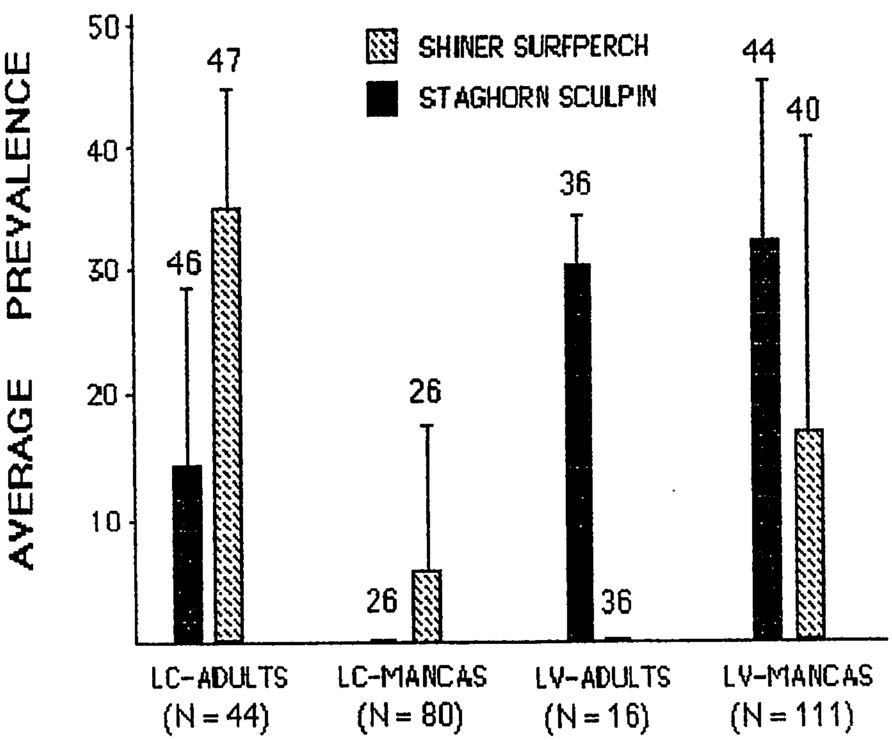
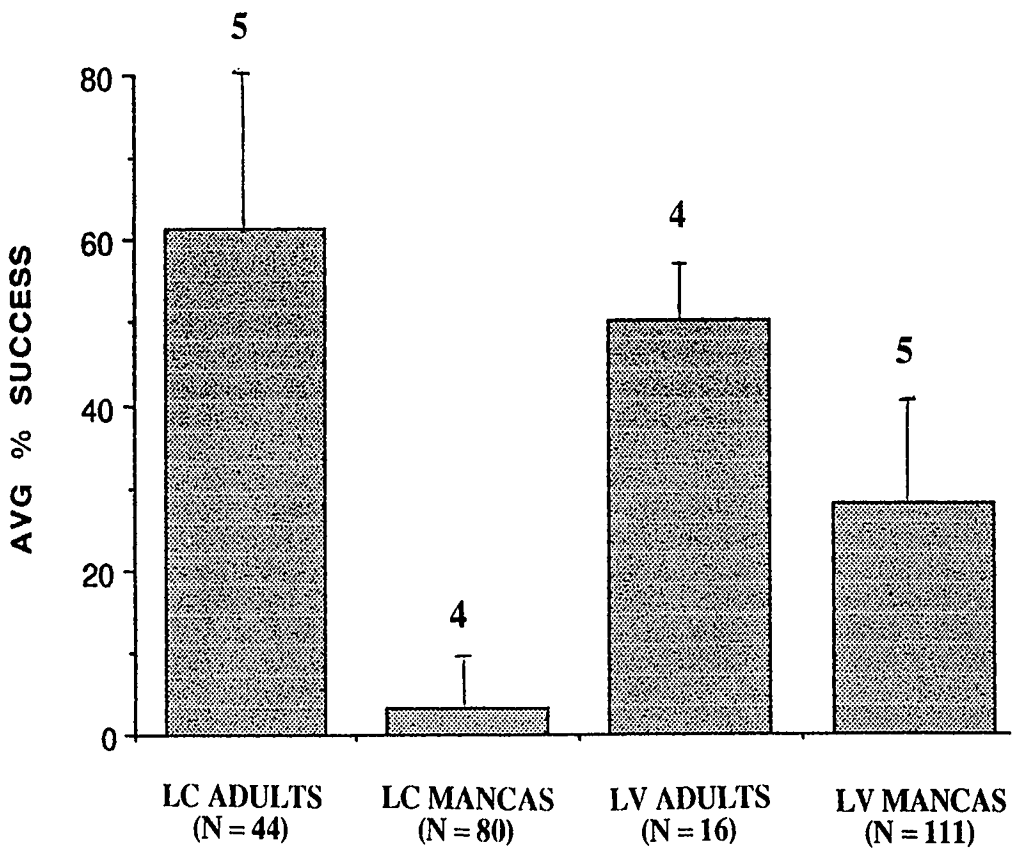

AVERAGE PREVALENCE
50
40
30
20
10
SHINER SURFPERCH
STAGHORN SCULPIN
47
46
26
26
36
36
44
40
LC-ADULTS (N = 44)
LC-MANCAS (N = 80)
LV-ADULTS (N = 16)
LV-MANCAS (N = 111)

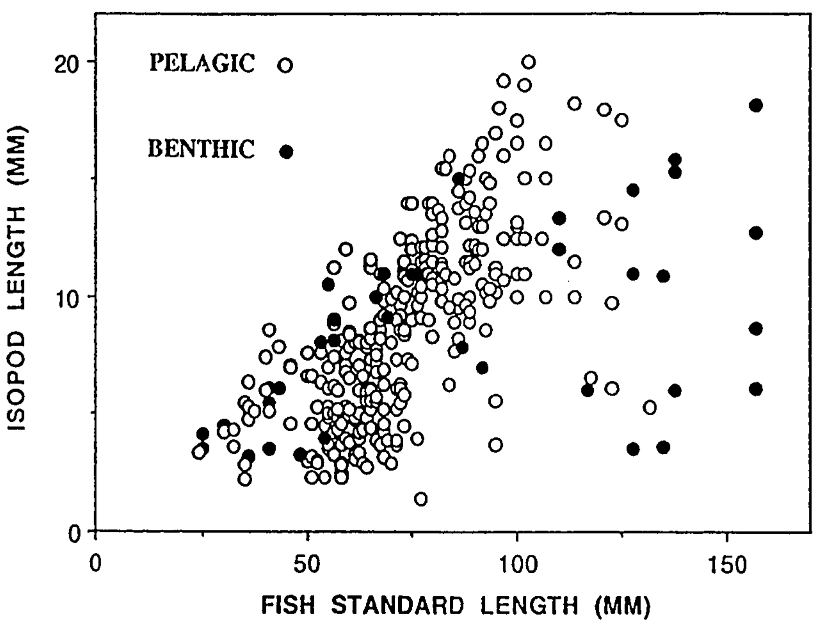
Figure 4. Average percent success of Lironeca californica and L. vulgaris (adult male and manca stage) on fishes (shiner surfperch, staghorn sculpin) in an aquarium. Number of experiments performed are shown at the top of the bars. Note: an arcsine transformation was performed on the data. Error bars are one standard deviation.



AVG % SUCCESS
80
60
40
20
0
5
4
4
5
LC ADULTS (N = 44)
LC MANCAS (N = 80)
LV ADULTS (N = 16)
LV MANCAS (N = 111)

Figure 5. Length of isopod versus standard length of infested fish host. open circles = fishes infested with Lironeca californica, dark circles = fishes infested with Lironeca vulgaris.

LENGTH OF ISOPOD VS STANDARD LENGTH OF FISH



Appendix 1a: List of all known hosts for Lironeca vulgaris. Prevalence (PREV) given when available. LACM = Los Angeles County Museum.

HOST	N	PREV(%)	HAB	GEOG. LOC.	SOURCE
Cetengraulis mysticetus			P	no. Gulf of CA	Brusca 1981
Onchorhynchus sp.			P	Coos Bay, OR	LACM
Synodus lucioceps	54	18.5	B	CA	this study
"				CA	LACM
"				so. CA	Turner et al. 1969
"				CA	Brusca 1978
Morone saxatilis	15	1	P	so. San Fran. Bay	this study
Paralabrax nebulifer				so. CA	Turner et al. 1969
Serranus aequidens				Gulf of Cal	Brusca 1981
Damalichthys vacca	12	8.3	P	CA	this study
"				so. CA	Turner et al. 1969
Cymatogaster aggregata			P	so. CA	Love and Moser 1983
Embiotoca jacksoni	47	4.2	P	CA	this study
"				CA	Brusca 1978
Hyperprosopon argenteum			P	CA	Richardson 1905
Phanerodon furcatus			P	so. CA	Turner et al. 1969
Micrometrus minimus			P		Iverson 1974
Amphistichus rhodoterus			P		Brusca 1978
Neoclinus blanchardi			B	so. CA	Turner et al. 1969
Clevelandia ios	27	4	B	CA	this study
Scorpaena guttata			B	so. CA	Turner et al. 1969
Sebastes chrysomelas			B	so. CA	Love and Moser 1983
Sebastes mystinus			P	so. CA	Love and Moser 1983
Sebastes serranoides			P	so. CA	Turner et al. 1969
Anoplopoma fimbria			B	so. CA	Love and Moser 1983
Ophiodon elongatus	2	100	B	Elkhorn Slough, CA	this study
"				CA	Richardson 1905
"				so. CA	Turner et al. 1969
"					Brusca 1978
Oxylebius pictus	2	100	B	San Nicolas Is.	this study
Leptocottus armatus	444	3.2	B	central CA	this study
"				OR	Love and Moser 1983
Scorpaenichthys marmoratus	54	7.4	B	Elkhorn Slough, CA	this study
"				central CA	Love and Moser 1983
Trachurus symmetricus			P	so. CA	Turner et al. 1969
Paralichthys californicus	33	3.0	B	central CA	this study
"				Anaheim Bay, CA	Ho 1975
Citharichthys stigmaeus	161	1.3	B	Elkhorn Slough, CA	this study
"	1119	57		Santa Barbara, CA	Robinson 1982
"		9.8		Monterey Bay, CA	Keusink 1979
"				Seal Beach, CA	LACM
"				Redondo Bch, CA	
"					Brusca 1978

Citharichthys sordidus	116	6.0	B	this study	this study
"		22.8		Monterey Bay, CA	Keusink 1979
"	41	97.6		Santa Barbara, CA	Robinson 1982
"					Brusca 1978
"				so. CA	LACM
Pleuronichthys vetulus	205	1.0	B	central CA	this study
"		14.9		Monterey Bay, CA	Keusink 1979
"	1619	0.06		OR	Olson 1978
Psettichthys melanostictus	10	100	B	Monterey Bay, CA	this study
"		57.1		Monterey Bay, CA	Keusink 1979
"				no. CA	Crane 1972
Hippoglossina stomata			B	Newport, CA	Brusca 1981
Hypsopsetta guttulata	13	7.7	B	so. San Fran. Bay	this study
Platichthys stellatus	5	20	B	Elkhorn Slough, CA	this study
"				Monterey Bay, CA	Orcutt 1950

Appendix 1b. List of all known hosts for Lironeca californica. Prevalence (PREV) given when available.

HOST	N	PREV(%)	HAB	GEOG. LOC.	SOURCE
Clupea pallasi			P	San Francisco Bay	Brusca 1981
Alosa sapidissima	13	15.4	P	San Francisco Bay	this study
Engraulis mordax			P	San Francisco Bay	Brusca 1981
Hypomesus pretiosus			P	WA	Hatch 1947
Fundulus parvipinnis	151	6.0	P	Venice canals, CA	this study
"				CA	Keys 1928
Lucania parva			P	San Fran. Bay	Brusca 1981
Atherinops affinis	1463	8.4	P	CA	this study
"	230	3.5		Bodega Harbor, CA	Waugh et al. 1989
"				CA	Brusca 1981
Leuresthes tenuis			P	San Diego, CA	Olson 1972
Gasterosteus aculeatus			P	San Francisco Bay	Brusca 1981
Aulorhynchus flavidus	58	8.6	P	Bodega Harbor, CA	this study
Morone saxatilis	18		P	central CA	this study
Cymatogaster aggregata	276	63.4	P	central CA	this study
"	455	0.4		Padilla Bay, WA	this study
"	191	28.8		Bodega Harbor, CA	Waugh et al. 1989
"				Departure Bay, B.C.	Fee 1926
"	138	8.0		B.C.	Arai 1969
"				CA	Richardson 1905
Hyperprosopon argenteum	10	10	P	central CA	this study
Phanerodon furcatus	32	6.2	P	central CA	this study
Micrometrus minimus			P	Baja Cal.	Iverson 1974
Brachyistius frenatus	4	25	P	Bodega Harbor, CA	this study
Mugil cephalus	92	4.3	P	so. CA	this study
"				Baja Cal.	LACM
Apodichthys flavidus	2	50	B	Bodega Harbor, CA	Waugh et al. 1989
Clevelandia ios	27	3.7	B	CA	this study
Quietula y-cauda	3	33.3	B	Venice canals, CA	this study
Enophrys bison	10	10	B	Bodega Harbor, CA	this study
Leptocottus armatus	444	1.6	B	central CA	this study
Citharichthys stigmaeus	161	0.6	B	central CA	this study

Appendix 2. Fishes not infested with Lironeca. Collection sites are shown as follows: PAD = Padilla Bay, BH = Bodega Harbor, SFB = south San Francisco Bay, EHS = Elkhorn Slough, SNI = San Nicolas Island, KH = King Harbor in Redondo Beach, PV = Palos Verdes Peninsula, GC = Gulf of California. Methods of capture are shown as follows: OT = otter trawl, BS = beach seine, HL = hook and line, PS = pole spear.

COMMON NAME	SCIENTIFIC NAME	N	LOCATION	METHOD
ratfish	Hydrolagus colliei	1	PV	OT
threadfin shad	Dorosoma petenense	6	SFB	OT
Pacific argentine	Argentina sialis	2	PV	OT
plainfin midshipman	Porichthys notatus	229	PV, SFB	OT
specklefin midshipman	Porichthys myriaster	1	PV	OT
spotted cusk-eel	Chilara taylori	4	PV, EHS	OT
blackbelly eelpout	Lycodes pacifica	126	PV	OT
jacksmelt	Atherinopsis calif.	1	SFB	OT
three-spine stickleback	Gasterosteus aculeatus	26	PAD, EHS	BS
California scorpionfish	Scorpaena guttata	14	PV	OT
rockfishes	Sebastes sp.	90	PV, EHS, SNI	OT,HL,PS
longspine combfish	Zaniolepis latipinnis	68	PV	OT
shortspine combfish	Zaniolepis frenata	6	PV	OT
kelp greenling	Hexagrammos decagram.	2	EHS, BH	OT, BS
yellowchin sculpin	Icelinus quadriseriatus	107	PV	OT
smoothhead sculpin	Artedius lateralis	4	BH	BS
bonyhead sculpin	Artedius notospilotus	3	SFB	OT
fluffy sculpin	Oligocottus snyderi	2	BH	BS
tidepool sculpin	Oligocottus maculosus	79	PAD	BS
sharpnose sculpin	Clinocottus acuticeps	1	BH	BS
blackedge poacher	Xeneretmus latifrons	3	PV	OT
pygmy poacher	Odontopyxis trispinosa	1	PV	OT
showy snailfish	Liparis pulchellus	2	SFB	OT
snailfish	Liparis sp.	2	PV, EHS	OT
spotted sandbass	Paralabrax maculatofas.	43	GC	HL
barred sandbass	Paralabrax nebulifer	1	KH	HL
leopard grouper	Mycteroperca rosacea	1	GC	PS
Panama graysby	Epinephelus panamensis	108	GC	HL
mojarra	Gerreidae	3	GC	PS
Pacific porgy	Calamus brachysomus	5	GC	PS
graybar grunt	Haemulon sexfasciatum	1	GC	PS
grunt	Haemulidae	59	GC	BS
white croaker	Genyonemus lineatus	20	SFB, PV	OT
opaleye	Girella nigricans	23	KH	HL
zebraperch	Hermosilla azurea	1	GC	PS
dwarf surfperch	Micrometrus minimus	10	EHS,SFB,BH	BS, OT
striped surfperch	Embiotoca lateralis	1	BH	BS
pink surfperch	Zalembius rosaceus	27	PV	OT
rainbow surfperch	Hypsurus caryi	21	EHS, PV	OT, BS

blacksmith	Chromis punctipinnis	3	SNI	PS
barracuda	Sphyraena lucasana	1	GC	HL
Mexican hogfish	Bodianus diplotaenia	1	GC	PS
senorita	Oxyjulis californica	3	SNI	PS
blenny	Blennidae	1	GC	BS
one-spot fringehead	Neoclinus uninotatus	2	EHS	OT
kelpfish	Gibbonsia sp.	16	EHS, BH	BS, OT
snake prickleback	Lumpenus sagitta	17	PAD	BS
bluebarred prcklebck	Plectobranchus evides	1	PV	OT
rockweed gunnel	Xererpes fucorum	2	BH	BS
penpoint gunnel	Apodichthys flavidus	6	BH, PAD	BS
saddleback gunnel	Pholis ornata	54	PAD	BS
chameleon goby	Tridentiger trigonocep.	45	SFB	OT
yellowfin goby	Acanthogobius flavim.	6	SFB, EHS	OT, BS
bay goby	Lepidogobius lepidus	9	SFB, PV	OT
bigmouth sole	Hippoglossina stomata	18	PV	OT
slender sole	Lyopsetta exilis	323	PV	OT
Dover sole	Microstomus pacificus	242	PV	OT
longfin sanddab	Citharichthys xanthostig.	45	PV	OT
gulf sanddab	Citharichthys fragilis	13	PV	OT
fantail sole	Xystreurys liolepis	10	PV	OT
hornyhead turbot	Pleuronichthys verticalis	33	PV	OT
c-o turbot	Pleuronichthys coenosus	4	PV	OT
spotted turbot	Pleuronichthys ritteri	1	PV	OT
curlfin turbot	Pleuronichthys decur.	1	PV	OT