Substrate Selection in Caprellid Amphipods of Southern California, with Emphasis on *Caprella californica* Stimpson and *Caprella equilibra* Say (Amphipoda)[1]

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ABSTRACT: The substrate affinities of Southern Californian caprellids were studied with principal interest in two species, *Caprella californica* and *Caprella equilibra.* Experiments designed to test the selectivity for three substrates at Long Beach Marina showed *C. californica* to "prefer" the bryozoan *Bugula neritina* over the algae *Polysiphonia pacifica* and *Ulva lobata. Caprella equilibra* showed no preference between *Bugula neritina* and *Polysiphonia pacifica,* but selected these substrates over *Ulva lobata.* Selectivity of *Caprella californica* was attributed to its cryptic adaptation.

THE CAPRELLIDEA CONSTITUTE a highly specialized suborder of amphipoda. Previous published works have dealt primarily in systematics and very little information is available concerning caprellid ecology.

Caprellids are most commonly found clinging to some living substratum. Among those most frequently cited in the literature are: algae, sponges, hydroids, and bryozoans. According to Mayer (1882, pp. 170–171) there are some caprellids which do not live on other organisms. *Pseudolirius kroyeri* (Halleri), for example, lives exclusively on sand or muddy sand. This species cannot clasp large objects since the hind legs do not possess a spine fold for the claw. Another species, *Pariambus minutus* (Mayer), is known to live, at least for the most part, on sand. Mayer does agree, however, that the vast majority of caprellids do prefer a living substrate. *Caprella equilibra* was reported by Mayer from the tunicate *Ciona intestinalis* (L), where he observed it sitting near the incurrent opening where it could utilize the water current and the outer muddy surface for feeding. Patton (1968, p. 119–120) described the caprellid, *Caprella grahami* Wigley and Shave, as a commensal on the starfish *Asterias forbesi* (Desor.).

The apparent dependence of most caprellids on other living organisms for support and protection makes this relationship an obvious place to begin an ecological investigation. The primary importance of this study is to establish whether substrate affinities exist among certain associated species of caprellids and to evaluate factors which could influence selectivity of these animals.

During the summer of 1961 at the Virginia Institute of Marine Science, I obtained some evidence to support the thesis that substrate affinities do exist in some species. The data collected from the various habitats showed the most common caprellid of the lower York River, during the months of June and July, to be *Caprella geometrica* Say, which was found in abundance on nearly all of the substrates examined. This species was particularly dominant on hydroids, bryozoans, and sponges. *Paracaprella tenuis* Mayer was the species next in abundance during these 2 months, being dominant on bryozoa. The third species was *Caprella equilibra,* which was not present on any substrate examined prior to early August, at which time it replaced *C. geometrica* as a dominant on sponges. *Paracaprella tenuis* seemed to show an affinity for the brown bryozoan *Victorella pavida* Kent. This species also occurred in large numbers on the sponge, *Haliclona permollis* Bowerbank, as

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it began to grow over the bryozoan in late July. The sample number was insufficient for statistical verification. The results did encourage further investigations into the caprellid-substrate relationships.

Locomotion should be considered in studies of substrate selection since the ability of an organism to move from one place to another might influence the results of experiments. The assumption is made that an individual is able to move from one substrate to another, selecting the one which is most suitable.

Caprellids move over their substrate with ease. They are also capable of swimming in an anteriorly directed manner by quick, jerky movements involving sudden ventral flexing and straightening of the body.

When placed in an aquarium, the caprellids often appear to have no direction to their swimming; they sometimes swim to the top of the water where they become trapped by the surface tension. In their natural habitat, however, caprellids swim with a sense of direction. When the bryozoan *Bugula neritina* (L) was detached from the dock float at Long Beach Marina so that it began to sink, the caprellids swam upward from the *Bugula* to the other bryozoan colonies attached to the floats.

Observations of caprellids kept in the laboratory show that they move from substrate to substrate, stopping for varying lengths of time. Their ability to swim and to move readily over the substrate eliminated locomotion as a problem in substrate selection experiments.

Feeding studies by Keith (1969) showed that caprellids in captivity feed principally on detritus and diatoms which are associated with the substrates. Food was removed from the substrates prior to each experiment to eliminate it as a possible factor influencing selection.

METHODS AND MATERIALS

Occurrences and Substrates

Samples were collected along the Southern California coast during April 1966 from Dana Point to San Simeon, and all of the information available from the literature on caprellid occurrences was tabulated in anticipation that certain caprellid-substrate relationships might be detected. Samples from Punta Peñasco, Mexico, and Santa Catalina Island were also utilized. Caprellid abundance was expressed in number per unit volume for each substrate.

Seasonal Effects at Long Beach Marina

Long Beach Marina is situated in Alamitos Bay; it is a small body of water used primarily for recreational purposes by the city of Long Beach. For a further description and history of Alamitos Bay, see Reish and Winter, 1954, pp. 106–107.

To determine seasonal effects on the total caprellid population and their abundance on various substrates, samples were taken from November 1965 through October 1967 from the sides of the floats which support the wooden boat docks. The floats are constructed of reinforced molded fiberglass plastic (Reish, 1964, p. 126). A total of 144 samples was taken at this station from April 1966 to October 1967.

Twenty-five samples were taken during each sampling period and preserved separately in 10 percent formalin. The caprellids were removed, counted, and stored in 70 percent alcohol. It was found that the most efficient means of removing the caprellids was to shake the preserved sample in a half-gallon jar filled about one-third with water, and then quickly removing the substrate and pouring the water through a screen with a pore size of .0070 mm. This process was repeated until caprellids could no longer be obtained in this manner. The substrate was examined under a dissecting microscope and any remaining caprellids removed. Caprellid abundance was expressed as number per cubic centimeter of substrate. During each sampling period the water temperature and relative substrate abundance were noted.

Substrate Selection

LABORATORY STUDIES: Caprellids were collected along with their substrates at Long Beach Marina from July 5 to September 8, 1967 to determine if substrate affinities could be detected. There were three principal substrates on which caprellids could be found in abundance at this location: the bryozoan *Bugula neritina* and the algae *Polysiphonia pacifica* Hollenberg and *Ulva lobata* (Kützing). Samples of these substrates were collected and placed in large plastic bags along with a generous supply of seawater and transported to the laboratory in Styrofoam containers. The caprellids and their respective substrates were kept in separate aquaria. The environmental temperature was determined each time specimens were collected so that the temperature of the experimental tanks could be adjusted to that of the environment.

The experimental tanks consisted of four 3-gallon plastic Aquaflair aquaria partially submerged in a 60-×-7-inch insulated Plexiglas tank designed to hold four of the small aquaria end to end. The large vessel was filled with distilled water and acted as a water bath to maintain the experimental tanks at the desired temperature.

The water bath was cooled by circulating distilled water from a beverage cooler through one-half-inch plastic tubing by means of a model 2U March submersible water pump (Bakus, 1965, pp. 230–231). The tubing made two loops in the bottom of the water bath and occupied almost its entire length. The temperature was controlled by using a thermostat on the cooler and also by adjusting the flow of water through the tubing. The temperature was kept as near as possible to that of the natural environment and ranged from 18° C on July 5 to 22° C on September 16, 1967, when the last selection experiment was completed.

Seawater for the aquaria was obtained from Marineland of the Pacific. Air was supplied to each aquarium by an electric pump. A fiberglass-charcoal filter was employed in conjunction with the air supply to keep the water free of suspended particles. The tanks were cleaned daily by removing fecal pellets and other settled material from the bottom with a syringe. At the end of each trial of an experiment, one-half the volume of each tank was removed and replaced with fresh seawater. The total volume was changed following the end of the second trial in the same tank.

Experiments were conducted to determine: (1) if *Caprella californica* and *Caprella equilibra* would show an affinity for one of the principal substrates, (2) the influence on the selectivity of the caprellids of the substrate from which they were originally obtained, and (3) the influence of one species on the substrate selection of the other.

Approximately equal volumes of each of the three substrates, from which all of the caprellids and food had been removed, were placed in the experimental tanks so that they made contact with one another. Twelve specimens were obtained from *Bugula neritina* and four were placed on each of the three substrates and observed over a 48-hour period. Seven observations, which consisted of counting the number of caprellids on each substrate, were made during this period at approximately equal intervals during the daytime. These numbers were then averaged to give a figure representing one trial. Averaging the number of independent counts helped to reduce the error due to periodic wandering of individuals. The substrates were carefully separated prior to counting to prevent the caprellids from moving from one to the other during the count. After counting, the substrates were again placed in contact. Ten trials were completed during one experiment and a *t*-test was used to determine the significance of the difference in numbers occurring on the three substrates. The entire experiment was repeated with specimens originally obtained from *Polysiphonia pacifica* and again with specimens from *Ulva lobata* to determine if the "parental" substrate was influencing the results of the selection experiments.

Experiments were repeated with *Caprella equilibra*. Because of the scarcity of this species at Long Beach Marina, a separate experiment was not conducted for specimens taken from the three substrates. Compensations were made for the influence of the original substrate by using individuals collected from each of the substrates rather than from a single one for all 10 trials.

To determine the influence of one species on the substrate selection of the other, two individuals of each species were placed on each of the three substrates. The same observational procedure was used as for the previous experiments.

FIELD STUDIES: Ten samples of the three principal substrates, *Bugula neritina, Polysiphonia pacifica,* and *Ulva lobata* were taken from Long Beach Marina during October 1967. The abundance of *Caprella californica* and *C.*

equilibra on each of the substrates was compared statistically and the results correlated with those previously obtained in the laboratory.

Size and Substrate Selection

To determine if any correlation existed between size and substrate, 72 samples were collected during August 1967 at Long Beach Marina. A single caprellid species, *C. californica,* was used. The average size of the individuals was determined for each of 10 samples from the three substrates. Measurements were made from the anterior edge of the cephalon to the tip of the abdomen.

It was decided that a valid average for one sample should consist of approximately 100 individuals or more. If a sample had less than 80 specimens, another sample was combined, and so forth, until the population approached 100. Every specimen 2 mm or larger in length was measured. In most cases, specimens smaller than 2 mm could not be positively identified to species. Ten averages were obtained for each of the three substrates. The number of individuals per sample ranged from 85 to 214. A *t*-test was applied to the data to determine the significance of the difference in mean size of the caprellids living on each of the three substrates.

RESULTS AND DISCUSSION

Occurrence and Substrates

Results obtained from collections along the Southern California coast showed that caprellids occupy a very wide variety of substrates. The principal ones are algae, bryozoans, hydroids, sponges, tunicates, eelgrass, and gorgonians. Although found primarily on living substrates, caprellids are also found in marine muds and in some instances on the frayed ends of ropes hanging into the water from boat docks.

Caprellids are most commonly found intertidally in tide pools, subtidally, and among fouling communities on pier pilings and dock floats. They have been reported, however, from depths of 3,501–4,004 meters (McCain, 1968, p. 91).

Local differences in environmental conditions such as wave action and temperature seem to be the primary factors affecting species distribution. The differences in substrate associations over a fairly extensive area obscure the detection of caprellid-substrate affinities. Results from this study made it evident that, if substrate preferences were to be detected, quantitative studies would have to be conducted within specific communities where environmental parameters were relatively uniform at a given time.

Seasonal Effects at Long Beach Marina

The most dense population of *C. californica* occurred on all substrates during the spring. The lowest number recorded per unit volume occurred during the winter. The total population of *C. equilibra* varied little in 1967, except for a slight increase during the spring.

Temperatures recorded at Long Beach Marina during the 1967 sampling periods ranged from 15.5° C in February to 22° C in August. The abundance of the substrates *Bugula neritina* and *Polysiphonia pacifica* varied considerably. During the winter their densities were very low, but as spring approached they began to increase. *Polysiphonia* reached its peak of abundance in April and *Bugula* reached its peak in July, becoming the dominant growth on the floats. A rapid decline in both of these substrates occurred in August. *Ulva lobata* showed only a slight increase during the winter and began to decrease again as temperatures reached about 19° C in July.

Seasonal variations in the total caprellid population did not appear to be controlled directly by fluctuations in substrate abundance, because the number of caprellids per unit volume of the substrate was low during the winter when the substrate abundance was also low. If substrate availability had been the limiting factor, the number of caprellids per unit volume would have increased as the amount of substrate decreased. Reproduction occurs year around, but the maximum rate in *Caprella californica* must occur in the early spring when an enormous population increase is evident.

Substrate Selection

LABORATORY STUDIES: The results of experiments to determine if *C. californica* exhibits a substrate affinity, and the influence of the substrate from which the caprellid was taken on its selection, are summarized in Tables 1, 2, and 3.

Table 1 indicates a highly significant difference ($P < .001$) between the number of *C. californica* selecting *Bugula* and the other two substrates. There was no significant selection shown, however, between *Polysiphonia* and *Ulva.*

When specimens were taken from *Polysiphonia pacifica* (Table 2), a strong affinity still existed for *Bugula neritina* ($P < .001$). A definite effect of the parental substrate, however, can be seen since a greater percentage of individuals selected *Bugula* when they were originally taken from this substrate ($P < .001$). The increase in numbers of individuals selecting *Polysiphonia pacifica* caused a significant difference in abundance to arise between this substrate and *Ulva lobata* ($P < .001$).

Table 3 shows that *Caprella californica* obtained from *Ulva* also exhibited an affinity for *Bugula* ($P < .001$), but again the influence of the parental substrate can be seen. The number of individuals selecting *Ulva* was greater among specimens originally collected from *Ulva* ($P < .001$).

The results of experiments to show if *Caprella equilibra* exhibited an affinity for any of the three substrates are summarized in Table 4. This table shows that *C. equilibra* did not select *Bugula neritina* over *Polysiphonia pacifica* as did *Caprella californica.* Both of these substrates, however, were favored over *Ulva lobata* ($P < .001$).

TABLE 1

AVERAGE NUMBER OF *Caprella californica* OCCURRING ON EACH SUBSTRATE

SELECTED SUBSTRATES	TRIALS									
	1	2	3	4	5	6	7	8	9	10
Bugula neritina	10	9	11	11	11	11	10	11	10	9
Polysiphonia pacifica	2	2	1	1	0	1	2	1	0	1
Ulva Lobata	0	1	0	0	1	0	0	0	2	2

NOTE: Specimens were obtained from *Bugula neritina.*

TABLE 2

AVERAGE NUMBER OF *Caprella californica* OCCURRING ON EACH SUBSTRATE

SELECTED SUBSTRATES	TRIALS									
	1	2	3	4	5	6	7	8	9	10
Bugula neritina	7	8	9	8	8	7	8	9	9	8
Polysiphonia pacifica	3	4	3	3	3	3	3	3	3	4
Ulva lobata	1	1	0	0	1	1	1	0	0	0

NOTE: Specimens were obtained from *Polysiphonia pacifica.*

TABLE 3

AVERAGE NUMBER OF *Caprella californica* OCCURRING ON EACH SUBSTRATE

SELECTED SUBSTRATES	TRIALS									
	1	2	3	4	5	6	7	8	9	10
Bugula neritina	6	7	7	7	6	7	7	8	7	8
Polysiphonia pacifica	4	1	4	3	3	1	3	1	3	2
Ulva lobata	2	3	1	3	4	4	2	3	2	1

NOTE: Specimens were obtained from *Ulva lobata.*

TABLE 4

AVERAGE NUMBER OF *Caprella equilibra* OCCURRING ON EACH SUBSTRATE

SELECTED SUBSTRATES	TRIALS									
	1	2	3	4	5	6	7	8	9	10
Bugula neritina	6	3	4	3	3	6	6	4	3	6
Polysiphonia pacifica	3	5	5	8	7	5	4	5	8	4
Ulva lobata	2	4	1	1	1	0	1	3	1	1

NOTE: Specimens were obtained from all three substrates.

The same results were obtained when the two species were placed together as when they were separated, indicating that, at least under conditions of the experiment, there was no interaction between the two species which affected their substrate selection. *Caprella californica* selected *Bugula* over *Polysiphonia* ($P < .01$), *Caprella equilibra* showed no selectivity between *Bugula* and *Polysiphonia,* and both species exhibited the least affinity for *Ulva.*

The preference of *Caprella californica* for *Bugula* seems to be best explained by the morphological similarities between this species and *B. neritina.* The coloration and external anatomy of this caprellid species appears quite similar to the bryozoan. The margins of the segments are often darker giving the illusion of thecae. In females of this species, tubercles occur on the dorsal surface of the thoracic somites which also aid in this illusion.

I suspect that, as conditions become crowded, certain members of the *Caprella californica* population move from *Bugula* to other substrates such as *Polysiphonia* and *Ulva.* Because the data from selection experiments show that the parental substrate affects the substrate selection of some individuals, one might infer that caprellids can adapt somewhat to their new substrate, resulting in less affinity for *Bugula.* Adaptation, however, to the degree that the affinity of *Caprella californica* for *Bugula* is reduced, may occur over a relatively long period of time since most of the individuals on *Polysiphonia pacifica* and *Ulva lobata* still select *Bugula neritina.*

Studies on adaptive coloration supported this thesis. *Caprella californica* and *C. equilibra* possess two types of chromatophores: melanophores and guanophores. *C. californica* has at least two means of regulating its color: (1) by cuticular tanning and (2) by physiological color changes brought about by expansion and contraction of chromatophores. *C. equilibra* was not observed to undergo tanning and was unable to adapt completely to dark substrates.

C. californica was able to adapt somewhat to the color of the substrate within about 5 hours, but adaptation did not appear to be complete until after ecdysis. The cuticular coloration appears to be permanent.

Ulva appeared to be the least "attractive" of the three substrates. The broad thallus probably makes it more difficult for caprellids to grasp than that of filamentous forms. It also seems that the caprellids studied could not adapt cryptically as well to *Ulva* as the other two substrates. Many specimens were found, however, on *Ulva* at Long Beach Marina.

Caprella equilibra did not show a preference for *Bugula* or *Polysiphonia.* This result was not surprising since *Caprella equilibra* is not as highly adapted morphologically to *Bugula neritina* as is *Caprella californica.* It should be pointed out, however, that in other areas where different substrates occur, *C. equilibra* might have strong affinities for certain ones. Because of its transparent, slender body, this species appears to be well adapted to hydroids.

These two species did not seem to affect one another's selection of a substrate under laboratory conditions, but it was suspected that, if conditions had been crowded, *C. equilibra* would have been more abundant on *Polysiphonia* than *Bugula.* It is logical to assume that, since *Caprella equilibra* showed no difference in its affinity for these two substrates, it would be the first to leave *Bugula* under crowded conditions.

TABLE 5

NUMBER OF *Caprella californica* AND *Caprella equilibra* PER CUBIC CENTIMETER OF SUBSTRATE AT LONG BEACH MARINA DURING FALL 1967

SUBSTRATES	*C. californica*		*C. equilibra*	
	51	33	33	1
	41	36	1	7
Bugula neritina	57	52	0	1
	44	34	1	2
	28	46	4	18
	17	16	5	15
	13	20	23	8
Polysiphonia pacifica	30	19	3	22
	4	9	12	10
	20	21	9	6
	3	2	0	0
	18	17	0	0
Ulva lobata	21	24	0	0
	7	10	0	0
	13	16	0	0

FIELD STUDIES: Data obtained during the fall of 1967 at Long Beach Marina to evaluate the laboratory findings are summarized in Table 5. Each number represents the abundance of caprellids expressed in number per cubic centimeter of substrate. The results showed that *Caprella californica* was more abundant on *Bugula neritina* than *Polysiphonia pacifica* or *Ulva* ($P <$ .001). No significant difference, however, was found in numbers occurring on *Polysiphonia pacifica* and *Ulva*. *Caprella equilibra* showed no significant preference for *Polysiphonia* or *Bugula,* but was more abundant on either of these substrates than *Ulva*. The conclusions of the field studies agreed with those obtained from the selection experiments.

Effect of Size on Substrate Selection

The average size of all *Caprella californica* occurring in each of 10 samples of the three principal substrates is summarized in Table 6. Each number represents an average of 85 to 214 specimens in terms of ocular micrometer units. These units may be converted to millimeters by dividing by six. A total of 3,756 specimens were measured.

The results show that no significant difference exists in the size of specimens found on *Bugula neritina* and *Polysiphonia pacifica*. A significant difference does exist, however, between the mean size of individuals occurring on *Ulva lobata* and the other substrates, those on *Ulva* being larger ($P < .01$).

CONCLUSIONS

1. California caprellids are able to occupy a wide variety of substrates. The majority of the substrates are living organisms such as hydroids, bryozoans, algae, and sponges; but living substrates are not a requirement.

2. Seasonal studies showed density fluctuations in both the caprellids and their substrates. Substrate abundance showed a positive correlation with the total caprellid density but was not considered to be the principal factor limiting the caprellid population size.

3. The most important substrates for caprellids at Long Beach Marina seemed to be the bryozoan *Bugula neritina* and the algae *Polysiphonia pacifica* and *Ulva lobata.*

4. Two caprellid species, *Caprella californica* and *Caprella equilibra,* occurred at Long Beach Marina. *C. californica* showed a highly significant preference for the bryozoan *Bugula neritina*. *Caprella equilibra* did not demonstrate any selective preference between *Bugula* and *Polysiphonia* but did seem to prefer these to *Ulva.*

5. The substrates from which the caprellids were collected did have some influence on their

TABLE 6

AVERAGE SIZE OF *Caprella californica*

SUBSTRATES	SAMPLES 1	2	3	4	5	6	7	8	9	10
Bugula neritina	34	34	34	34	39	36	33	40	38	32
Polysiphonia pacifica	30	34	36	25	30	38	23	42	36	28
Ulva lobata	35	31	35	49	43	47	45	44	37	40

NOTE: Size given in terms of ocular micrometer units. Units may be converted to millimeters by dividing by six.

substrate selections in the laboratory, but the preference for *Bugula* by *Caprella californica* was apparently so strong that it was evident even in individuals taken from the other substrates.

6. *Ulva lobata* was found to have individuals of larger average size than the other two substrates. This phenomenon was attributed to the nature of the thallus.

7. The affinity which was demonstrated by *Caprella californica* for *Bugula neritina* was attributed to its cryptic adaptations to that substrate.

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LITERATURE CITED

BAKUS, G. J. 1965. A refrigerated seawater system for marine organisms. Turtox News, vol. 43, no. 9, pp. 230–231.

KEITH, D. E. 1969. Aspects of feeding in *Caprella californica* Stimpson and *Caprella equilibra* Say (Amphipoda). Crustaceana, vol. 16, no. 2, pp. 119–124.

MAYER, P. 1882. Die Caprelliden des Golfes von Neapel. Fauna and Flora des Golfes von Neapel, vol. 6, pp. 1–201.

MCCAIN, J. C. 1968. The Caprellidae (Crustacea: Amphipoda) of the Western North Atlantic. Bulletin. United States National Museum, vol. 278, pp. 1–147.

PATTON, W. K. 1968. Feeding habits, behavior and host specificity of *Caprella grahami*, an amphipod commensal with the starfish *Asterias forbesi*. Biological Bulletin, Woods Hole, vol. 134, no. 1, pp. 148–153.

REISH, D. J. 1964. Studies on the *Mytilus edulis* community in Alamitos Bay, California: I. Development and destruction of the community. Veliger, vol. 6, no. 3, pp. 124–131.

REISH, D. J., and H. A. WINTER. 1954. The ecology of Alamitos Bay, California, with special reference to pollution. California Fish and Game, vol. 40, no. 2, pp. 105–121.