

Feeding Mechanisms and Possible Resource Partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, USA

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Abstract

Caprellid amphipods feed by browsing, filter-feeding, predation, scavenging, and scraping. Food acquisition is related to the presence or absence of plumose setae on the second antenna; those species with such setae obtain a significant amount of their diet from filtering and scraping periphyton while those species without such setae usually rely on predation. Two primary predators and 8 primary filter-feeders and scrapers were investigated. Substrates inhabited by the predators did not overlap, but some filter-feeders were found together. Feeding overlap has been decreased among filter-feeders that occur together, as they either feed on different sized particles or they filter at different heights from the substrate. Species filtering the same sized particles at the same heights that were found together utilized alternate feeding mechanisms, e.g. browsing on algal filaments.

Introduction

Although caprellid systematics is partially based on mouthpart morphology, structural variations have been thought to have little effect on feeding mechanisms or behavior (Laubitz and Mills, 1972). This conclusion was partially derived from feeding studies conducted on one genus, *Caprella* (Saunders, 1965; Patton, 1968; Keith, 1969), although McCain (1968) thought that morphological differences might reflect different feeding mechanisms.

McCain (1970) reorganized the suborder Caprellidea and recognized four groups based on mandible morphology, one group consisting of the whale lice (Family Cyamidae). Within the three non-parasitic groups, 6 distinct categories may be obtained by including the presence or absence of plumose setae on the antennae (Table 1). (Although there are 6 morphological combinations possible, no caprellids are known from Category 6.) Family reorganization by Laubitz (1976) does not alter these categories.

Feeding mechanisms of 3 species, one each from Categories 3, 4, and 5, were previously investigated (Caine, 1974), with indications that species in Category 3 are predators, species in Category 4 are filter-feeders and scrapers, and species in Category 5 are without

feeding preferences. These previously examined species are common in the Gulf of Mexico, and the disparate feeding mechanisms may be the result of resource partitioning within the community. Species diversity in the US North Pacific includes numerous sympatric species within Categories 1 through 4 (Laubitz, 1970), and an investigation was undertaken to examine the feeding mechanisms of the Caprellidae. While studying feeding, it became apparent that some of the sympatric caprellids fed in a similar manner, and possible resource partitioning was also examined.

Table 1. Categories of the Caprellidae, excluding the Cyamidae, based on mandibular morphology and swimming setae. +: present; -: absent

Category	Group ^a	Swimming setae	Mandibular palp	Molar process
1	I	-	+	-
2	II	+	+	+
3	II	-	+	+
4	III	+	-	+
5	III	-	-	+
6	I	+	+	-

^aAfter McCain (1970).

Materials and Methods

Ten species of caprellids were collected from waters surrounding the San Juan Islands, Washington (USA). Within the intertidal zone, *Caprella californica* Stimpson, *C. laeviuscula* Mayer, *C. mendax* Mayer, *C. natalensis* Mayer, and *Metacaprella kennerlyi* (Stimpson) were found. Subtidally, *C. irregularis* Mayer, *C. laeviuscula*, *C. mendax*, *C. striata* Mayer, *Duetella californica* Mayer, *Mayerella banksia* Laubitz, *Metacaprella kennerlyi*, and *Tritella pilimana* Mayer were collected by dredging or SCUBA diving.

Feeding mechanisms were observed for each species with specimens of varying sizes and both sexes with the aid of a stereomicroscope. Ten-minute feeding observations were made for each specimen with the caprellid on natural substrates. Feeding mechanisms and time spent utilizing each method was recorded. At least 50 observations were made for each species; those species with more diverse feeding patterns (*Caprella laeviuscula*, *C. mendax*, and *Tritella pilimana*) had 74 observations each. Filtering ability was determined with the aid of sized diamond particles (25, 30, and 45 μm) and sized silicon carbide particles (60, 90, and 125 μm). Each particle size was presented separately, and particles were considered "captured" if retained by the antennae.

Stomach content analyses, using the methods of Saunders (1965), were made for at least 35 specimens of each species to verify feeding modes. Eighty specimens of *Duetella californica* and *Mayerella banksia* were examined, as their diets differed from the other caprellids. Feeding appendages were examined and plumose setal spacing on the antennae was measured with the aid of an ocular micrometer. As no discrepancies with the illustrations of Laubitz (1970) were found, the reader is referred to the appropriate figures in her monograph. Species identification was based on that monograph (Laubitz, 1970).

Feeding Mechanisms

There are 5 types of adult feeding mechanisms: browsing, filter-feeding, predation, scavenging, and scraping.

Browsing is the ingestion of filamentous algae. The second gnathopods take no part in algal ingestion and remain laterally extended while the first gnathopods retain the algal filaments not being ingested. Algae are pulled into the oral area by the action of the inner and outer lobes of the maxillipeds and

the maxillules. Both pair of appendages move in an anteroventral-to-posterodorsal plane, 180° out of synchrony. Thus, the maxillipeds complete the posterior movement as the maxillules complete the anterior movement. Setae and spines on the appendages pull the algae orally as the appendages move medially, grasping the algae, at the onset of the anterior stroke, and laterally, releasing the algae, at the onset of the posterior stroke. The *lacinia mobilis* and the incisor processes of the mandibles cut the algal filaments into small pieces and the material is masticated by the molar processes. Apparently the cut pieces are held within the oral area by the second maxilla until a sufficient amount of material has been obtained, then the second maxilla close and mastication takes place without the addition of more algal filaments.

The other 4 feeding modes have been described previously (Caine, 1974). Briefly, filter-feeding occurs as the setae on the first and second pairs of antennae entrap material, either passively or actively; if the adhering material is ingested the organism is filter-feeding, but if the material is discarded the specimen is cleaning itself (Caine, 1976). Predation occurs when the caprellid assumes an upright position and waits for a small organism to swim between the outstretched second gnathopods and the antennae. Scavenging is the grasping of non-living material, usually dead organisms or pieces of detritus, and either scraping material from the object or ingesting the entire object. Scraping consists of removal of encrusting material, e.g. periphyton and detritus, from the substrate on which the caprellid is epibiotic. The primary feeding modes of caprellids are listed in Table 2.

Although there are 5 feeding mechanisms, each species has subtle differences in the actual methods or frequency a method is utilized. Browsing is similar for both *Tritella pilimana* and *Caprella laeviuscula*, but *T. pilimana* utilizes this method less frequently than does *C. laeviuscula*.

Filter-feeding occurs to some extent in all caprellids, as material entrapped by the antennae and subsequently cleaned from the antennae is occasionally ingested but, of the species examined herein, neither *Duetella californica* and *Mayerella banksia* frequently utilized this feeding mechanism. Active filtering occurred in *Caprella laeviuscula*, where anterodorsal water currents, created by the beating of the maxillipeds and first gnathopods, pass through the setae of the ventrally

Table 2. Primary means of obtaining food materials by caprellids. Feeding modes: B, browsing; F, filter-feeding; P, predation; S, scavenging; Sc, scraping

Category	Feeding mode	Species	Source
1	P	<i>Phtisica marina</i>	Costa (1960)
2	B,F,Sc	<i>Tritella pilimana</i>	Present study
3	P,S,Sc	<i>Duetella californica</i>	Present study
3	P,S,Sc	<i>Luconacia incerta</i>	Caine (1974)
3	P,S	<i>Mayerella banksia</i>	Present study
4	F,Sc	<i>Caprella californica</i>	Saunders (1965), Keith (1969) and present study
4	F,Sc	<i>C. equilibra</i>	Keith (1969)
4	F,Sc	<i>C. irregularis</i>	Present study
4	B,F,S,Sc	<i>C. laeviuscula</i>	Saunders (1965) and present study
4	B,F,S,Sc	<i>C. mendax</i>	Present study
4	F,Sc	<i>C. natalensis</i>	Present study
4	F,S,Sc	<i>C. penantis</i>	Caine (1974)
4	F,Sc	<i>C. striata</i>	Present study
4	Sc	<i>C. unica</i>	Patton (1968)
4	F,Sc	<i>Metacaprella kennerlyi</i>	Saunders (1965) and present study
5	B,F,P,S,Sc	<i>Paracaprella tenuis</i>	Caine (1974)

flexed antennae, while *Tritella pilimana* utilizes a random rocking motion which pulls the antennae through the water. *C. irregularis*, *C. natalensis*, *C. striata*, and *Metacaprella kennerlyi* relied on natural, rather than produced, water currents. The filtering heights (body length minus the last two pereonites plus the length of the second antenna) and particle retention relationships for those species with swimming setae are given in Fig. 1 and Table 3. Particle retention varies due to different flexation of the antennae and subsequent setal overlap. It is possible that filtering selectivity can be controlled through antennal flexure, but this was not observed with the inorganic particles used to test particle retention. Particles retained were $115 \pm 9.8\%$ the setal spacing, probably due to setal movement. These findings agree with those of Boyd (1976). As the slopes of the regression lines are not 1.0, setal spacing is not merely a chance or growth artifact.

Predation was frequently observed only in *Duetella californica* and *Mayerella banksia*. Both species used a "stand and wait" method, where the caprellid remained practically motionless except for the capture strike (medial movement of the second gnathopods combined with the ventral movements of the antennae, forcing the prey into the grasp of the first gnathopods and maxillipeds).

Scraping behavior was noted for all species examined, but occurred more frequently in species with swimming setae than in the other genera. *Caprella natalensis* grasped the substratum with its second gnathopods while scraping, and remained in a scraping position for up to 8 sec. Other species seldom used the

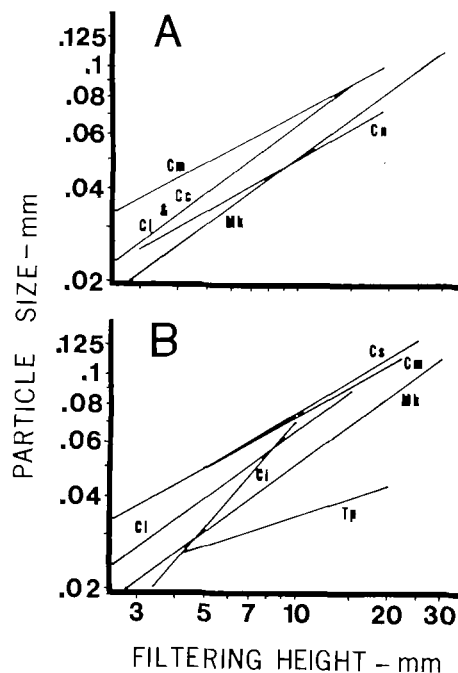


Fig. 1. Regressions of filtering height versus particle retention of those species utilizing filter-feeding as a primary feeding mechanism from (A) intertidal and (B) subtidal habitats. $n = 25$ for each species. Cc: *Caprella californica*; Ci: *C. irregularis*; Cl: *C. laeviuscula*; Cm: *C. mendax*; Cn: *C. natalensis*; Cs: *C. striata*; Mk: *Metacaprella kennerlyi*; Tp: *Tritella pilimana*

second gnathopods to grasp the substrate, and a scraping posture was maintained for less than 1 sec. *C. laeviuscula*, *C. mendax*, *Metacaprella kennerlyi*, and *Tritella pilimana* were observed to strip large amounts of material while scraping, and

then sort the material after resuming a standing posture.

Ontogenetically, juveniles (newly escaped from the brood chambers) feed by scraping. Definitive feeding mechanisms of the adults become increasingly important as individual size increases.

Stomach content analysis verified the predominate feeding modes observed in the laboratory. Those species with swimming setae, and correlated dense setae on the maxillae and maxillipeds, had more than 75% of the volume of the digestive tract contents composed of diatoms and detritus and the remainder composed of algae, copepod fragments, and small sand grains. Those species without swimming setae and dense mouthpart setation had copepod and nematode fragments comprising more than 20% of the diges-

tive tract contents and detritus more than 60%. As indicated previously (Caine, 1974), mandibular mastication probably renders material unidentifiable, i.e., detritus, and the diet is best evaluated by the second most common constituent of the digestive tract. No determination was made of the size of the filtered particles within natural populations; determination of particles assumed to be filtered and not scraped proved impossible.

Habitats

When sorting the collections, it became apparent that some caprellid species were found only on one substrate while other species were less habitat specific. In addition, the caprellid community on any substrate varied as to species composition. The substrates and associated caprellids collected in this study are listed in Table 4.

Table 3. Regression analysis of Fig. 1. $n = 25$ for each species. $t > 0.01$ for all slopes. Y -int.: Y intercept

Species	Habitat ^a	Y-int.	Slope	r^2
<i>Caprella californica</i>	I	13.5	.586	.844
<i>C. irregularis</i>	S	5.0	1.135	.894
<i>C. laeviuscula</i>	I,S	11.9	.743	.792
<i>C. mendax</i>	I,S	20.7	.540	.926
<i>C. natalensis</i>	I	13.5	.586	.884
<i>C. striata</i>	S	19.3	.587	.853
<i>Metacaprella kennerlyi</i>	I,S	9.6	.727	.535
<i>Tritella pilimana</i>	S	16.2	.323	.873

^aI: intertidal; S: subtidal.

Discussion

Feeding mechanisms of free-living members of the suborder Caprellidea are a function of mouthpart morphology. Structural variations influencing feeding involve the antennae, maxillae, and maxillipeds. The more setose the antennae, the more setose the other appendages; the converse also being true. Tables 1 and 2 indicate that those species with swimming setae (Categories 2 and 4) utilize filter-feeding and scraping as

Table 4. Substrates and cohabiting caprellids of San Juan Island based on 379 separate substrate colonies (hydroids) or clumps (algae) with caprellids present

Species no.	Species	Zone ^a	Substrate	Cohabiting species
1	<i>Caprella californica</i>	I	<i>Zostera marina</i>	none
2	<i>C. irregularis</i>	S	<i>Obelia longissima</i>	3,7
3	<i>C. laeviuscula</i>	I	<i>Z. marina</i>	none
		S	<i>Aglaophenia</i> sp.	4,9,10
		S	<i>Obelia dichotoma</i>	9
		S	<i>O. longissima</i>	2,4,6,7,9,10
4	<i>C. mendax</i>	S	<i>Aglaophenia</i> sp.	3,10
		S	<i>Obelia longissima</i>	3,7,9,10
5	<i>C. natalensis</i>	I	<i>Odonthalia floccosa</i>	none
6	<i>C. striata</i>	S	<i>Obelia longissima</i>	3,7,9,10
7	<i>Duetella californica</i>	S	<i>O. longissima</i>	2,3,4,6,9,10
8	<i>Mayerella banksia</i>	S	Free on bottom	none
9	<i>Metacaprella kennerlyi</i>	S	<i>Aglaophenia</i> sp.	3,10
		S	<i>Obelia dichotoma</i>	3
		S	<i>O. longissima</i>	3,4,6,7,10
10	<i>Tritella pilimana</i>	S	<i>Aglaophenia</i> sp.	3,4,9
		S	<i>Obelia longissima</i>	3,4,6,7,9

^aI: intertidal; S: subtidal.

major mechanisms for food acquisition. Those species without swimming setae (Categories 1 and 3) are primarily predators. Although Category 5 lacks swimming setae, only one species has been examined (Caine, 1974) and it was without feeding preference.

Caine (1974) discussed the morphological differences among Categories 3, 4, and 5, and found that specimens from Category 3 had elongated, sparsely setose appendages (predation), Category 4 had stout appendages with swimming setae (filter-feeding and scraping), and Category 5 had appendages intermediate in stoutness and setation (without feeding preference, a generalist-opportunist). Oral appendage setation of *Tritella piliimana* Category 2, is similar to species of Category 4, except that the dactylus and propodus of the second gnathopods are densely setose and the mandibular palp assists in antennal cleansing. Setae on the second gnathopods impede predation as they interfere with prey capture, thereby dictating a filtering/scraping mode.

No live specimens of Category 1 were found in this study, but Costa (1960) reported that *Phtisica marina* Slabber is a predator. Figures of *P. marina* by McCain (1968) indicate that the appendages are similar to specimens of Category 3 except that there is no molar process. Laubitz (1976) states that such a mandible indicates a carnivorous diet. Figures of other representatives of Category 1 by McCain (1968) and Laubitz (1970, 1972) indicate that the similarity in appendage structure between Categories 1 and 3 is universal.

While the primary feeding trends are listed in Table 2 and discussed above, all species utilize the 5 feeding modes to some extent. Thus, McCain (1968) reported that *Caprella equilibra* accepted small pieces of bivalves or bryozoans and preyed on gammarids and polychaetes. Keith (1969) also indicated scraping, filtering, and scavenging as important mechanisms for this species, with predation being somewhat rarer in occurrence.

Given these feeding preferences (Table 2), some type of substrate restrictions or food partitioning mechanisms must occur for the geographic association of multiple caprellid species. This assumes that successful colonization of suitable substrates will occur and inhabitants compete, either directly or indirectly, among themselves. Although caprellid niche diversity may be physiological, behavioral, or morphological, spatial sympatric occurrence may be independent of small physiological differences. Intertidal and subtidal isolation

occurred between some species, but all were found in the waters surrounding San Juan Islands. Because of the vertical zonation, intertidal and subtidal caprellids were considered separately (Fig. 1).

Behavioral isolation, e.g. aggressive exclusion and substrate preferences, may not be determinate as many species were collected together (Table 4) and no behavior suitable to explain the presence or absence of any species of caprellid was observed. McCain (1968) and Laubitz (1970, 1972) have indicated that most species of caprellids are not habitat, i.e., substrate, specific and occur on most suitable substrates. Keith (1971) considered the problem of substrate selection in two species of the genus *Caprella*, and found that both preferred the same substrate in the laboratory. In the field, the cryptic species preferred those habitats to which it was cryptically adapted. However, Keith also found that the caprellids readily occurred on other substrates in the field. Collections conducted in this study indicate that some species may have more rigid substrate preferences than other species, but most of the caprellids were collected on a variety of substrates. Therefore, the partitioning mechanism could be morphological.

Duetella californica and *Mayerella banksia*, the only primary predators collected, are morphologically dissimilar from caprellids that are primary filter-feeders. As the predators do not occur together, they are without serious caprellid competition for food. The other 8 species do compete to some extent, as filter-feeding is their primary means of obtaining food.

Although most co-occurring, filter-feeding caprellids do not utilize the same size particles at the same height, the variance in particle retention does not allow complete resource partitioning (Fig. 1, Table 3). Examination of the other feeding mechanisms indicates that those species with extensive filtering overlap do not occur together (e.g. *Caprella californica* and *C. laeviuscula*; *C. natalensis* and *Metacaprella kennerlyi*; *C. mendax* and *C. striata*). Those other species that occur together have less filtering competition and usually have different secondary feeding mechanisms.

While explaining static populations, this analysis ignores the competition of juvenile forms and disregards the final limiting factor for population size. If conclusions on physiological and behavioral aspects are correct, then there must be some mechanism(s) that allows the juveniles to coexist with each other and adults and that allows the adult com-

munity to maintain diversity. Both problems are partially answered by the transient nature of the substrates and the constant colonization and dispersion activities. Secondarily, visual predation by various fish probably removes non-cryptic caprellids; carnivorous invertebrates, e.g. the sessile stauromedusae *Haliclystus auricula* (Rathke), the anthozoan *Epiactis prolifera* Verrill, and the opisthobranch *Melibe leonina* (Gould), remove individuals without regard to size or species.

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