Amphipoda of the Northeast Pacific (Equator to Aleutians, intertidal to abyss): XIV.
Gammaroidea – an updated and expanded review
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Preface

The purpose of this review is to bring together information on all of the species reported to occur in the NEP fauna. It is not a straight path to the identification of your unknown animal. It is a resource guide to assist you in making the required identification in full knowledge of what the possibilities are. Never forget that there are other, as yet unreported species from the coverage area; some described, some new to science. The natural world is wonderfully diverse, and we have just scratched its surface.

Introduction to the Gammaroidea

The superfamily, while having both marine and freshwater members, is most prominent in epigean fresh-waters. Marine occurrences are coastal, with no superfamily members belonging to pelagic or deep-sea communities. There is a vast literature on the fresh-water members of the superfamily, particularly in European waters, where they have been studied for centuries. According to Bousfield (1982) they are a fairly recently derived group which appeared in the Tertiary. The superfamily contains a number of families not represented in the NEP, including the Acanthogammaridae, Caspicolidae, Macrohectopidae, Micruropidae, Pachyschesidae, and the Typhlogammaridae. These families are most prominent in Indo-European fresh-water habitats. The Gammaridae is poorly represented in the NEP, with only one widely distributed arctic-boreal form, and two species introduced from the Atlantic. One additional member of the family has been introduced to the waters of the saline relict Salton Sea, now landlocked in southern California (J. L. Barnard and Gray 1968, 1969). Most regional species in the superfamily are in the family Anisogammaridae, a North Pacific endemic family, with representatives on both the west and east coasts of that waterbody. The family Mesogammaridae has a similar distribution, but fewer species. The Gammaroporeidae are monotypic, containing a single species from the NEP. Lowry and Myers (2013) transferred this family to the Hadziida, and it is no longer considered a gammaroid.

The reorganization of the old Gammaridae s. l. by Bousfield (1977, but initiated in 1973 with creation of the new families Melitidae and Crangonycidae) has not been either universally adopted, or uncritically accepted. J. L. Barnard and Karaman (1980), Karaman and J. L. Barnard (1979), and Holsinger (1974, 1977) all took issue with some aspect of this concept. While these criticisms have reasonable basis, the basic outlines of the reorganization have been widely accepted, and we accept them here. The Gammaridae s. l. was still used in the J. L. Barnard and C. M. Barnard (1983) reexamination of the freshwater amphipods of the world. Even so, within that broad family umbrella they tended to use (at least for discussion purposes) a series of groups most of which are now viewed as family level taxa. The concepts of the Barnards and of the currently used Bousfield derived classification are not entirely congruent. Groups treated as gammaroids s. l. by the former are now distributed through a series of other superfamilies in several other infraorders. It is, therefore, dangerous to compare the groups adopted by the Barnards in our current discussion of the gammaroids s. s. It is safest to do this at the generic level, and becomes increasingly confusing as one ascends the taxonomic hierarchy. Despite this caveat there is considerable value in their discussions of the gammaroids s. l., and these should be examined by parties interested in the group and its relationships to other groups now

separated off. In the recent erection of the Subclass Senticaudata (Lowry and Myers 2013) the gammaroids were placed there, and revised so that they are now considered in the restricted rather than the broad sense of earlier workers.

Diagnosis of the Gammaroidea

"*Plesiomorphic gammarideans having both antennae (especially peduncle of A2) strongly developed, segment 2 of A1 not elongate, accessory flagellum prominent (rarely lacking): head with inferior antennal sinus deeply emarginate; eye well developed, basically reniform; body often carinate and/or processiferous, and /or rostrum moderately to well-developed; urosome segments with well developed dorsal groups of spines and setae; sexual dimorphism usually strongly expressed in body size, and in characters of antennae, gnathopods, peraeopods and uropod 3, but not in a specialized male instar; calceoli of antenna 2 cup- or plate-shaped. Mandibular palp strongly 3-segmented, terminal segment strong, usually with D-setae; lower lip, inner lobes lacking or weakly developed; maxilla 1, inner plate large, strongly setose; maxilliped with large, marginally spinose inner plates, palp strong, dactylate; coxal plates 1-4 deep, continuous (overlapping), coxae 5-7; anterior lobe usually deeper than posterior lobe. Gnathopods 1 and 2 strongly subchelate, subequal, 2 usually larger; peraeopod 3 larger than 4, may be sexually dimorphic in armature (not form): peraeopods 5-7, basis usually expanded, 7 longest; pleopods with well developed rami, subequal; epimeral plates subquadrate or acute behind; uropod 1, peduncle with basofacial spine; uropod 3, rami usually subequal, spinose and setose (natatory), terminal segment of outer ramus present; telson basically bilobed, spinose and setose marginally and apically, apices rounded. Coxal gill of peraeon 7 usually present; accessory (sternal) gills lacking; brood lamellae large (or distally expanded), marginally with strong simple setae*." (Bousfield 1977).

Ecological Commentary

The genus *Gammarus* is a good exemplar for the entire superfamily, and most of the literature on the ecology of the group is drawn from work done with various *Gammarus* species. Donald and Virginia Steele (and coauthors) produced a considerable body of work on the biology of *Gammarus* species in the northwest Atlantic (Steele 19976; Steele and Steele 1969, 1970a, b, 1972, 1973, 1974, 1975a, b, c, 1986, 1991; Steele and Whittick 1991; Steele and Steele 1970, 1972; Steele, Steele and MacPherson 1977; and Steele and Steele 1986). They documented the geographic distribution, reproductive bionomics, and other aspects of the biology of many species found in the area. Several of these species also occur in the NEP, and are of greater current interest that those distributed only in the Atlantic. In addition to the coverage provided by Steele and Steele, general natural history of species occurring in the northwest Atlantic or NEP is provided by Blegvad (1922), Kinne (1959), J. L. Barnard (1959), Hynes and Harper (1972), LaFrance and Ruber (1985), and Naylor et al (1988).

Members of the superfamily occupy both marine and freshwater biomes, and consequently osmoregulation is an important part of their physiological ecology. Several of the species can be found in waters of variable salinity. The mechanisms of ion control, retention and excretion, are discussed by Kinne (1959), Sutcliffe (1971), Lockwood et al (1976), Bettison and Davenport (1976), and Bulnheim (1979) among others. Calcium handling is central to the control of sodium, and thus the physiological response to changes in salinity.

Gammaroids have diversified ecologically in many respects other than their response to salinity. Their feeding ranges from detritivory to carnivory, stopping along the way at herbivory.

Studies of the sympagic species *Gammarus wilkitzkii* including in situ observations, gut analysis, and mouthpart morphology (Arndt et al 2005) suggest that food bet-hedging in the form of omnivory is the actual nutritive strategy of the species. This is an adaptation to a particularly unstable habitat (under sea ice) in which *G. wilkitzkii* lives, but similar seasonal instability is a feature of many habitats in which species of gammaroids occur. It is likely that opportunistic omnivory is advantageous to a number of species. Kelly et al (2002) also report dietary flexibility, but emphasize carnivory. At least in some situations predation may be a means to a competitive end. Dick et al (1990) suggest that *Gammarus pulex* may selectively feed on the molted females of *G. duebeni*, allowing it to competitively displace the latter in struggles to dominate resources. Other species time their reproductive cycle to take advantage of seasonal algal growth (Steele and Steele 1975, Steele and Whittick 1991). This would suggest that, at least for this subset of species, herbivory is the dominant (if not the only) nutritive mode adopted. Since the morphology of most gammaroids allows them the luxury of choice (they have the physical equipment for several different types of feeding), the animals can respond to whatever resource is available at the time; feeding on the most energetically advantageous of the food sources surrounding them.

Associations between gammaroids and other organisms include a bit of reported commensalism between ostracods and gammaroids (J. L. Barnard 1959, Baker and Wong 1968). The ostracods hide among the brood in the brood pouch. While this benefits the ostracod in some fashion, it apparently has no noticeable adverse effect on the amphipod. Other invertebrates, including ciliate protozoans (Bierhof and Roos 1977), and turbellarians (Maren 1979), have associations that are either suspected or known to be parasitic. Microsporidians are definitely parasitic on gammaroids, and affect sexuality in the infected animals (Bulnheim 1966, 1972, 1978; Bulnheim and Vavra 1968). Although placement of microsporidians remains controversial, they are probably best considered as obligate parasitic molds.

Gammaroids are apparently good fish food, and are also undoubtedly consumed by birds feeding in their shallow estuarine homes. They also fall prey to other gammaroids (as mentioned above and discussed in Dick et al 1990). Like other amphipods, gammaroids will fall prey to nemerteans that share the same habitat.

In the NEP, as in other waters, gammaroids are proving to be highly invasive compared to other amphipod groups. This may be in part due to their opportunistic diet, which allows them to exploit nearly any un- or under-utilized food source. It may be in part due to their tolerance of adverse environmental conditions: Sagasti et al (2000) found *Gammarus mucronatus* to be tolerant of hypoxic events in estuaries, while Waldichuck and Bousfield (1962) reported *Anisogammarus pugettensis* from partially anoxic waters; and *G. duebeni* is highly resistant to osmotic stress (Rock et al 2007). It may also be due in part to their reproductive potential. Gammaroids averaged 82% of the average brood number of the highest ranked group, the hadzioids, but averaged over twice as many eggs per brood (Saint Marie 1991). In consequence their average fecundity was considerably higher.

Iteroparity is the norm for the group, with life spans ranging from two months (*G. mucronatus*) up to four years (*G. oceanicus*), but averaging about a year (Saint Marie 1991). The number of broods per female in her lifetime ranges from 3-4 up to 26 in *G. chevreuxi*. Because of this relatively high reproductive output, which has considerable cost to the population (Steele and Steele 1986),their importance in energy flow in shallow embayments may be locally high. Secondary productivity in *Gammarus* species was examined by Kinne (1959), Fredette and Diaz (1986) and LaFrance and Ruber (1985).

Eogammarus possjeticus male guarding his smaller mate (Photo: Gyo Tansui)

Male gammaroids are precopulatory mate guarders (Conlan 1991, Borowsky 1991), and are typically larger than the females they clasp (Saint Marie 1991). The nature of the mate guarding relationship was explored experimentally by Dunham and Hurshman (1991). Life history characteristics of invasive and non-invasive species of European Gammarus (s. l.) were tabulated by Grabowski et al (2007). They found indications that successful invaders are both highly fecund, and relatively more tolerant of environmental extremes than native species.

Much of the invasive force of *Gammarus* populations is directed against indigenous congeners rather than other organisms. Competition for resources with congeners is strong given the opportunistic adaptations of most members of the genus. This may be tolerance based (Dennert 1974), or result from more active conflict between populations (Dick et al 1990). In Europe, where many indigenous species of the genus are present, a number of stocks have been severely impacted by introductions of exotic gammaroids, including species of *Dikerogammarus*, *Gammarus*, and *Echinogammarus*.

Key to NEP Gammaroid genera

Bousfield (1979) provided a series of keys to the families of the Gammaroidea in the NEP and their constituent genera. These are synthesized here to provide a unitary key to the genera in the superfamily in the NEP. The key elements have not been changed (except for an added statement in the first part of couplet 3), just reorganized to produce a single key. Genera not occurring south of the Aleutians have been omitted.

1. Eyes usually medium to large, subreniform, multifacetted; pleopods normal, rami long, multisegmented; urosome segments dorsally with groups of spines and/or setae; uropod 3 strong, at least one ramus longer than peduncle.....2
   Eyes small, round, with few facets; pleopods small, rami short, less than 10-segmented; urosome segments dorsally with paired setae only; uropod 3 small, rami shorter than peduncle.....*Gammaroporeia* [now in Hadziida]

2. Uropod 3, rami elongate, closely subequal, margins with spine groups but lacking plumose setae; telson lobes short, apically spinose, fused more than half their length; peraeopod 7 lacking coxal gill.....*Paramesogammarus*
   Uropod 3, rami not closely subequal, inner variously shorter, margins usually with spines and plumose setae; telson lobes longer than wide, apically spinose and setose, fused basally 1/3 or less; peraeopod 7 with coxal gill (rarely lacking).....3
3. Gnathopods (♂) dissimilar in size and form, palms (especially 1) oblique with simple spines; gnathopod dactyls slender, simple; coxal gills simple, lacking accessory lobes on P6 and P7; urosome segments with posterodorsal spines in groups of 3 (a median cluster and paired dorsolateral clusters).....*Gammarus*
   Gnathopod (♂) subsimilar in size and form (1 larger), palmar margins nearly vertical, lined with blunt peg-spines; gnathopod dactyls massive, with posterior accessory blade; coxal gills with accessory lobes; urosome segments with posterodorsal spines in clusters of 2 or 4 on either side of midline (middle pair may be closely approximate).....(Anisogammaridae).....4
4. All pleon segments prominently middorsally carinate; uropod 3, outer ramus lacking terminal segment; all coxal gills with single accessory lobe..... *Carineogammarus*
   Pleon segments not (or weakly) middorsally carinate; uropod 3, terminal segment of outer ramus present (may be very small): coxal gills of peraeopods 2 and 3, usually peraeopod 5 and/or 6 with 2 (or more) accessory lobes.....5
5. Urosome 2 with prominent median tooth and smaller pair of dorsolateral teeth; uropod 3, rami subequal; antenna 1 distinctly shorter than antenna 2; inferior antennal sinus with narrow posterior notch.....*Anisogammarus*
   Urosome 2 with dorsal groups of spines (or single spines on elevated bases) only; uropod 3, inner ramus less than half length of outer ramus; antenna 1 subequal to, or longer than, antenna 2; inferior antennal sinus smoothly concave posteriorly.....6
6. Some pleon segments with dorsal groups of spines and/or setae.....8
   All pleon segments dorsally bare (may have one or two isolated marginal setae).....7

7. Uropods 1 and 2 short, rami of 2 (excluding apical spines) not extending beyond peduncle of uropod 3; uropod 3, terminal segment of outer ramus very small, masked by distal spines of segment 1; antenna 2, peduncular segments 4 and 5 with 4-7 posterior marginal groups of long setae.....*Locustogammarus*
   Uropods 1 and 2 longer, rami of 2 extending well beyond peduncle of uropod 3; uropod 3, terminal segment of outer ramus distinct; antenna 2, peduncular segments 4 and 5 with 2-3 posterior marginal groups of medium length setae.....
   ....*Eogammarus*
8. Pleon segments dorsally with groups of stout spines only; urosome segments 1 and 2 dorsally with stout spines in groups of 3-7, elevated; antennae 1 and 2, peduncular segments each with 4-7 groups of long posterior marginal setae.....9
   Pleon segments dorsally with few groups of slender spines and/or setae; urosome segments 1 and 2 with slender spines, in groups of 1-3, not elevated; antennae 1 and 2 peduncular segments each with 1-4 groups of short to medium length posterior marginal setae.....*Ramellogammarus*
9. Urosome segment 2 with 4 posterodorsal groups of spines; antenna 1, peduncular segment 2 shorter than 1; coxal gill of peraeopod 6 with single accessory lobe;

telson lobes fused in basal ¼; small animals (10-13mm).....*Spasskogammarus*
Urosome segment 2 with 2 posterodorsal groups of spines, strongly elevated; antenna 1, peduncular segments 1 and 2 subequal in length; coxal gill of peraeopod 6 with 3 accessory lobes; telson lobes fused only near base; mostly large animals (15-30mm).....*Spinulogammarus*

NEP Gammaroidea from McLaughlin et al. (2005). Valid taxa **bolded**, synonyms not. None of these taxa are reported by SCAMIT agencies in the SCAMIT Ed. 9 taxonomic listing (Cadien & Lovell 2014), as they occur in habitats little sampled by marine monitoring programs.

Family Gammaridae

Gammarus daiberi Bousfield 1969 – North Atlantic; Introduced into estuaries in the NEP: 0-5m

Gammarus lacustris Sars 1863 – Circumboreal; south to Puget Sound; 0-3m

[**Gammarus mucronatus** Say 1818] – North Atlantic; Introduced to the Salton Sea inland in southern California; 0-5m

Gammarus setosus Dementieva 1931 – North Atlantic, North Pacific circumpolar; NEP south to British Columbia; 0-5m

Lagunogammarus setosus see Gammarus setosus Dementieva 1931

Family Acanthogammaridae – no NEP representatives

Family Anisogammaridae

Anisogammarus amchitkana Bousfield 2001 – Aleutian Ids., Alaska; 0-10m

Anisogammarus epistomus Bousfield 2001 – Vancouver Id., British Columbia; 0m

Anisogammarus oregonensis Shoemaker 1944 (see Ramellogammarus oregonensis)

Anisogammarus pugettensis (Dana 1853) – Aleutian Ids., Alaska to Northern California; 0-5m

Anisogammarus slatteryi Bousfield 2001 - Bering Sea to Willapa Bay, Washington; 0-13m

Carineogammarus makarovi (Bulycheva 1952) – NWP Kamchatka Peninsula to Japan Sea, NEP Aleutians to SE Alaska; 0-100m

Eogammarus confervicolus (Stimpson 1856) – Prince William Sound, Alaska, to central California; 0-5m

Eogammarus oclairi Bousfield 1979 – British Columbia to Oregon; 0-5m

Eogammarus makarovi Bulycheva 1952 (see Carineogammarus makarovi)

Eogammarus psammophilus Bousfield 1979 – Aleutian Ids., Alaska; 0m

Gammarus atchensis Brandt 1851 (see Spinulogammarus atchensis)

Gammarus locustoides Brandt 1851 (see Locustogammarus locustoides)

Gammarus ramellus Weckel 1907 (see Ramellogammarus ramellus)

Gammarus pugettensis Dana 1853 (see Anisogammarus pugettensis)

Gammarus subcarinatus Bate 1862 (see Spinulogammarus subcarinatus)

Locustogammarus levingsi Bousfield 1979 – Kenai Peninsula, Alaska to Vancouver Id., British Columbia; 0-5m

Locustogammarus locustoides (Brandt 1851) – NWP, NEP from Aleutian Ids., Alaska to Queen Charlotte Ids., British Columbia; 0-5m

Maera confervicola Stimpson 1856 (see Eogammarus confervicolus)

Ramellogammarus columbianus Bousfield and Morino 1992 –
Ramellogammarus littoralis Bousfield and Morino 1992 –
Ramellogammarus oregonensis (Shoemaker 1944) – Oregon; 0-5m
Ramellogammarus ramellus (Weckel 1907) - British Columbia to northern California; 0-2m
Ramellogammarus vancouverensis Bousfield 1979 – Vancouver Id., British Columbia; 0-1m
Spasskogammarus tzvetkovae Bousfield 1979 – Aleutian Ids., Alaska; 0m
Spinulogammarus atchensis (Brandt 1851) – Aleutian Ids., Alaska; 0m
Spinulogammarus subcarinatus (Bate 1862) – Bering Sea to Vancouver Id., British Columbia; 0m

Family Mesogammaridae

Paramesogammarus americanus Bousfield 1979 – Alexander Archipelago, SE Alaska; 0-2m

Comments by Family

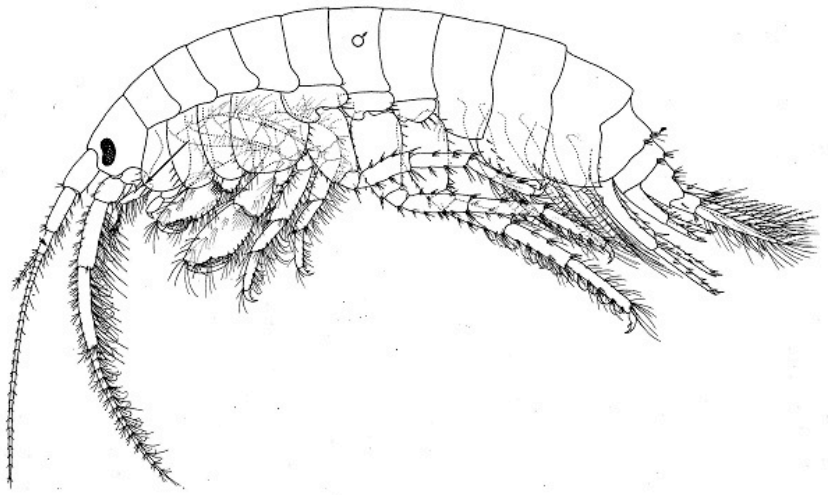
Family Gammaridae – Diagnosis: "Non-carinate, weakly rostrate, mainly epigean gammaroideans with strongly developed accessory flagellum, natatory uropods, and dorsal spine groups on urosome. Maxilla 1 outer plates with 11 apical spine-teeth." (Bousfield 1977).

Gammarus – The genus is believed to have evolved in fresh or perhaps brackish water, and then invaded the diluted coastal sea-waters of the holarctic region (J. L. Barnard and C. M. Barnard 1983). Steele and Steele (1974) elaborate this history, suggesting the origin was tethyan, with spread of the group into more northern waters as it speciated. They point out that closely related genera (originally included in *Gammarus*) are restricted to warmer waters, and are not distributed in the cooler waters favored by *Gammarus* itself. They also conclude from the current distribution and close similarity of many of the members of the genus that it is not a primitive precursor but a recently derived and actively speciating genus.

Diagnosis: "*Body smooth, compressed; urosome segments 1-3 with groups of dorsal spines, with or without associated setae. Coxal plates moderately large, margins rounded; plate 4 excavate posteriorly. Epimeral plates 2-3 rounded, quadrate or weakly acute. Head often with small rostrum, lateral lobes rounded or truncated; eyes variable, small and rounded to large elongate-reniform. Antennae variable, usually elongate; accessory flagellum typically well developed; calceoli present or absent. Mouthparts basic; maxilla 1 and 2 inner plate densely setose medially. Gnathopods 1 and 2 subchelate, subequal or gnathopod 2 larger than 1. Pereopods usually spinose, often setose. Uropods biramous; uropod 3 rami foliaceous, inner ramus more than half length of outer; outer ramus 2-articulate; rami often spinose and densely setose. Telson cleft, each lobe with lateral and apical spines, with or without setae*." (from Lincoln 1979)

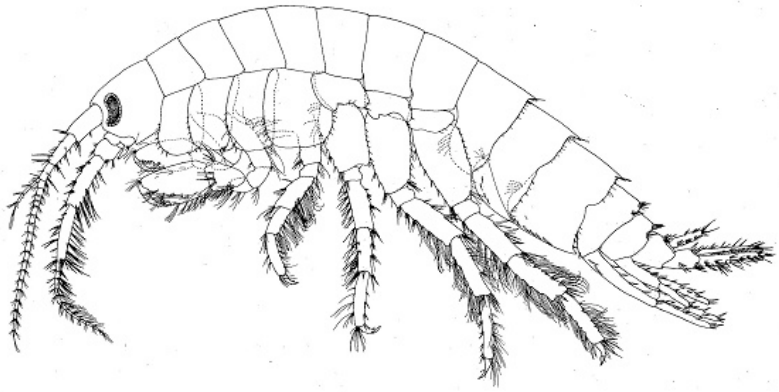
Although the genus is very large, with over 100 members, few occur in marine waters in the NEP. *Gammarus lacustris*, as its name suggests, is a predominantly freshwater organism, occurring in coastal and inland lakes. It is, however, also taken in hyposaline nearshore waters receiving the drainage of such water bodies (Chapman 2007), and thus could be taken in estuarine and rivermouth waters of reduced salinity along the boreal coast of the NEP. J. L. Barnard and C. M. Barnard (1983) indicate that records of this species do not approach the

coastal zone south of the Canadian border, so nearshore marine distribution of *G. lacustris* should only occur north of that point.



Gammarus daiberi (from Bousfield 1973)

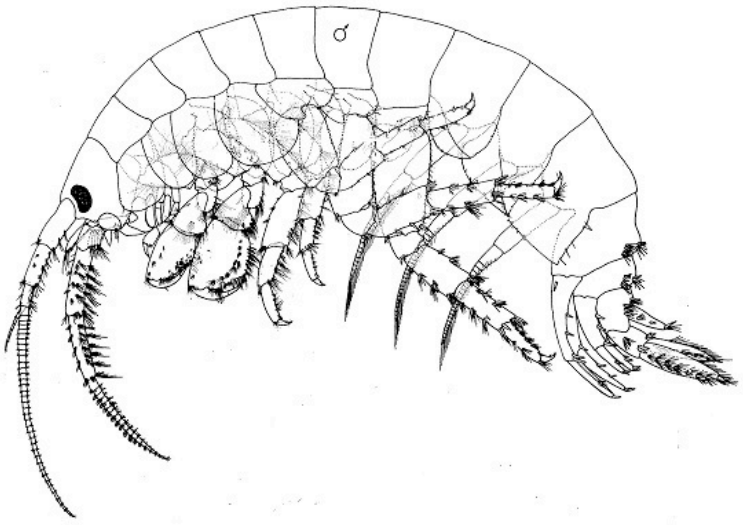
Another northwest Atlantic species in the genus has been introduced to coastal estuarine hyposaline situations, *Gammarus daiberi*. This species is currently known only from the San Francisco Bay and adjacent San Joaquin Delta waters (Benson 2007, Chapman 2007), but could show up in other NEP coastal waters of reduced salinity (less than 15ppt). The species is fully illustrated both in the original description (Bousfield 1969) and in his handbook of western Atlantic amphipods (Bousfield 1973). Chapman (2007) suggests that the noted invasive amphipod *Gammarus tigrinus* will probably eventually invade the NEP, but that has not yet happened (Kripp 2007). Illustrations and description of this species can be found in Bousfield (1973), while its biology is discussed by Steele and Steele (1972).



Gammarus mucronatus (from J. L. Barnard and Gray 1968)

A third species, *Gammarus mucronatus*, has been introduced into the saline Salton Sea in southern California (J. L. Barnard and Gray, 1968,1969). This is a catchbasin for agricultural runoff in the Coachella Valley accumulating in the low point left by retreat of the Gulf of California since the Miocene. As this runoff contains salts dissolved from the soils of the area, the waterbody is saline tending to hypersaline (during periods of high evaporative loss and low supply). It has no connection to the sea, so there is little likelihood that this introduction will

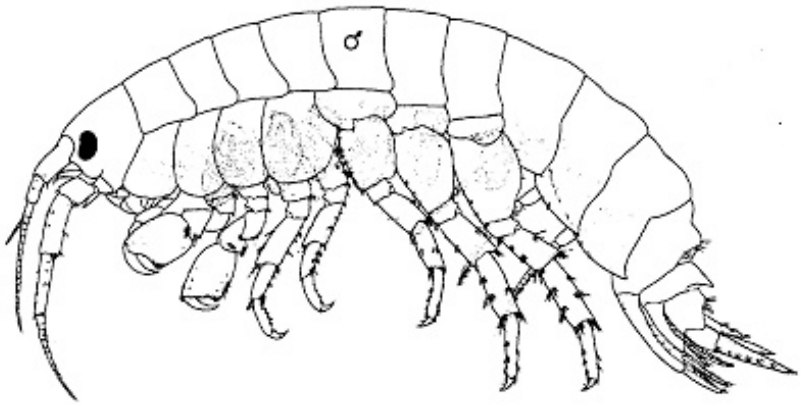
spread to coastal waters. The species is native to the northwest Atlantic. J. L. Barnard and Gray (1968) fully describe the organism (see also Bousfield 1973).



Gammarus setosus (from Bousfield 1979)

The most widely distributed *Gammarus* in the NEP is *G.* (*Lagunogammarus*) *setosus*. Originally described in the northwest Pacific, this form is distributed from the western North Atlantic (Steele and Steele 1970), through the northwest Pacific, and down the arctic and boreal coast of the NEP (Steele and Steele 1974) to British Columbia (Bousfield 1979, as *Lagunogammarus setosus*). The species occurs in estuaries and brackish bays where it occupies fine muddy and silty bottoms in intertidal to shallow subtidal depths. It is favored in areas of very low salinity, being found in areas of freshwater seepage and stream mouths (Steele and Steele 1974). Bousfield (1979) provides full illustration and description of the species.

Family Anisogammaridae – Diagnosis: "Eyed, epigean, coastal marine and brackish-fresh water gammaroideans characterized by: urosome (occasionally pleosome) strongly dorsally spinose and setose, occasionally urosome 2 processiferous; coxae 1-4 deep, contiguous, setose; coxae 5-7, anterior lobe deeper; antennae strong, accessory flagellum short; antennae 2 occasionally calceolate. Mouthparts basic; lower lip with weakly developed inner lobes; maxilla 1, outer plate with 11 apical spine-teeth. Gnathopods powerfully subchelate, 1 stronger than 2 (especially ♂): palmar margins lined with blunt pet-spines (♂ and ♀). Uropod 3 of "parviramus" or "variramus" types, rami spinose and/ or setose; telson lobes separated, spinose apically; coxal gills with accessory lobes on peraeon segments 2-7." (Bousfield 1977)



Anisogammarus pugettensis (from Bousfield 2001)

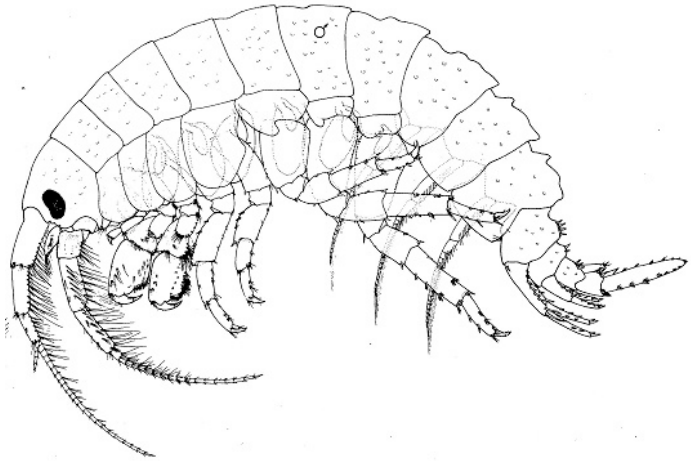
Anisogammarus – The genus is endemic to the North Pacific region, and well represented both in its Northwestern (Tzvetkova 1975b), and Northeastern (Bousfield 2001) portions. Members of the genus are usually associated with algae on intertidal beaches or shallow sedimentary bottoms (Bousfield 2001). While probably pursuing the omnivorous feeding habits of most gammaroids, the association with algae, particularly rapidly growing leafy and filamentous greens (*Ulva* and *Enteromorpha*) may signal herbivory as a primary feeding mode during periods of algal availability. Omnivory is, however, supported by the report of *A. pugettensis* feeding opportunistically on drowned humans in Japanese waters (Koseki et al 1962). A key to, and descriptions of all NEP taxa in this genus is provided by Bousfield (2001). J. L. Barnard (1954) also illustrated specimens of *A. pugettensis* from Oregon. Reports of and general distribution of Anisogammarus species were treated by Tzvetkova (1975a).

Diagnosis: "*Head, rostrum very short; inferior antennal sinus large, occasionally with narrow posterior notch. Antennae medium, subequal, accessory flagellum prominent, Antenna 2, peduncle large, flagellum occasionally calceolate.*

Mouthparts regular, little modified. Lower lip, inner lobes variously developed. Mandible: left lacinia 5-dentate; spine-row strong.

Peraeon dorsally smooth. Coxal plates 1-4medium deep, regular; plates 5 & 6 shallowly anterolobate. Gnathopods powerfully subchelate (male); gnathopod l larger than 2; palmar margins hearing peg spines (male), simple or pectinate (female);carpus short, lobe small. Peraeopods 5-7, bases weakly heterpodous; dactyls short. Peraeopods 2-7 with large coxal gills, 25 with 2, P6 with 3, and P7 with 1-2 accessory gills.

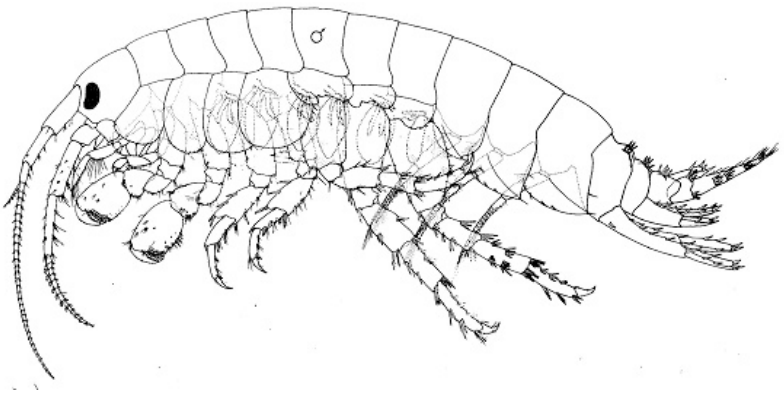
Pleosome and urosome variously dorsally carinate, toothed, spinose, or smooth. Uropods 1& 2, rami usually short, linear, spinose. Uropod 3 large, subaequiramous, terminal segment small. Telson bilobate, with marginal and apical spines. Female brood plates large, unequal, with numerous long marginal setae." (from Bousfield 2001)



Carineogammarus makarovi (from Bousfield 1979)

Carineogammarus – A monotypic North Pacific endemic genus consisting only of *Carineogammarus makarovi*. Originally described from the Western North Pacific as *Eogammarus*, it was transferred to the newly created *Carineogammarus* by Bousfield (1979). The ecology of the species differs from many other NEP anisogammarids in favoring more saline waters (20-34 ppt), which allows a much broader bathymetric distribution (to over 100m depths). It can be separated from other genera of NEP gammaroids using the generic key provided above. The species is fully illustrated and described in Tzvetkova (1975b). This is not the same genus as Bulycheva's *Carinogammarus*, whose species were split between *Carineogammarus* and *Barrowgammarus* by Bousfield.

Diagnosis*: " Medium-sized animals characterized by: Posterior peraeonal and all pleon segments middorsally carinate; body cuticle pitted. Eyes medium, reniform. Anterior head lobe notched medially. Antennae subequal, peduncles strong, richly long-setose, noncalceolate. Mandibular palp segments relatively short and broad, segment 1 strongly setose on distal margin. Lower lip, inner lobes fully defined, fused to outer lobes. Maxilla 1, palp lacking marginal setae. Maxilla 2, inner plate with short row of facial setae (8-10). Maxilliped, inner plate relatively short, broad. Gnathopods (0) large, powerful, subsimilar in size and form, palms oblique, peg-spines subacute, lining posterior ¥3 of palm; dactyls, unguis normal, accessory blade short. Gnathopods (~) dissimilar in form, palm of 1 oblique, convex; palm of 2 nearly vertical, convex. Coxal plates relatively narrow and deep, lacking tooth at lower posterior angle. Peraeopod 4, segment 4 shorter and more inflated anteriorly than in peraeopod 3. Peraeopods 5-7, basis with shallow posterodistal lobe, posterior margins finely setulose. Coxal gills medium, thick, saclike, each with one short, thick, accessory lobe; gill 7 small. Pleopods normal, outer margin of peduncle setose. Pleon lacking dorsal groups of spines; side plates with obtuse lower hind corners. Urosome segments each with dorsally paired groups of spinules on raised prominences. Uropods 1-2 short, barely exceeding peduncle of uropods 3, peduncles and rami marginally spinose. Uropod 1 with elongate interramal spines. Uropod 3, inner ramus very short; outer ramus large, margins spinose, lacking plumose setae; terminal segment lacking. Telson lobes broad, fused in basal Y3, setulose marginally, apices with single spine.*" (from Bousfield 1979)

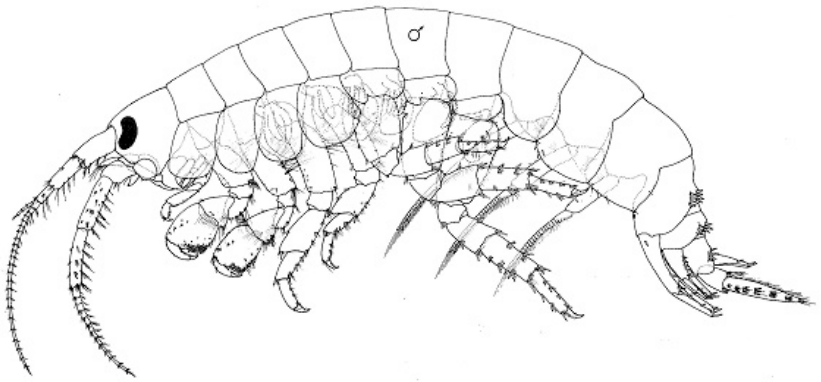


Eogammarus confervicolous (from Bousfield 1979)

Eogammarus – Most members of the genus are from the Northwest Pacific, but three are recorded from the NEP. By far the most widely distributed is *Eogammarus confervicolus* described over 150 years ago by Stimpson. Other species have restricted distributions in the Aleutians, or British Columbia to Oregon. This latter distribution is that reported for *Eogammarus oclairi*. Chapman (2007) makes a case for this being merely a growth form distinguished from *E. confervicolus* solely by ontogenically variable characters. While this may be the case, we retain *E. oclairi* here pending further investigation of its standing. The distribution reported for *E. oclairi* fits neatly within that of *E. confervicolus*. A key to all members of the genus is provided by Bousfield (1979), as are descriptions of all species reported from the NEP.

Diagnosis: "*Small to medium-sized species characterized by: Pleon dorsally non-carinate and non-spinulose. Eyes large, reniform. Antenna 1 subequal to, or longer than 2; peduncle segments well developed and setose, antenna 1 peduncle 1 usually with posterodistal spine; flagellum of antenna 2 cup-calceolate in 0 and often in S? Mandible, palp segment 1 unarmed. Lower lip, inner lobes incompletely defined laterally; distally only slightly separated from outer lobes. Maxilla 1, outer margin of palp with 3-6 setae. Maxilla 2, inner plate with strong (10-25) facial setae. Maxilliped inner plate relatively short. Gnathopods (♂) subsimilar, powerful; palms nearly vertical, peg-teeth large, usually blunt, striated, lining entire inner and outer sides of palmar margin below weak hinge prominence; dactyls with normal unguis, and elongate posterior blade, elevated basally. Gnathopods of ♀ dissimilar in size and form (not markedly so); palmar margins oblique (less so in 2), gently convex, inner spine row extending into anterior half of palmar margin, posterior spines pectinate; dactyls normal, posterior accessory blade medium long. Coxal plates deep, with spine at posterior angle. Peraeopods 3 and 4 slender, subsimilar, spinose and setose. Peraeopods 57, posterodistal lobe distinct, especially well developed in peraeopod 5; basis of peraeopod 7 more or less broadly expanded, especially proximally, posterior margin setose-spinose. Coxal gills medium large, relatively large on peraeopod 7; accessory lobes elongate, slender, double on peraeopods 2,3,4 and 5, treble on peraeopod 6, single on peraeopod 7. Pleon side plates 2 and 3, hind corners acute, variously produced. Pleopods normal, peduncles lacking marginal setae. Urosome segments 1, 2 and 3 with 4, 2 and 4 dorsal groups of slender spines respectively, not elevated nor interspersed with setae. Uropods 1 and 2 stout, rami long, apically and marginally spinose. Uropod 3, inner ramus short (less than 30% outer); outer ramus strong, margins lined with groups of spines and plumose setae, setae most numerous on inner margin; terminal segment well developed. Telson*

lobes fused basally (proximal 20%), each bearing apical and distal-lateral spine(s)." (from Bousfield 1979)

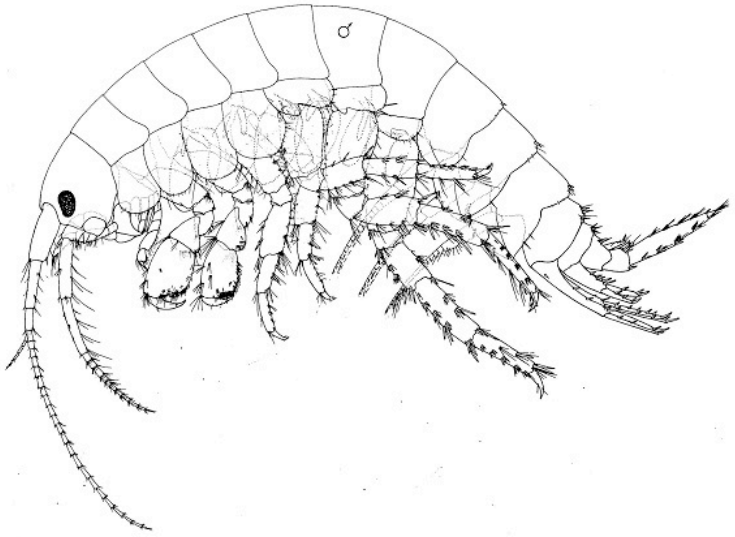


Locustogammarus locustoides (from Bousfield 1979)

Locustogammarus – A genus created by Bousfield (1979) to house a small group of North Pacific intertidal and estuarine species with affinities to *Spasskogammarus* and *Spinulogammarus*, but lacking pleonal dorsal setation/spination. Two species are reported from the NEP, and a third from the NWP. *Locustogammarus locustoides* is discussed in illustrated in J. L. Barnard (1954 as *Anisogammarus*) and Bousfield (1979). The latter author also describes *L. levingsi* as a new taxon in the same publication, and includes a key to the genus.

Diagnosis: "*Pleon not carinate, spinulose or setose dorsally. Eye large, reniform. Antennae subequal or 1 slightly longer; peduncular segments elongate and strongly long-setose posteriorly. Antenna 2, flagellum weakly (0 only) or not calceolate; accessory flagellum short (4-5 segments); inferior antennal sinus deep, lacking posterior notch. Mandible, palp slender, segment 3 with long mediodistal setal row; segment 2, proximomedial setae sparse, segment 1 variably setose distally or not. Lower lips, inner lobes not completely defined laterally, slightly separated distally from outer lobes. Maxilla 1, palp outer margin with variable numbers of weakly plumose setae. Maxilla 2, inner plate with 12-18 facial setae. Maxilliped inner plate stout, inner distal margin with 3-4 bent spines, palp relatively short. Gnathopods (0) subsimilar, powerful; palmar margins steeply oblique, peg-spines short, blunt, relatively widely spaced along inner and outer margins posterior to medium-strong (hinge) prominence; dactyls with relatively slender unguis and medium-long posterior accessory blade. Gnathopods (S?) dissimilar but not markedly so; palmar margin of propods oblique, more strongly so in 1, subacute marginal peg-spines extending into anterior half of margin, pectinate spines at posterior angle present in gnathopod 2, lacking in gnathopod 1; dactyls, unguis slender, posterior accessory blade medium-long. Coxal plates (especially 3 and 4) relatively shallow, slightly deeper than long, hind corner with spine. Peraeopods 3 and 4, distal segments (especially 4) stout, spinose. Peraeopods 5-7 bases medium broad, with posterodistal lobes, weakly developed in 6 and 7. Coxal gills relatively small, shallow, but well developed in peraeopod 7; accessory lobes about half gill length, paired on peraeopods 2, 3, 4, and 5, single on peraeopods 6 and 7. Pleon side plates 2 and 3, hind corners subquadrate or obtuse; pleopods normal. Urosome segments 1,2, and 3, each with 4 elongate groups of dorsolateral spines (on slight elevations), middle pair widely separated, spines (in outer series) in groups of 2-6. Uropods 1 and 2 short, rami extending little beyond peduncle of uropod 3 (except in L. aestuariorum) , armed with few (0-2) marginal spines. Uropod 3, inner ramus short; outer ramus long, broad, thick, outer margin with several spine groups and few, mostly single, setae,*

inner margin with, few .spine groups and lined with. plumose setae; terminal segment very small. Telson lobes broad, fused in basal Y3, each with apical and distolateral spine groups.'

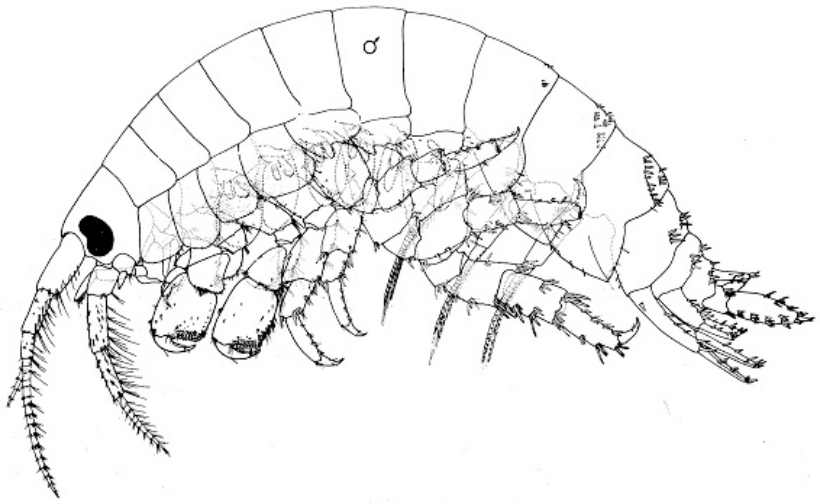


Ramellogammarus vancouverensis (from Bousfield 1979)

Ramellogammarus – Basically a freshwater genus found in lakes rivers and streams on the Pacific slope of North America (Bousfield and Morino 1992). There are occasional reports of these species from beaches and rivermouths receiving the runoff of such freshwaters. They can apparently survive, if not prosper, in hyposaline coastal situations as well as in freshwaters. Chapman (2007) provides reports from shorelines and coastal waters for several of these taxa. The genus was erected by Bousfield (1979) in his revision of the gammaroids of the Northern Pacific. It is endemic to the NEP, and has no representatives on western shores of the North Pacific. Most of the known species have been detected in hyposaline coastal habitats as well as in freshwaters. Five are reported here. They are described in Bousfield and Morino (1992), and can be distinguished using the key provided there. Additional discussion of *R. ramellus* is provided in J. L. Barnard (1954 as *Anisogammarus*).

Diagnosis: "*Medium to small, essentially freshwater anisogammarids, characterized by: Pleosome dorsally spinulose and/or setulose. Eyes medium to small, subreniform. Antenna 1 markedly longer than 2; peduncles well developed, slender, moderately setose; flagella not strongly setose, noncalceolate; accessory flagellum moderate (3-5 segments). Mandible, palp segment 3 with 1-2 facial groups of setae. Lower lip, inner lobes completely defined, weakly separated distally at throat of outer lobes. Maxilla 1, palp with few (0-3) outer marginal setae. Maxilla 2, inner plate with 1218 facial setae. Maxilliped, inner plate tall, nearly equal in length to outer. Gnathopods (0) powerful, subsimilar in size and form; palmar margins nearly vertical; peg-spines large, blunt, striated, lining inner and outer palmar margins below strong proximal (hinge) prominence; dactyl, unguis normal, accessory blade of medium length, basally elevated. Gnathopods (S?) dissimilar in form, palmar margins of both oblique, of 1 more strongly oblique and convex, of 2 shallow-concave proximally; spines confined to distal half of palmar margin; dactyls with slender unguis, accessory blade medium to medium-short. Coxal plates medium deep, lower margin setulose, posterior angle with spine. Peraeopods relatively slender, spinose and setose; segment 4 of peraeopod 4 not stoutly expanded,. Peraeopods 5-7, posterior margins of basis setose, or spinose-setose, posterodistal lobes distinct only on peraeopod 5. Coxal gills very large, broadly overlapping, gill 7 relatively large; accessory lobes short-slender, paired on*

peraeopods 2, 3, 4, 5, single on 6 and 7. Pleon side plates 2 and 3, hind corner subacute, slightly produced. Urosome segment 1 with 1 or 2 pairs, and segments 2 and 3 with 1 pair, of dorsolateral spine groups; spines slender, singly, doubly or triply inserted, usually accompanied by slender setae. Uropods 1 and 2 normally developed, rami slender, with few (0-3) marginal spines; interramal spines short, slender. Uropod 3, inner ramus very short (less than 1/6 outer); outer ramus long, slender, both margins with clusters of long slender spines and spinesetae (nonplumose); terminal segment well developed. Telson lobes moderately long, fused in basal 1/5; apically with single spine, and often also 1 lateral marginal spine and fine setae." (from Bousfield 1979)

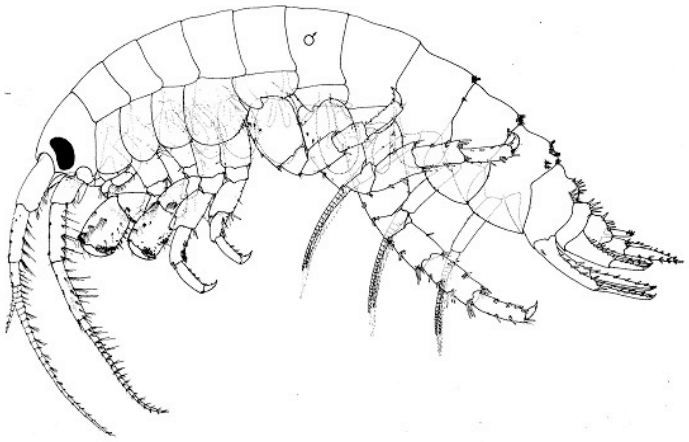


Spasskogammarus tzvetkovae (from Bousfield 1979)

Spasskogammarus – Yet another new genus created by Bousfield (1979) in his revision of the North Pacific gammaroids. It contains only two species; S. spasski from the Sea of Japan, and S. tzvetkovae from the NEP. With just the single NEP representative, this species can be keyed using the generic key to gammaroids provided above, or in the key to the genus provided by Bousfield (1979). Like *Carineogammarus*, *Spasskogammarus* species prefer fully saline situations, with *S. tzvetkovae* found on intertidal algal covered rocky flats in the Aleutian Islands.

Diagnosis: "*Small to medium-sized anisogammarids characterized by: Pleosome segments dorsally spinulose. Eye large, reniform. Antennae short, subequal; peduncles stout, strongly setose, noncalceolate; accessory flagellum 5-6 segmented. Mandible, palp slender, segment 1 unarmed. Lower lip, inner lobes completely defined, separated only slightly at throat from outer lobes. Maxilla 1, palp with 3-5 outer marginal setae. Maxilla 2, plates tall, inner distally angulate, facial row of setae long (about 15 setae). Maxilliped, outer plate· broad. Gnathopods (in ♂) subsimilar, powerful, palmar margins nearly vertical, peg-spines large, heavy, blunt, striated, lining palmar margin posterior to strong proximal (hinge) prominence; dactyls with heavy unguis, and medium-long prominent accessory blade. Gnathopods (♀) dissimilar in form, palmar margin of 1 oblique, convex, of 2 vertical, nearly straight; in both, palmar spines confined to posterior half of margin; dactyls with short posterior accessory blade. Coxal plates 3 and 4.rather shallower and broader than 1 and 2, hind corners with spine. Peraeopod 4 with short broad segment 4; peraeopods 5-7 short, posterior margin of basis spinose-setose, basis ()f 5 with shallow posterodistal (hind) lobe. Coxal gills medium large, relatively large on peraeopod 7; accessory lobes short, paired on peraeopods 2, 3, 4 and 5, single on 6 and 7. Pleopods normal, peduncles marginally setose; pleon side plates 2 and 3, hind*

corners subacute. Urosome segments 1-3 each dorsally with 2 pairs of slightly elevated groups of slender spines. Uropods 1 and 2 medium long, rami with few (2-3) marginal spines; uropod 3, inner ramus small; outer ramus broad, margins spinose (lacking plumose setae), terminal segment well developed. Telson lobes broad, fused basally about Y4 their length; each with distolateral and apical groups of spine(s)." (from Bousfield 1979)



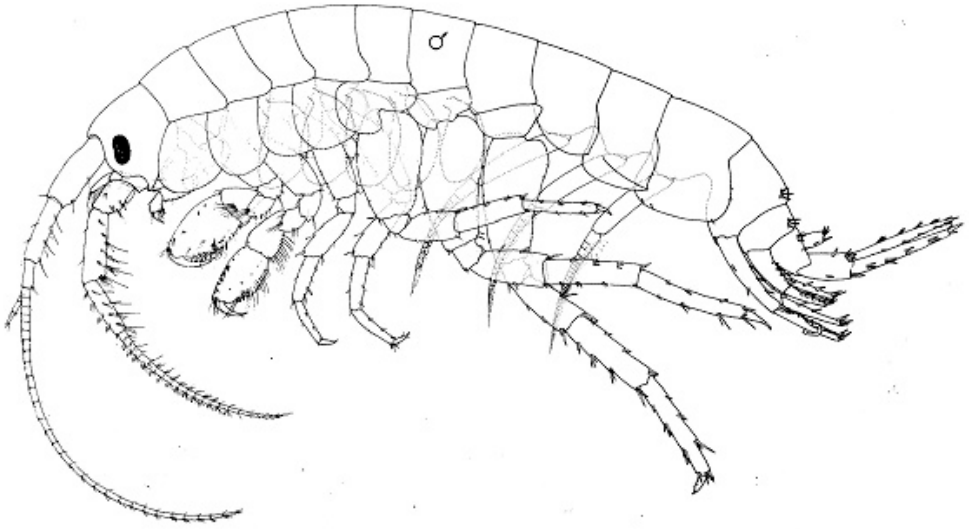
Spinulogammarus subcarinatus (from Bousfield 1979)

Spinulogammarus – Originally proposed as a subgenus by Tzvetkova, full generic status was suggested by Bousfield (1979). The genus consists of three species, two of which are reported from the NEP. Of these *S. atchensis* is restricted to a few of the western members of the Aleutian Island chain, while *S. subcarinatus* also occurs as far south as British Columbia. Both are described and S. subcarinatus illustrated in Bousfield (1979), who also provides a key to all members of the genus. Tzvetkova (1975) treats the two species described at the time. Members of the genus are found intertidally, generally on protected rocky beaches, and under polyhaline conditions. They may also be found in fully saline waters, but this is more typical of *Spasskogammarus* species.

Diagnosis: "*Medium to large anisogammarids characterized by: Dorsally spinulose but weakly or noncarinate pleon segments. Eyes large, reniform. Antennae subequal, peduncles well developed and strongly setose posteriorly, noncalceolate; accessory flagellum long (6+ segments). Mandibular palp slender, segment 1 lacking distal setae. Lower lip, inner lobes not fully defined, broadly fused to outer lobes. Maxilla 1, palp with 5-6 marginal setae. Maxilla 2, plates tall, inner plate with numerous (12-20+) facial setae. Maxilliped, inner and outer plates subequal in length. Gnathopods (0) somewhat dissimilar in form, palm of 1 oblique, of 2 nearly vertical, palmar peg spines relatively small, mostly subacute, lining all but anterior quarter of margin; dactyl, unguis normal, accessory blade long, base elevated. Gnathopods of Si? dissimilar in form; palmar margin of 1 strongly convex-oblique, acute peg-spines lining more than half of its length; palmar margin of 2 nearly vertical, slightly concave; peg-spines acute in both, lining half or more of palmar margin; dactyls with normal unguis and medium-to-short accessory blade. Coxal plates medium deep, hind corners with spine. Peraeopods stout, posterodistal lobe of basis shallow in peraeopods 5 and 6, lacking in peraeopod 7; posterior margins weakly spinose. Coxal gills medium large; accessory gills long, paired (double) on peraeopods 2-5, treble on 6, single on 7. Pleopods normal, peduncle with setose outer margin; epimeral plate 3 with subacute hind corner. Urosome segments 1 and 3 with 2 pairs, segment 2 with 1 pair, of elevated dorsolateral spine groups. Uropods 1 and 2 stout, rami long, marginally spinose (3-4 each), interramal spines short. Uropod 3, inner ramus relatively long (Y4 outer);*

outer ramus broad, margins spinose, with few plumose setae; terminal segment well developed. Telson lobes short, barely fused basally, each with one group of marginal spine(s) and an apical group." (from Bousfield 1979)

Family Mesogammaridae - Diagnosis: "*Epigean, eyed, coastal marine gammarids combining the following characters: body (pleosome) dorsally toothed, urosome spinose: ambulatory appendages strongly spinose, asetose, antennae normally developed; antenna 1, peduncular segments 1 and 2 subequal; accessory flagellum prominent; antenna 2 cup-calceolate (in ♂and ♀); mouthparts about normal: lower lip with weak inner lobes; maxilla 1, outer plate with 11 apical spine-teeth; maxilla 2 with reduced marginal and facial setae; coxae 1-4 medium-deep, contiguous; 5-7, anterior lobe deeper; gnathopods strongly subchelate, 1 distinctly larger than 2; palmar spines simple, not peg-like; uropod 3, rami subequally biramous, spinose (few setose), outer ramus 2-segmented; telson lobes short, basally fused, spinose apically and laterally. Coxal gills simple, lacking on peraeon 7. Brood lamellae sub-linear, little expanded distally, marginal setae long.* " (Bousfield 1977).



Paramesogammarus americanus (from Bousfield 1979)

Paramesogammarus – A monotypic genus created by Bousfield (1979) to accommodate a new species related to *Mesogammarus* from the north west Pacific. *Paramesogammarus americanus* is distributed in the Arctic-Boreal of the NEP, occurring from the Bering Sea to the Alexander Archipelago in SE Alaska. It can be separated from other superfamily members with the key to genera above. Bousfield (1979) reports it is found in fully marine waters rather than hyposaline rivermouths. Females are ovigerous in summer.

Diagnosis: "*Medium small, slender bodied gammaroideans. Eye medium small, subovate. Antenna 1 longer than 2; peduncles 1 and 2 subequal, lightly setose, peduncle 1 with posterodistal spine, peduncle 3 short; accessory flagellum short (3-4 segmented). Antenna 2, peduncle 5 shorter and more slender than 4, both moderately· setose posteriorly; peduncle 4 with spines and setae; peduncle 5 and proximal flagellar segments with/prominent cup-calceoli in both <3 and ~; superior and inferior antennal sinuses shallow. Upper lip founded, lightly pilose below. Lower lip, inner lobes narrow, barely defined laterally, slightly separated from outer lobes at throat. Mandibular palp slender, segment 2 with short medial setae, segment 1 distally setose. Maxilla 1, outer margin of palp lacking setae. Maxilla 2, inner plate, facial row*

of setae short, adjacent to inner margin. Maxilliped, inner and outer plates subequal in length. Gnathopods 1 and 2 alike in ♂ and ♀; gnathopod 1 larger but propod subsimilar to gnathopod 2; gnathopod 1, carpal lobe short, narrow, propod subovate, palm oblique, with single row of simple spine-teeth, and 2 additional medial spine clusters near posterior angle. Gnathopod 2, carpus longer than deep, posterior margin with numerous setal groups; dactyls of both gnathopods slender, simple. Coxal plates medium shallow, rounded below. Peraeopod 5, basis with shallow free posterodistal lobe. Peraeopods 6 and 7 longer than 5, slender, bases wide proximally, lacking posterodistal lobe, posterior margin weakly armed. Coxal gills medium large, simple, saclike. Pleon segments dorsally smooth; side plate 3 shallow, rounded posteriorly. Urosome segments 1, 2, and 3 each with a pair of dorsolateral spine groups, 2-3 slender spines per group. Uropods 1 and 2 short, slender, rami extending little beyond peduncle of uropod 3; outer ramus of uropod 1 (0), outer margin with large curved clasping spine and distal row of comb spines, in S?, with simple spines only. Uropod 2, inner ramus shorter than outer, peduncle and outer ramus strongly spinose. Telson lobes short, broad, fused in basal ~, each with group of apical and lateral spines." (from Bousfield 1979)

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