

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.

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.

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 1997; 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 than 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 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. Male gammaroids are precopulatory mate guards (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.

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).

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, multifaceted; 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*
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

Gammaroidea of the NEP (Equator to Aleutians, intertidal to abyss): a review
Donald B. Cadien 22 July 2004 (revised 12Oct 2007)

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.

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

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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 Gammaroporeidae

Gammaroporeia alaskensis (Bousfield and Hubbard 1968) – Olsen Bay, Alaska to

Vancouver Id., British Columbia; 0m

Micruropus alaskensis Bousfield and Hubbard 1968

Family Mesogammaridae

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

Family Caspicolidae – no NEP representatives

Family Micruropidae - no NEP representatives

Family Pachyschesidae - no NEP representatives

Family Typhlogammaridae - no NEP representatives

Family Macrohectopidae - no NEP representatives

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.



Gammarus fasciatus (Photo: Colin van Overdijk)

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.

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).

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 and figure the organism (see also Bousfield 1973).

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, epigeal, 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 pereon segments 2-7.” (Bousfield 1977)

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).

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) and in Bousfield (1979). This is not the same genus as Bulycheva's *Carinogammarus*, whose species were split between *Carineogammarus* and *Barrowgammarus* by Bousfield.

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. Additional description and illustration of *E. confervicolus* is provided by J. L. Barnard (1954 as *Anisogammarus*).



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

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.

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*).

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. tzvetkova* 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. tzvetkova* found on intertidal algal covered rocky flats in the Aleutian Islands.

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.

Family Gammaroporeidae – Diagnosis (as gammaridean family group 10): “Body form sub-fossorial, with broadened and setose coxal plates and appendages; eye sub-rotund, few-faceted; antennae short, accessory flagellum small; mouthparts about normal: lower lip lacking inner lobes; maxilla 1, inner plate with 11 (not 9) apical spine-teeth; gnathopods medium, subchelate, 1 larger than 2, palmar margins with blunt peg-spines (♂ only); peraeopod 4 of different form than peraeopod 3 (both sexes); peraeopods 5-7 (especially 7) with strongly expanded basis; pleopods weak, inner ramus shorter; outer margin of peduncle plumose-setose; urosome dorsally weakly armed; uropods 1 and 2 short; uropod 3 rami very short, unequal, lacking armature; telson small, bilobed, weakly armed. Coxal gills simple, lacking on peraeon 7. Brood plates broadly expanded.” (Bousfield 1977).

Gammaroporeia – A highly specialized mid- to upper intertidal genus. Bousfield (1979) reports it favors muddy to muddy gravel beaches subject to the outflow of cold creeks. Gills are reduced in this genus, presumably because it is always found in well oxygenated waters. The urosome is compact, with short uropods and resembles that of some talitroids. The animal is fossorial, and elongate uropods would be a liability in the sediments it favors. The type and only species *Gammaroporeia alaskensis* is found only from the Gulf of Alaska south to British Columbia in appropriate habitats, so the genus and family are endemic to the NEP. It is well described and illustrated in Bousfield 1979, and in Bousfield and Hubbard 1968, where it was originally described as *Micruropus alaskensis*. While sharing some similarities with *Micruropus* in the Micruropidae, that group is almost exclusively distributed in Lake Baikal and the Ponto-Caspian area of the Old World (Bazikalova 1962). *Gammaroporeia* could be considered a New World ecological analogue.

Family Mesogammaridae - Diagnosis: “Epigeal, eyed, coastal marine gammarids combining the following characters: body (pleosome) dorsally toothed, urosome spinose: ambulatory appendages strongly spinose, aetose, 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 pereon 7. Brood lamellae sub-linear, little expanded distally, marginal setae long. “ (Bousfield 1977).

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.

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