

# Notes on Norwegian marine Amphipoda. 10. Scavengers and fish associates

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The dominant group of carrion-eating amphipods in Norway are the Lysianassoidea; they play an important role as scavengers in Norwegian and arctic waters. A number of genera damage fish caught in nets and on long-lines; in Norway the most serious damage is done by *Anonyx* and *Tmetonyx* species. *Tmetonyx cicada* and the isopod *Cirolana borealis* have also regularly been found in Cod roe.

Symbionts of living fish belong to the genera *Lafystius*, *Normanion*, *Opisa* and *Trischizostoma*. *Lafystius* and *Normanion* have low host specificity, *Opisa eschrichtii* is found on gadids and Halibut *Hippoglossus hippoglossus* and *Trischizostoma raschi* on the small shark *Etmopterus spinax*. Little is known on the biology of these species.

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This paper is part of a continuing series documenting the occurrence and frequency of symbiotic relationships between amphipods and other aquatic animals (Vader 1970, 1971, 1972a, 1979, 1983, 1984). The present paper is restricted to Norwegian amphipod species; a similar paper on Canadian fish-associated amphipods is in preparation (Bousfield, pers. comm.). Similar associations no doubt occur in other parts of the world, but we have not come across any references.

Fishes are, besides whales, the only vertebrates in northern Europe that harbour amphipod associates. In warmer seas, amphipods, especially *Caprella acutifrons*, *Hyachelia tortugae*, *Hyale grimaldii* and *Platophium chelonophilum* have also regularly been collected from different species of sea turtles (e.g. Chevreux & de Guerne 1893, Mayer 1903, Chevreux & Fage 1925, Barnard 1967, Ruffo 1975). Migratory birds (cf. Segerstråle 1954, Swanson 1984), and occasionally even aquatic mammals (Peck 1975), may play some role in the dispersal of especially freshwater amphipods, but such temporary transport associations hardly qualify as symbiosis.

Before treating the specialized fish associates, we think it useful to present some data on the role of amphipods as scavengers in Norwegian waters, both because fish is the most important

type of carrion, and because carrion-feeding amphipods often damage commercially caught fish in nets or on long lines.

## SCAVENGERS

Scavenging amphipods primarily feed by definition on dead organisms to which they are attracted by a powerfully developed sense of chemoreception (cf. Dahl 1979, Busdosh et al. 1982, Hargrave 1985). For this reason they can easily be collected, often in large numbers, in various types of traps baited with fish or meat (e.g. Barnard 1959, Vader 1972b, Hessler et al. 1978, Thurston 1979). Amphipods appear to be especially important as scavengers in arctic/antarctic and cold-temperate waters and in the deep sea. In warmer seas bacterial decomposition occurs much more quickly and competition with small decapods and fishes is fierce.

The overwhelming majority of scavenging amphipods belongs to the Lysianassoidea. In Norway and the Norwegian Arctic representatives of the following genera have often been taken in baited traps: *Onisimus* Boeck (= *Boeckosimus* Barnard) (but not *O. normani* and *O. plautus*), *Orchomene* Boeck, *Anonyx* Krøyer, *Scopelocheirus* Bate, *Tryphosella* Bonnier (= *Tryphosa* auct), *Eurythenes* Smith, *Tmetonyx* Stebbing (but not *T. caeculus*), *Orchomenella* G.O. Sars, and *Orchomenopsis* G.O. Sars (Sars

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1890—95, Chevreux 1899, Oldevig 1959, Vader 1972b).

Baited traps have also attracted *Atylus* spp (Heldt 1952, Sekiguchi 1982), *Hyperioipsis voringii* (Chevreux 1899), and a number of species in the Eusiroidea: *Apherusa chiereghinii* (Heldt 1952), *Cleonardo* spp. (Chevreux 1908), *Dolobrotus mardeni* (Bowman 1974), *Leptamphopus sarsi* (Vader 1972b), and *Pontogeneia* spp (Bowman 1974, Sekiguchi 1982). In brackish waters *Gammarus* spp have occasionally been taken in baited nets (Haahtela 1969). These non-lysianassid species are never caught in abundance, however, and lysianassids are everywhere the dominant scavenging amphipods.

Some specialized deep-sea carrion-feeding Lysianassoidea show extensive morphological and physiological specializations for such a 'feast-or-famine' regime, as demonstrated by Dahl (1979) for species in the genera *Eurythenes*, *Hirondellea*, *Orchomene* and *Paralicella*. Shallow-water lysianassids also show adaptations for carrion-feeding (cf. Oleröd (1975) for *Orchomene*, Sainte-Marie (1984) for *Anonyx*), but boundaries between carrion-feeding, predation and detritus feeding are by no means clear-cut in these species. In *Anonyx* spp the proportion of carrion in the diet varies both between species and between age-classes (Sainte-Marie & Lamarche 1985).

#### AMPHIPODS ATTACKING FISH IN NETS AND ON LONG-LINES

As carrion-feeding amphipods have a well-developed sense of distance chemoreception, it comes as no surprise that they are also attracted to living fish in nets and on long-lines, and often do considerable damage (Heldt 1952, Templeton 1967, Sekiguchi 1982, Stepien & Brusca 1985, own observations); as noted by Chevreux the problem was even greater in the days of the sailing ships (cf. Chevreux & Fage 1925, p. 56, sub *Scopelocheirus hopei*). Similar problems have also occasionally been noted in brackish and fresh waters, where *Gammarus* species have attacked fish caught in different types of nets (Redeke & de Vos 1925, Segerstråle 1944, Ruoff 1968).

In Norwegian waters the most serious damage is usually done by *Anonyx* and *Tmetonyx* species. Further south, in the North Sea and off the French coast, *Orchomenella nana* is the most common culprit in shallow water and *Scopelocheirus hopei* in deeper waters (Chevreux & Fage 1925, Schellenberg 1942). *Tmetonyx ci-*

*cada* and the isopod *Cirolana borealis* have in addition been discovered many times in Cod roe (Raitt 1929, Berland 1983, own observations). The crustaceans probably penetrate into the roe first after the Cod has been caught: usually a few crustaceans are present, damage is not extensive and the culprits are first discovered at the dinner table.

#### AMPHIPODS ASSOCIATED WITH FREE-SWIMMING FISHES

In Norwegian waters only four amphipod genera belong to this category; the lysianassoid genera *Normanion*, *Opisa* and *Trischizostoma*, and the lafystiid *Lafystius*.

Stephensen (1929) also included *Laphystiopsis planifrons* in his list of 'amphipods that live on fishes' and his statement has been repeated by several authors (e.g. Bousfield 1978), but this appears to have been based exclusively on the superficial similarity of this amphipod with *Lafystius*, and on Sars' speculation: 'Whether *Laphystiopsis* in reality leads, like *Lafystius*, a semi-parasitic life, or not still remains an open question.' (Sars 1890—95, p. 388). The few records of *Laphystiopsis planifrons* have all been from deep fjord bottoms, with no signs of any symbiotic association. On the other hand, its little-known congener *L. iridometrae* is an apparently obligate associate of a crinoid (Shoemaker 1919).

*Tryphosella* (= *Tryphosa* auct.) *nanoides* (Lilljeborg), a common amphipod in baited traps in comparative shallow water in Norway (Vader, unpubl. obs.), has also been reported a few times as having been collected from living fishes. Robertson (1888) found *T. nanoides* (and '*T. horingi*' in reality probably also *T. nanoides*, cf. Moore 1984, p. 38) 'on the back of a codfish' in Scotland, Sars (1890—95) recorded the same species 'in great numbers from the back of a living skate (*Raja batis*) just brought up by a fishing line' in western Norway, and Norman (1900, Norman & Scott 1906) also collected *T. nanoides* 'from a skate' in Cornwall. In all the above cases, the fish had probably been restricted in its movements for some time prior to collection.

#### *Lafystius sturionis* Kröyer (Lafystiidae)

This, as yet the only species in the family Lafystiidae (further spp are under description, Bousfield pers. comm.), is an obligate associate of fishes, with low host specificity. It is widespread,

but not common in the North Atlantic and the Mediterranean. It has often been found on the Cod *Gadus morhua* (Bate 1857, Miers 1879, Robertson 1888, Walker 1895, Kingsley 1902, Chevreux & Fage 1925, Stephensen 1926, 1940, Oldevig 1959, Kabata 1970, Sanderson 1973, Appy & Burt 1982, Moore 1984, own observations), with 'the pectoral fins' as the most commonly mentioned site. But *Lafystius sturionis* has also been collected from the Haddock *Gadus aeglefinus* and from Cottids (Bousfield 1973), from the Angler Fish *Lophius piscatorius* (Della Valle 1893, Oldevig 1959), the Sturgeon *Acipenser sturio* (Kröyer 1842), the Blue Skate *Raia batis* (Sars 1890—95, Oldevig 1959), and the Tope *Galeorhinus galeus* (Kröyer 1842). It has in other words a very wide host-spectre both from a taxonomic and a biological point of view. One aberrant record is from the spider crab *Maia squinado* (Chevreux 1887, Chevreux & Fage 1925).

Taxonomically, the Lafystiidae are close to the Acanthonotozomatidae. Both families have been included by Bousfield (1978) in his superfamily Stegocephaloidea, while also Barnard's (1969, 1974) classification indicates close relationships between Lafystiidae, Acanthonotozomatidae and Stegocephalidae.

#### *Normanion* spp (Lysianassoidea)

This eastern Atlantic and Mediterranean genus needs taxonomic revision (cf. Diviacco & Vader in press, Vader in prep.); for this reason and because the 2 or 3 Norwegian species do not seem to differ much in biology, treatment here will be at the generic level. Sars (1890—95) collected *Normanion* from sand and gravel bottoms, as well as 'clinging to living and dead fishes taken on long lines' in deep water. The unique holotype of the mediterranean abyssal species *Normanion abyssi* Chevreux was collected from a baited trap (Chevreux 1903), but in Norway we have never found *Normanion* in baited traps. Specimens were, however, found regularly in bottom-sledges in the Bergen area. The first author also found a number of specimens on fish caught on long-lines, and Dr. Bjørn Berland (Bergen) sent him a sample taken from the skin (in part even inside the mouth!) of an Angler Fish *Lophius piscatorius* caught by rod and line in western Norway.

#### *Opisa eschrichtii* (Kröyer) (Lysianassoidea)

This rarely collected North Atlantic (and N. Pacific?) species has now been found several times

on gadoid fish, and has to be considered an obligate, albeit possibly temporary fish associate. The only published records we have found are those by Stephensen (1923, from Cod *Gadus morhua*) and Schneider (1926, from Haddock *G. aeglefinus*). In Northern Norway *Opisa* has in later years been found a few times on both Cod and Haddock, as well as on the Halibut *Hippoglossus hippoglossus* (Vader, unpubl. obs.). Similar records exist for Canadian waters (Bousfield, pers. comm.).

#### *Trischizostoma raschi* (Boeck) (Lysianassoidea)

This is a much more host-specific fish associate than *Normanion* and *Opisa*. As first described by Sars (1890—95, p. 673—674), *T. raschi* was 'found clinging to the skin of the common black dog-fish (*Spinax niger*), in most cases to the belly, near the anal opening. It very easily detached itself from the fish, and swam about with great rapidity.' The fish host is now usually known as the Velvet Belly *Etmopterus spinax*, a small viviparous bottom-living shark. Its distribution in western and northwestern Europe (cf. Pethon 1985) corresponds well with that of *T. raschi*: coast of Norway, off southern Iceland, off West Ireland. The Velvet Belly also occurs in the Mediterranean, together with *Trischizostoma nicaeense* (Costa), also a fish associate, though apparently of lower host specificity (for references see Sexton 1908). A number of other *Trischizostoma* species have been described, of which two S. African species, *T. remipes* Stebbing and *T. paucispinosum* K.H. Barnard, seem to be associates of sponges (Barnard 1925). All *Trischizostoma* species have also been collected apparently free-living in the bathypelagic zone.

The association of *T. raschi* with the Velvet Belly *E. spinax* has been confirmed by Nordgaard (1911), Stephensen (1935—42) and Vader (many unpubl. obs. from western Norway). The type specimens of *T. raschi* were collected from 'the skinned body of a newly shot bird, submerged in the dredge' (cf. Sars 1890—95), while Bovallius (1886) recorded the species from starfish(!) as well as from sharks.

## DISCUSSION

As is the case with amphipod associates of many marine invertebrate groups (Vader 1979, 1983, 1984) those found on fishes are not a monophyletic group. *Lafystius* belongs to the Stegocephaloidea (Bousfield 1978), and while *Normanion*,

*Opisa* and *Trischizostoma* all are Lysianassoidea the three genera are not especially closely related.

Very little is known about the biology of any of these species. *Lafystius* is usually described as an ectoparasite of fishes, and this species is not very often found free-swimming. In Norway we have never collected it from baited traps, although Robertson (1892, cited from Norman 1900, p. 203) seems occasionally to have found many *Lafystius* in baitcreels in Scotland. The dorsoventrally depressed *Lafystius sturionis* with its strong, smooth, curved pereopod dactyli and its piercing mouthparts arranged in a conical bundle, seems to be well adapted to an existence as a more or less permanent ectoparasitic 'louse' on the surface of fishes. A similar life-style, albeit with large coelenterates as 'host' and less permanent attachment to the host, has recently been suggested for the related Stegocephalidae (Moore & Rainbow 1984).

*Trischizostoma raschi* (and *T. nicaeense*) also have piercing mouthparts in a conical bundle (while the possible sponge-living S. African *Trischizostoma* species have more generalized mouthparts (Barnard 1962)). The very agile *Trischizostoma* species, with their telsonic fan, very large eyes, rich sensory armaments and powerful, very mobile, grasping first gnathopods (cf. Sexton 1908, Pirlot 1932) appear to be fully able to move from host to host at will. It is therefore somewhat unexpected that *T. raschi* appears to be quite host specific. Its choice of host and its location on the host are less surprising: as its vernacular name suggests, the Velvet Belly *Etmopterus spinax* has an unusually soft skin for a shark, especially in the belly region. In *T. raschi* the midgut has large dilatations (Pirlot 1932); in combination with piercing and sucking mouthparts this gives the impression of a blood-sucking ectoparasite with a leech-like way of life.

A broadly similar configuration of the mouthparts is found in the 'Conicostomatid' genera (Lowry & Stoddart 1983) and also those species are probably 'micropredators', in their case of sessile invertebrates (cf. Vader 1983 for *Acidostoma* spp).

Both *Normanion* and *Opisa* spp have enlarged first gnathopods; those of *Normanion* are quite similar to, though smaller than, those of immature *Trischizostoma*. They are very long and possibly used to grasp the host. *Normanion* has a very conspicuous and capacious swollen midgut and is not a rapid swimmer. The mouthparts are not really styliform and in the small maxillipeds the palps are shorter than the outer plates (Pirlot

1932). Pirlot (op. cit.) also pointed out that the very little known lysianassoid species *Podopriorella norvegica* Sars from Norwegian fjords has similar mouthparts and may have a similar way of life. The amphipods of the genus *Normanion* are clearly temporary symbionts of slow, bottom-living fishes (certainly not pelagic fishes, contra Lincoln 1979) with possibly a 'feast-or-famine' feeding strategy, but we are ignorant of the exact nature of their food. Very little is known about *Opisa eschrichtii*. It is evidently also a temporary associate of fish, but not having seen living specimens, we do not want to make conjectures on its way of life.

Although fish-living amphipods are no doubt often overlooked, none of the species appear to be really common and successful, especially compared to the large numbers of fish associates among other crustacean groups such as the Copepoda and the Isopoda (Kabata 1970). This is in spite of the fact that amphipods are among the dominant scavengers of dead and debilitated fish in cold seas, where they usually greatly outnumber the scavenging cirrolanid isopods. All fish-associating amphipod taxa seem to have developed independently into fish symbionts, and in no case (except possibly *Tryphosa nanoides*, see p. 4) do the direct ancestors of the fish-associated amphipods appear to have been generalized scavengers, in contradistinction to the probable evolution within the flabelliferan isopods (Brusca 1981). One of the reasons for the modest success of amphipods as fish symbionts may be that these laterally compressed organisms are much better suited for crawling through three-dimensional lattice structures than for attachment to, and crawling on, a slippery and largely two-dimensional fish skin.

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