

Parasitic and commensal polychaetes (Fams. Arabellidae and Sphaerodoridae) and copepods (Fam. Saccopsidae) associated with lamella-worms (*Terebellides* spp.) in Scottish, and nearby, waters.

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ABSTRACT

Records are provided for the parasitic polychaete, *Haematocleptes terebellidis* and the commensal polychaete, *Commensodorum commensalis*, both associated with the lamella-worm, *Terebellides stroemii*, in the outer Clyde Estuary, Scotland. New records and basic morphometrics are also provided for the parasitic copepods *Melinnacheres terebellidis* and *M. steenstrupi*, both ectoparasites of lamella-worms. *Melinnacheres terebellidis* is recorded for the first time from British waters in the North Sea and the Celtic Sea, and also from Sweden. Its host is identified as *Terebellides shetlandica* – a recently described species of lamella-worm. *Melinnacheres steenstrupi* is newly recorded from Mull, the Clyde Estuary, Campbeltown Loch, the Celtic Sea, and also from Sweden. The male of *M. terebellidis* is described for the first time and compared with other males of the genus.

INTRODUCTION

The trichobranchid polychaete *Terebellides stroemii* M. Sars 1835 is a tube-dwelling marine worm found in soft sediments and widely distributed in Scottish seas. It is characterised by the possession of 4-lobed lamellate branchiae (gills) superficially resembling the gills of fish or bivalve molluscs. The branchiae of polychaetes are external and typically cirriform or arborescent. The lamellate structure in the genus *Terebellides* is relatively unusual, making this genus readily identifiable and providing the common name of lamella-worm.

The lamella-worm, *T. stroemii*, is known to act as a host to one parasitic and one commensal polychaete species and also to two parasitic copepod species. Although published records of these associates are rare, they are overlooked by most marine ecologists and may be more widely distributed. During routine monitoring of seabed invertebrates by SEPA (and the former Clyde River Purification Board, CRPB) around a sewage discharge off Greenock, in the lower Clyde Estuary, both of the above polychaete species and one of the copepod species associated with *T. stroemii* were observed. These

finds were initially cited in O'Reilly, 1995. This note provides details of these finds and further records from the Clyde Estuary, along with new records of both parasitic copepod species collected from lamella-worms elsewhere in Scottish waters. Some additional notes are also included on material of the parasitic copepods from nearby waters in the southern North Sea, the Celtic Sea and from Sweden.

Material cited here was collected by seabed grabs or dredges. Recovered sediment was sieved in sea-water and the residue fixed with formosaline. Invertebrate fauna was subsequently sorted from the residue and transferred to methylated spirit. Specimens were examined on stereo (Olympus SZH10) or compound (Olympus BH-2 with phase contrast) microscopes with camera attachments. Mounted slides were prepared in polyvinyl lactophenol and drawings carried out with the aid of a *camera lucida* drawing tube.

POLYCHAETES FROM THE LAMELLA-WORM (*T. stroemii*)

The polychaete family Arabellidae contains a small number of species which are endoparasitic within other polychaetes (Pettibone, 1957). One of these, *Haematocleptes terebellidis* Wirén 1886, lives inside the coelom of *T. stroemii* or other terebellomorph polychaetes. *Haematocleptes terebellidis* is up to 25 mm long with a rounded prostomium and reduced parapodia with very short embedded chaetae. It was originally described from Gullmarfjord, Sweden, and until recently there have been no records elsewhere, due, no doubt, to its clandestine habits. It was included in the synopsis of British Amphinomida, Spintherida, and Eunicida (George & Hartmann-Schroder, 1985) under the assumption that it is likely to occur in British waters.

In 1989, during a survey in the Clyde Estuary, off Greenock, a single specimen of *H. terebellidis* was found loose among the washings of a benthic faunal grab sample collected at Station G2 (see O'Reilly *et al.*, 1997 for survey details). The grab sample also contained several large *T. stroemii*, some of which

had ruptured during sample processing and it is assumed the parasite originated from one of these. This Clyde specimen, the first from UK waters, was identified by A. Mackie at the National Museum of Wales where it is now deposited. Since then, two *H. terebellidis* have been recovered by A. Mackie in the Irish Sea, apparently from *T. stroemii* and also from *Ampharete falcata* Eliason 1955 (see Mackie & Garwood, 1995). It is evident that *H. terebellidis* is considerably under-recorded in UK waters and diligent examination of potential hosts would probably reveal it to be widely distributed.

The polychaete family Sphaerodoridae comprises a variety of small worms which are characterised by rows of spherical tubercles ornamenting the body surface (Fauchald, 1974). They are mostly free-living but one species, *Commensodorum commensalis* (Lutzen 1961), is associated with the polychaete *T. stroemii*, living commensally within the tentacular crown of its host. In British waters *C. commensalis* is known from only a handful of specimens collected from St. George's Channel (Mackie *et al.*, 1995), north east England (Garwood, 2000), the Bristol Channel (Mackie *et al.*, 2006), the southern Irish Sea (Robinson *et al.*, 2009), and off the Antrim coast of Northern Ireland (DASSH, 2011). *Commensodorum commensalis* is around 5mm long and, like *H. terebellidis*, was also originally described from Gullmarfjord, Sweden. Of over 1000 *T. stroemii* examined in Gullmarfjord by Lutzen (1961), around 3.5% harboured *C. commensalis* co-habitants. Surveys by CRPB/SEPA in the Clyde Estuary, off Greenock, indicate about 2% infestation with 28 *C. commensalis* recovered from a total of 1364 *T. stroemii*. These were collected over a nine-year period, but mostly from one survey in 1995. Extensive macrobenthic monitoring throughout the Firth of Clyde by CRPB/SEPA has only revealed one other single *C. commensalis*, from Campbeltown Loch in 2001.

The number of *C. commensalis* recovered during four of the monitoring surveys carried out in the Clyde Estuary between 1989 and 1998 is shown in Table 1. The arrangement of sampling stations is illustrated in O'Reilly *et al.* 1997 (except Stns. B4 and E4 which represent subsequent extensions to transects B and E, each 1km from the discharge.) Only the stations where *C. commensalis* was observed are shown in the table. *Terebellides stroemii* was also recovered from grabs at many of the other stations and the total number of grab samples and *T. stroemii* is also provided. Locality details for the polychaetes *H. terebellidis* and *C. commensalis* are given in Appendix 3.

While Lutzen (1961) examined live hosts to locate the *C. commensalis*, none of the Clyde *C. commensalis* specimens was actually found with their host but were recovered from the sample residue following sample fixation. The process of sieving and fixing benthic samples with formalin appears to separate

C. commensalis from its host, although *T. stroemii* specimens were always recorded within the same sample as the *C. commensalis* records.

PARASITIC COPEPODS FROM LAMELLA-WORMS

The family Saccopsidae was established by Lutzen (1964) for a small group of copepods parasitic on ampharetid or trichobranchid polychaetes. The family name was changed to Melinnacheridae by Bresciani & Lutzen (1975) but recently Boxshall & Halsey (2004, p.650-1) pointed out this was an invalid emendation and reverted to the use of Saccopsidae. The saccopsids are highly transformed ectoparasites. Their ovoid bodies are almost devoid of appendages, except for some minute vestigial antennae and mouthparts and a pair of conspicuous egg-sacs in reproductive (ovigerous) females. The males are minute and attach to the female genital area.

The family comprises a single genus, *Melinnacheres*, with only four species: *Melinnacheres ergasiloides* M.Sars 1870 from *Melinna cristata* (M.Sars 1851) in the North Atlantic, *M. levinseni* (McIntosh 1885) from *Ehlersiella atlantica* McIntosh 1885 in the mid-Atlantic between Bermuda and the Azores, and *M. terebellidis* (Levinsen 1878) and *M. steenstrupi* (Bresciani & Lutzen 1961) both recorded from the lamella-worm, *T. stroemii*, in the North Atlantic and Mediterranean.

Bresciani & Lutzen (1961) tabulated the differences between the mature females of *M. terebellidis*, based on two specimens from Greenland, and their new species *M. steenstrupi*, from Greenland, Iceland, Denmark and Sweden. Some of the features (which are summarised in Table 2.) such as the transverse fissure and the cement glands, can be difficult to see in formalin fixed material unless it is cleared in lactic acid. However, other characteristics, such as the body shape, and the attachment location are more readily observed. Adult *M. terebellidis* attach to the host dorsum and have a tapered body shape, while *M. steenstrupi* attach to the host branchiae and have an oval body shape.

There are no published records of *M. terebellidis* in British waters but over a number of years specimens have been received by the author from various surveys in Scottish and nearby seas. All the specimens were attached to the host dorsum (see Fig. 1, 2 & 3). Around 50 parasitised lamella-worms were collected in the northern North Sea from the Magnus, Tern, Lyell, NW Hutton, Brent, Golden Eagle, Western Isles, Emerald, Cheviot, Gryphon, Cairngorm and Braemar oilfields (around 150km north east of the Shetland Isles), and south east of Fair Isle. A few additional specimens of *M. terebellidis* were collected in the southern North Sea, the Celtic Sea, and in Kosterfjord, Sweden.

Table 1. Number of *C. commensalis* from Clyde Estuary Survey stations, 1989-98.

| Year | No. of <i>C. commensalis</i> at sampling Stations: | | | | | | | | | | Total no. of <i>T. stroemii</i> | Total no. of samples |
|------|--|----|----|----|----|----|----|----|----|----|------------------------------------|----------------------|
| | A1 | A3 | B2 | B4 | C1 | D2 | D3 | E3 | E4 | H1 | | |
| 89 | 1 | | | | | | 2 | | | | 147 | 64 |
| 92 | | | | | 1 | | | | | | 234 | 66 |
| 95 | 1 | | 3 | 2 | 3 | 1 | | 3 | 8 | 2 | 805 | 84 |
| 98 | 1 | 1 | | | | | | | | | 178 | 14 |

Table 2. Comparison of *M. terebellidis* and *M. steenstrupi* by Bresciani & Lutzen in 1961.

| <i>M. terebellidis</i> (Levinsen, 1878) | <i>M. steenstrupi</i> (Bresciani & Lutzen, 1961) |
|---|--|
| Body up to 4 mm long. | Body up to 1.8mm long. |
| Body shape oblong, cone shaped. | Body shape ovoid. |
| Chitinous swellings small, separated. | Chitinous swellings large, close together. |
| Single median transverse fissure in front of chitinous swellings. | Median transverse fissure absent, but two vaginal openings in this area. |
| Cement gland is ¼ length of body. | Cement gland is ½ length of body. |
| Attaches to host dorsum. | Attaches to host branchiae. |

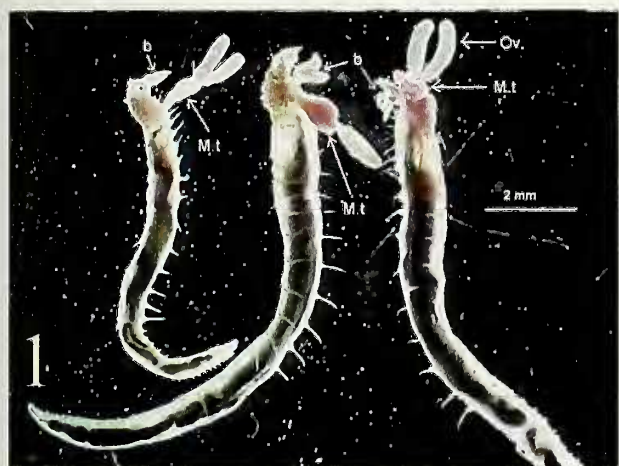


Fig. 1. Parasitic copepods, *Melinnacheres terebellidis* (M.t.), on lamella-worms from NW Hutton Oilfield. (b = branchiae of worm, Ov. = Ovisacs of copepod)

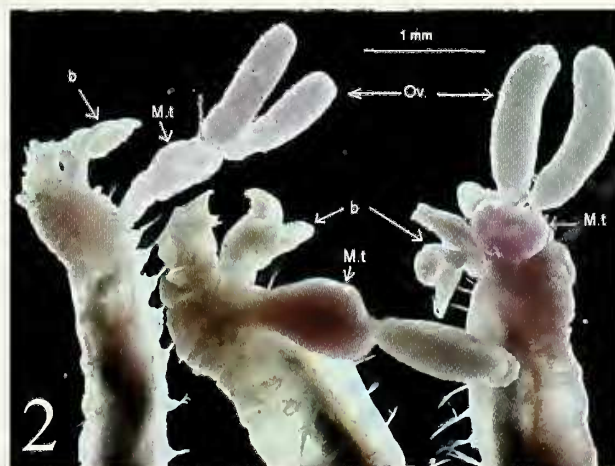


Fig. 2. Anterior region of same lamella-worms showing details of *Melinnacheres terebellidis* (M.t.) attached to dorsum. (b = branchiae of worm, Ov. = Ovisacs of copepod).

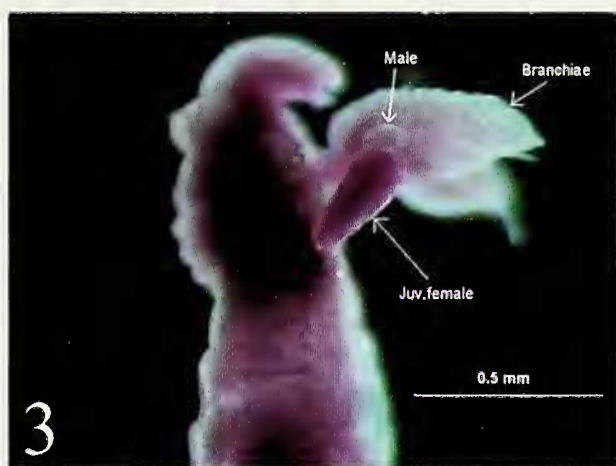


Fig. 3. Lamella-worm from Lyell Oilfield with juvenile female copepod, *Melinnacheres terebellidis*, attached to dorsum. A dwarf male copepod is visible attached to the female.

Melinnacheres steenstrupi is already known from British waters (see Gotto, 2004) and has been found by the author attached to the gills of *T. stroemii* in Irvine Bay in 1981, off Greenock in 1992 and 1995, in Loch Spelve, Mull in 1996, and in Campbeltown Loch in 2004 (see Fig. 4 & 5). Around the British Isles the only other record of this species is from Western Ireland (Gotto & O'Connor, 1980). Additional material of *M. steenstrupi* was also received from the Celtic Sea and from Kosterfjord, Sweden. The discovery of *M. steenstrupi* in the Mediterranean (Laubier, 1969) suggests that its distribution may be much more extensive than the sparse records indicate.

Details of all the "new" material of *M. terebellidis* and *M. steenstrupi* are provided in Appendices 1, 2, and 3. The average length of ovigerous females of *M. terebellidis* is around 1.1mm (range 0.61-1.6mm, n=29) which is smaller than "up to 4mm" stated by

Bresciani & Lutzen (1961). They knew of only two specimens, both from Greenland, of which the one figured appears to be around 3.5mm. The biggest Scottish specimen is 1.6mm long and has ovisacs, 2.2mm long. The ovisacs of *M. terebellidis* appear to be straight or only slightly curved and are about equal to the length of the body. Up to three *M. terebellidis* attach laterally to the anterior dorsum of their host, between setigers 1 and 5, and positioned to the right or left, or on both sides.

For *M. steenstrupi* the average length of ovigerous females is around 1.6 mm (range 1.24 -1.88mm, n=8), similar to "up to 1.8mm" given by Bresciani & Lutzen (1961). Their figured *M. steenstrupi* is 1.2mm long, with 1.4mm ovisacs. The ovisacs of *M. steenstrupi* are up to three times the body length and often strongly curved. The biggest specimen, from Irvine Bay, is 1.88mm long and has 6mm ovisacs (Fig. 4).

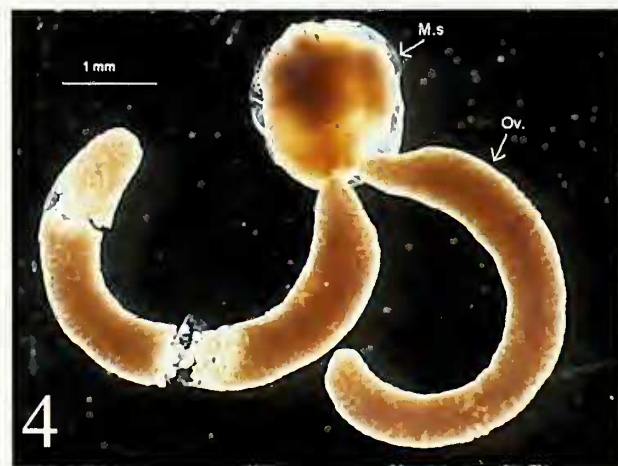


Fig. 4. Parasitic copepod, *Melinnacheres steenstrupi* (M.s.) detached from host lamella-worm (*T. stroemii*) from Irvine Bay. (Ov. = ovisacs of copepod).



Fig. 5. Parasitic copepod, *Melinnacheres steenstrupi* (M.s.) attached to gill stem of host lamella-worm (*T. stroemii*) from Campbeltown. (Ov. = ovisacs of copepod).

MORPHOLOGY OF THE MALES

The male of *M. terebellidis* has, until now, remained unknown. Among the present material of *M. terebellidis*, eight female specimens harboured males attached to their genital area. It appears the males may initially attach while the female is immature (see Fig. 3). Four males were detached from their female partners and permanently mounted on slides in polyvinyl lactophenol to enable a description and comparison with the other known males of the genus. Detaching, mounting and orientating the males to view and draw the cephalic appendages proved problematical and several of the specimens were damaged in the process. Discerning the fine detail of the morphology is difficult even using a x1000 oil immersion lens.

The body is ovoid 0.14mm long and 0.09mm wide. (Fig. 6) It is unsegmented and comprises an anterior cephalic portion, with rudimentary appendages, and a posterior portion which includes, internally, a pair of spermatophore sacs. There appears to be three pairs of cephalic appendages. However in none of the specimens could each one of every appendage pair be observed. It seems that some of the appendages may have been torn off during detachment from the female. The cephalic appendages are interpreted as antennules (A.1), antennae (A.2), and maxillae (Mx.2). The antennule is weakly divided into four segments with two short setae terminally on the distal segment and three (or four) short setae along anterior border of the other three segments. The antennae are 2-jointed, comprising a broad basal segment and a terminal segment with, distally, a pair of chitinous denticulate protuberances. The maxillae consist of two (three?) segments with the terminal segment armed with a similar pair of chitinous protuberances distally. The posterior part of the body is rounded and appears to be devoid of any appendages or ornamentation. A pair of large internal spermatophores is visible through the body wall. In one male two oval spermathecae had been extruded from the posterior end of the male in readiness to be transferred to the female genital area.

DISCUSSION

Bresciani & Lutzen (1961) provided a detailed description of both the external morphology and internal anatomy of *M. steenstrupi*. They figured the rudimentary antennae and mouthparts of the female which had previously been overlooked within the genus. Similar minute antennules, antennae and maxillae are visible in the present material of female *M. terebellidis* but no mandibles have been observed. The antennule of female *M. terebellidis* is considerably smaller than that of the male (see Fig. 6). Bresciani & Lutzen (1961) also illustrated the copepodite and male of *M. steenstrupi* and, in 1975, figured both the male and female of *M.*

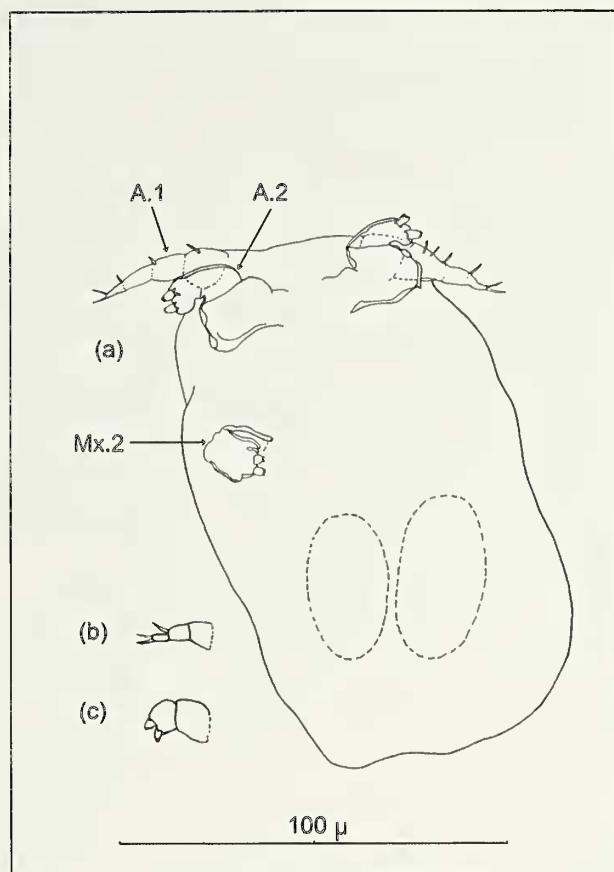


Fig. 6. *Melinnacheres terebellidis*, (a.) male habitus, ventral (A.1 - Antennule, A.2 - Antenna, Mx.2 - Maxilla, dashed ovals - spermatophores), (b.) female Antennule (A.1) and (c) female Antenna (A.2).

ergasiloides. Little new has been published on the genus since, other than a brief re-description of *M. levinseni* by Boxshall (1977).

Mature or ovigerous female *M. terebellidis* and *M. steenstrupi* are easily distinguished by their body shape and attachment location on the host. It appears that Levinsen (1878), in the original description of *M. terebellidis*, also found a juvenile specimen attached to the gill of the same host specimen as the adult. This is the only record of this species attached in such a location. It is possible that this could have been a juvenile *M. steenstrupi* although it would be the only record of both species attached to the same host specimen.

Until recently *T. stroemii* has been the only lamella-worm recorded from British or Scandinavian waters (Howson & Picton, 1997, Holthe 1986). It was initially assumed that specimens of the two *Melinnacheres* species discussed here occurred on the same host species, *T. stroemii*, albeit with different attachment locations. However it was noticed that the hosts of *M. terebellidis* did not match *T. stroemii* being generally smaller, with gill lobes unfused for most of their length and the gill lobes with distinct filamentous papillar projections

posteriorly (on lobes 1 and 2). Material was forwarded to Dr Julio Parapar who determined this to be a completely new species of lamella-worm which has recently been described as *Terebellides shetlandica* Parapar, Moreira, & O'Reilly 2015. Although this species has not previously been recognised in British seas it appears to be widely distributed in offshore waters.

The males in the genus *Melinnacheres* were first described by Sars (1870) for *M. ergasiloides*. Bresciani & Lutzen (1975) redescribed *M. ergasiloides* including the male and corrected a number of Sars' errors with regard to the original description. The male of *M. steenstrupi* was described by Bresciani & Lutzen (1961) and shows a number of small differences from that of *M. ergasiloides*.

The male of *M. terebellidis* appears to be very similar to that of *M. steenstrupi*. The only obvious difference is that the antennule of *M. steenstrupi* appears to comprise only three segments and is armed with five terminal setae only. In the male of *M. ergasiloides* the antennule is more developed being 6-jointed with five long setae and two very short setules. The posterior body portion of *M. ergasiloides* is ornamented with numerous short spinules and bears a pair of swellings plus a pair of rami armed with minute stylets. In *M. steenstrupi* and *M. ergasiloides* a pair of minute mandibles is present. The occurrence of these in *M. terebellides* could not be confirmed although there did appear to be a remnant of a mandible in one specimen. Further study, perhaps with the aid of scanning electron microscopy, may be required to elucidate the fine details of the male morphology (and clarify whether vestigial mandibles are present in either sex). Although the males are all very small it is evident that the three species discussed here could be distinguished on the male morphology alone.

It is clear from the historical records and those added here that the distribution of the two species of *Melinnacheres* from lamella-worms is probably widespread. While their distributions may overlap, it appears they may each be restricted to separate host species. It is not clear whether the host for the original description of *M. terebellidis* from Greenland in 1878 was actually *T. stroemii* or one of its subsequently described congeners. In a study of *Terebellides* from Icelandic waters, Parapar *et al.* (2011) recognised *T. stroemii*, *T. gracilis* Malm, 1874, *T. atlantis* Williams, 1984, and another new species *T. bigeniculatus* from the area. Any of these four might act as hosts of *M. terebellidis* in nearby Greenland seas. There remains a possibility that the *M. terebellidis* material found on *T. shetlandica* in Scotland is a new cryptic species. However, other than its smaller size, its morphology is consistent with the original *M. terebellidis* description. Re-examination of material of *M. terebellidis* (and its

host) from the type locality would be required to investigate this matter. In particular, examination of male specimens or DNA analysis may help resolve this question.

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Appendix 1. Scottish (and other) specimens of *M. terebellidis*. (Letters a,b,c.....each represents a single host, mat.= mature, imm.= immature, ovig.= ovigerous, ♀ = female, ♂ = male) Attachment locations are on the right (R) or left (L) dorsum with the setiger number indicated. For smaller copepods only a selection of the widths were measured.

| Sampling Location / Year | Specimens on host | Copepod length mm | Copepod width mm | Attachment location | Ovisac length mm | Ovisac width mm |
|--------------------------|-------------------|-------------------|------------------|---------------------|------------------|-----------------|
| Magnus 88 | ♀ mat. | 1.0 | 0.76 | R3 | | |
| Kosterfjord 89 | ♀ mat. | 0.72 | 0.36 | L3 | | |
| Tern 89a | ♀ ovig. | 0.8 | 0.36 | R3 | 0.8 | 0.2 |
| Tern 89b | ♀ ovig. | 0.72 | 0.44 | detached | 0.8 | 0.2 |
| Lyell 91a | ♀ post ovig. | 1.6 | 0.48 | R1 | | |
| Lyell 91b | ♀ ovig. | 1.0 | 0.52 | R3 | 0.96 | 0.28 |
| Lyell 91c | ♀ mat. | 0.8, | 0.44 | L1, | | |
| Lyell 91c | ♀ imm. | 0.2 | - | L1 | | |
| Lyell 91d | ♀ imm. | 0.32 | - | L1 | | |
| Lyell 91e | ♀ imm. | 0.4 | - | L2 | | |
| Lyell 91f | ♀ imm. x2 | 0.32, 0.4 | - - | R1, R2 | | |
| Lyell 91g | ♀ imm. | 0.2 | - | R3 | | |
| Lyell 91h | ♀ imm.+♂ | 0.28 | 0.16 | L3 | | |
| Lyell 91i | ♀ imm. | 0.36 | - | L3 | | |
| Lyell 91j | ♀ imm. x3 | 0.2,0.24,0.4 | - - - | L3, L4, L5 | | |
| Lyell 91k | ♀ imm. | 0.08 | - | R4 | | |
| Lyell 91l | ♀ imm. | 0.16 | - | L1 | | |
| Lyell 91m | ♀ imm. | 0.16 | - | L2 | | |
| Lyell 91n | ♀ post ovig. | 1.4 | 0.48 | detached | | |
| Lyell 91o | ♀ ovig. | 1.4 | 0.6 | detached | 0.92 | 0.48 |
| n. North Sea 91a | ♀ ovig. | 1.28 | 0.8 | L2 | 1.2 | 0.36 |
| n. North Sea 91b | ♀ mat. | 1.0 | 0.56 | R3 | | |
| n. North Sea 91c | ♀ ovig.+2♂ | 0.8 | 0.4 | L4 | 0.8 | 0.24 |
| n. North Sea 91d | ♀ imm. | 0.48 | 0.2 | L4 | | |
| n. North Sea 91e | ♀ imm. | 0.6 | 0.28 | R4 | | |
| n. North Sea 91f | ♀ imm. | 0.16 | - | R2 | | |
| n. North Sea 91g | ♀ ovig.+♂ | 1.12 | 0.48 | detached | 0.92 | 0.28 |
| n. North Sea 91h | ♀ ovig. | 1.04 | 0.52 | detached | 1.04 | 0.24 |
| NW Hutton 1,91a | ♀ mat. | 1.0, | 0.4 | L4 | | |
| NW Hutton 1,91a | ♀ mat.+♂ | 1.24, | 0.52 | L6 | | |
| NW Hutton 1,91a | ♀ ovig.+♂ | 1.0 | 0.46 | R4 | 0.96 | 0.32 |
| NW Hutton 1,91b | ♀ mat.+♂ | 1.12 | 0.56 | R3 | | |
| NW Hutton 1,91c | ♀ ovig. | 1.2 | 0.8 | L3 | 1.2 | 0.4 |
| Fair Isle 93a | ♀ mat.+♂ | 0.8, | 0.4 | L2, | | |
| Fair Isle 93a | ♀ imm. | 0.4 | 0.2 | L3 | | |
| Fair Isle 93b | ♀ juv. | 0.6 | 0.2 | R3 | | |
| s. North Sea 93 | ♀ mat. | specimen | lost ! | detached | | |
| NW Hutton 2,02a | ♀ ovig. | 1.4 | 0.76 | L2 | 1.28 | 0.36 |
| NW Hutton 2,02b | ♀ ovig. | 1.0 | 0.6 | R3 | 1.6 | 0.36 |
| NW Hutton 2,02c | ♀ ovig. | 0.96 | 0.52 | L2 | 0.8 | 0.2 |
| NW Hutton 2,02d | ♀ ovig. | 0.96 | 0.48 | R4 | 1.08 | 0.3 |
| NW Hutton 2,02e | ♀ mat.+2♂ | 1.4 | 0.56 | R5 | | |
| Celtic Sea 1, 06a | ♀ ovig. | 1.3 | - | L4 | - | - |
| Celtic Sea 1, 06b | ♀ mat. | 0.8 | - | R3 | | |
| Brent 07 | ♀ ovig. | 1.2 | - | R3 | - | - |
| Golden Eagle, 08 | ♀ ovig.+♂ | 1.42 | 0.61 | detached | 1.59 | 0.29 |
| Western Isles 10 | ♀ ovig. | 1.59 | 0.93 | L2 | 2.2 | 0.37 |
| Emerald 10a | ♀ ovig. | 1.22 | 0.61 | L3 | 1.59 | 0.36 |
| Emerald 10a | ♀ ovig. | 1.35 | - | R2 | 1.59 | 0.36 |
| Cheviot/Alwyn 10 | ♀ mat. | 1.54 | 0.85 | L3 | - | - |
| Cheviot 10 | ♀ ovig. | 1.22 | 0.54 | L3 | 1.10 | 0.29 |
| Gryphon 10a | ♀ ovig. | 0.66 | 0.46 | L3 | 0.73 | 0.29 |

| | | | | | | |
|-------------------|-------------|------|------|----------|------|------|
| Gryphon 10b | ♀ ovig. +2♂ | 0.86 | 0.61 | L5 | - | - |
| Gryphon 10c | ♀ ovig. +2♂ | 0.73 | 0.49 | L2 | - | - |
| Celtic Sea 2, 11a | ♀ ovig. | 0.61 | 0.49 | R3 | 0.86 | 0.25 |
| Celtic Sea 2, 11b | ♀ ovig. | 0.61 | 0.49 | L2 | 0.81 | 0.25 |
| Celtic Sea 2, 11c | ♀ ovig. +2♂ | 0.91 | 0.61 | R3 | 1.35 | 0.29 |
| Celtic Sea 2, 11d | ♀ ovig. | 0.78 | 0.56 | R3 | 1.00 | 0.29 |
| Cairngorm 12 | ♀ mat. | 1.88 | 0.78 | detached | - | - |
| Braemar 1, 12 | ♀ ovig. | 1.22 | 0.68 | detached | 1.10 | 0.29 |
| Braemar 2, 12a | ♀ ovig. +♂ | 0.73 | 0.49 | L3 | 0.86 | 0.26 |
| Braemar 2, 12b | ♀ mat. | 0.61 | 0.29 | R1 | - | - |

Appendix 2. Scottish (and other) specimens of *M. steenstrupi*. (Letters a,b,c.....each represents a single host, mat.= mature, imm.= immature, ovig.= ovigerous, ♀ = female, ♂ = male) Attachment locations are always on the gill. Some copepods have become detached from their host and several hosts show additional attachment scars.

| Location, Year and host specimen no. | Specimens on host | Copepod length mm | Copepod width mm | Attachment location | Ovisac length mm | Ovisac width mm |
|--------------------------------------|-------------------|-------------------|------------------|---------------------|------------------|-----------------|
| Irvine Bay 81a | ♀ ovig. | 1.88 | 1.6 | detached | 6.0 | 0.72 |
| Irvine Bay 81a | ♀ ovig. | 1.76 | 1.2 | Gill | broken | 0.64 |
| Kosterfjord 86a | ♀ mat.+ 1♂ | 1.04 | 0.64 | Gill | | |
| Kosterfjord 86a | ♀ mat.+ 1♂ | 0.96 | 0.64 | Gill | | |
| Kosterfjord 86a | ♀ mat.+ 2♂ | 0.8 | 0.6 | Gill | | |
| Kosterfjord 86a | ♀ imm. | 0.28 | 0.2 | Gill | | |
| Kosterfjord 86b | ♀ mat. | 0.52 | 0.48 | Gill * | | |
| Kosterfjord 86b | ♀ mat.+ 1♂ | 0.4 | 0.48 | Gill | | |
| Kosterfjord 86b | ♀ mat.+ 2♂ | 0.4 | 0.36 | Gill | | |
| Kosterfjord 86c | ♀ mat. | 0.6 | 0.36 | Gill *** | | |
| Kosterfjord 86c | ♀ mat. | 0.64 | 0.4 | Gill | | |
| Kosterfjord 86c | ♀ imm. | 0.44 | 0.28 | Gill | | |
| Kosterfjord 86 | ♀ mat. | 0.76 | 0.6 | detached | | |
| Kosterfjord 86 | ♀ mat. | 0.64 | 0.44 | detached | | |
| Kosterfjord 86 | ♀ imm. | 0.36 | 0.32 | detached | | |
| Greenock 92a | ♀ mat. | 1.4 | 1.4 | Gill | | |
| Greenock 95a | ♀ mat. | 1.52 | 1.6 | Gill | 4.0 | 0.56 |
| L.Spelve 96a | ♀ ovig. | 1.48 | 1.4 | Gill | 3.4 | 0.8 |
| L.Spelve 96a | ♀ ovig. | 1.76 | 1 | detached | 2.2 | 0.48 |
| L.Spelve 96a | ♀ imm. | 1.08 | 0.8 | Gill | | |
| L.Spelve 96a | ♀ imm. | 0.72 | 0.6 | Gill | | |
| L.Spelve 96a | ♀ imm. | 0.48 | 0.36 | Gill | | |
| Campbeltown 04a | ♀ ovig. | 1.68 | 1.4 | Gill | 2.5 | 0.56 |
| Campbeltown 04b | ♀ ovig.+ 2♂ | 1.4 | 1.12 | Gill | 3.2 | 0.52 |
| Campbeltown 04 | ♀ ovig.+ 1♂ | 1.24 | 1.04 | detached | 2.0 | 0.48 |
| Celtic Sea 3, 06a | ♀ imm. | 0.8 | - | Gill | | |
| Celtic Sea 3, 06a | ♀ imm. | 0.8 | - | Gill | | |
| Celtic Sea 3, 06a | ♀ imm. | 0.8 | - | Gill | | |
| Celtic Sea 4 06 | ♀ ovig. | specimen | lost! | detached | | |
| Rame Head 07 | ♀ ovig. | 1.35 | 1.22 | | 1.96 | |

*plus 1 attachment scar on gill
 ***plus 3 attachment scars on gill

Appendix 3. Sampling station details.

(i) Localities for polychaetes *C. commensalis* & *H. terebellidis*:

Clyde Estuary, Stn. A1, 55° 58.33' N, 04° 48.40' W.
Clyde Estuary, Stn. A3, 55° 58.33' N, 04° 49.02' W.
Clyde Estuary, Stn. B2, 55° 58.48' N, 04° 49.81' W.
Clyde Estuary, Stn. B4, 55° 58.50' N, 04° 49.21' W.
Clyde Estuary, Stn. C1, 55° 58.38' N, 04° 48.30' W.
Clyde Estuary, Stn. D2, 55° 58.42' N, 04° 47.84' W.
Clyde Estuary, Stn. D3, 55° 58.47' N, 04° 47.62' W.
Clyde Estuary, Stn. E3, 55° 58.32' N, 04° 47.57' W.
Clyde Estuary, Stn. E4, 55° 58.32' N, 04° 47.33' W.
Clyde Estuary, Stn. H1, 55° 58.28' N, 04° 48.35' W.
Clyde Estuary, Stn. G2, 55° 58.06' N, 04° 48.09' W.

(ii) Localities for copepod *M. terebellidis*:

- Magnus Field (61° 40' N, 01° 20' E), 16/8/1988, coll. A. Mackie, loaned from National Museum of Wales (1988.143).
- Kosterfjord, SW of Yttre Vattenholm, dredged 60-80m, 28/10/1989, coll. A. Mackie, loaned from National Museum of Wales.
- Tern Field, Stn. 5A (61° 30' N, 00° 55' E), 1989, coll. B. Cleator.
- Lyell Field, (60° 53.94' N, 01° 16.29' E, depth 140m), July 1991, coll. S. Hamilton.
- Northern North Sea (location details unknown), 1991?, coll. S. Hamilton.
- NW Hutton Field, Location 1 (61° 10' N, 01° 12' E, depth 160m), 1991?, coll. S. Hamilton.
- Southern North Sea, Block 48, Stn. 14, (53° 26.35' N, 01° 45.61' W, depth 22m), 4/1993, coll. S. Hamilton.
- NW Hutton Field, Location 2 (details unknown), 2002?, coll. P. Garwood.
- Fair Isle, Stn. 1 Braer Survey, (59° 03' N, 01° 59' W, depth 130m) 4-5/1993, coll. S. Hamilton.
- Celtic Sea, Location 1, CEFAS Stn. ISB 25c (49° 45' N, 05° 30' W, depth 135m), June 2006, coll. D. Hall, T. Worsfold.
- Brent Field, GDL Stn. BRS GR15 FA (ED50 TM CM 0 E - Easting 590864.86, Northing 6763053.33), June 2007.
- Golden Eagle Field, GDL Stn. 01-FB (57° 58.94' N, 00° 55.36' W), Mar. 2008.
- Western Isles, GDL Stn. Dev. Site 20-MFB (61° 11.99' N, 00° 45.01' E), Jul. 2010.
- Emerald Field, GDL Stn. EMD 06-MFB (details unavailable), Sep. 2010.
- Cheviot to Alwyn route, GDL Stn. 8496ENV07-A (60° 48.40' N, 01° 39.90' E), Sep. 2010.
- Cheviot Field, GDL Stn. ENV02-MFA (details unavailable), Oct. 2010.
- South Gryphon, GDL Stn. SGG-F1-E-3-MFA (details unavailable), Jan. 2011.
- Celtic Sea, Location 2, Haig Fras, Stn. 63 (50° 30' N, 07° 18' W, depth 100m), June 2011, coll. Steve Jarvis.

- Cairngorm Field, GDL Stn. ENV05-MFA (details unavailable), Aug. 2012.
- Braemar Location 1, Stn. HG06 31C (details unavailable), 2012?
- Braemar Location 2, Stn. BRMR01 24A (details unavailable), 2012?

Stations with GDL prefix were sampled by Gardline Environmental Ltd.

Copepod material from Tern, Lyell, northern North Sea, NW Hutton, and Fair Isle has been deposited in the National Museum of Scotland (NMSZ:2013.071.01-07, NMS.Z 2015.023.1).

Parasitised material of *T. shetlandica* from Western Isles, Emerald, Cheviot, South Gryphon, and Braemar fields has also been deposited (NMS.Z 2015 023.1-5) and material from the Celtic Sea (Location 2) has been deposited in the Natural History Museum, London (NHMUK ANEA 2015.201-02). Note the host of the "Western Isles" specimen is mistakenly attributed to "near the Western Isles" (suggesting the Outer Hebrides off western Scotland) in Parapar, Moreira, & O'Reilly (2015), when in fact it originates from the "Western Isles Development Project" in the northern North Sea, about 160km east of the Shetland Isles.

(iii) Localities for copepod *M. steenstrupi*:

- Kosterfjord, SW of Yttre Vattenholm, dredged 40-65m, 27/08/1986, coll. A. Mackie, loaned from National Museum of Wales (1986.108).
- Irvine Bay, Stn. Q1 (55° 35.72' N, 04° 43.80' W, depth 20m) 1981.
- Greenock, Ironotter Point, Stn. H1 (55° 58.28' N, 04° 48.35' W depth 20m) April 92.
- Greenock, Ironotter Point, Stn. H1, (55° 58.28' N, 04° 48.35' W depth 20m) May 95.
- Loch Spelve, Mull, Fish Farm A Stn. 9 (location details unknown), 14/5/1996.
- Campbeltown Loch, Stn. 3 (55° 25.96' N, 05° 33.09' W depth 20m) 2/11/2004.
- Celtic Sea, Location 3, CEFAS Stn. ISB 20b (51° 14.98' N, 07° 30.00' W, depth 93m) June 2006, coll. D. Hall, T. Worsfold.
- Celtic Sea, Location 4, CEFAS Stn. ISB 21c (51° 00.02' N, 07° 59.98' W, depth 100m) June 2006, coll. D. Hall, T. Worsfold.
- Rame Head, CEFAS Stn. G33 (50° 16.8' N, 04° 12.6' W), 2007.

Material from Irvine Bay, Greenock, Loch Spelve, and Campbeltown Loch has been deposited in the National Museum of Scotland (NMSZ:2013.071.08-13).