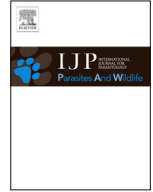




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Invited Review

Global diversity of fish parasitic isopod crustaceans of the family Cymothoidae

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ABSTRACT

Of the 95 known families of Isopoda only a few are parasitic namely, Bopyridae, Cryptoniscidae, Cymothoidae, Dajidae, Entoniscidae, Gnathiidae and Tridentellidae. Representatives from the family Cymothoidae are obligate parasites of both marine and freshwater fishes and there are currently 40 recognised cymothoid genera worldwide. These isopods are large (>6 mm) parasites, thus easy to observe and collect, yet many aspects of their biodiversity and biology are still unknown. They are widely distributed around the world and occur in many different habitats, but mostly in shallow waters in tropical or subtropical areas. A number of adaptations to an obligatory parasitic existence have been observed, such as the body shape, which is influenced by the attachment site on the host. Cymothoids generally have a long, slender body tapering towards the ends and the efficient contour of the body offers minimum resistance to the water flow and can withstand the forces of this particular habitat. Other adaptations to this lifestyle include small sensory antennae and eyes; a very heavily thickened and calcified cuticle for protection; and sharply curved hooks on the ends of the pereopods which allows these parasites to attach to the host. Most cymothoids are highly site and host specific. Some of these parasitic cymothoids have been reported to parasitise the same host fish species for over 100 years, showing this species specificity. The site of attachment on the host (gills, mouth, external surfaces or inside the host flesh) can also be genus or species specific. This paper aims to provide a summary of our current knowledge of cymothoid biodiversity and will highlight their history of discovery, morphology, relationships and classification, taxonomic diversity and ecology.

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1. Introduction

Cymothoid isopods are obligate fish parasites, occurring in all oceans with the exception of polar waters. The family is primarily marine, with limited occurrence in African and Asian freshwaters, but a moderate diversity in tropical South American river systems, notably the Amazon and its tributaries. Most cymothoids occur on hosts within the 200 m bathymetric, with fewer than 10 species extending beyond 500 m in depth. The family is among the larger of the isopod families comprising some 40 genera and more than 380 species (Ahyong et al., 2011). Greatest diversity occurs within the tropics, with a rapid attenuation in diversity towards high latitudes.

The Cymothoidea belongs within the suborder Cymothoidea Wägele, 1989, and the superfamily Cymothoidea Wägele, 1989. This superfamily forms a clade of families that show a gradient from commensal and micropredation in the families Corallanidae, Aegidae and Tridontellidae to obligate parasitism in the Cymothoidea (Brandt and Poore, 2003). Cymothoids are large isopods, with few species below 10 mm in length or more than 50 mm in length. Characteristic of the family is that the females are far larger than the males, this trait being most strongly expressed in the buccal and gill attaching genera.

Cymothoids are one of the best-known groups of isopod among the general public. They are familiar to fishers and anglers as sea lice (incorrectly – not to be confused with arguloid or caligoid copepods), tongue-biters and fish doctors, and are of interest to fish biologists and to the aquaculture industry as potential pests or disease vectors. The account of the tongue-replacing isopod (Brusca and Gilligan, 1983) achieved widespread and sustained publicity.

2. History of discovery

The family Cymothoidea is unique in being among the first isopods described and being the first isopod family subjected to a comprehensive world revision (Schioedte and Meinert, 1881, 1883, 1884). Cymothoids, being relatively large (10–50 mm), came to the attention of taxonomists early in the history of crustacean taxonomy, in large part through the work of the early fish taxonomists, notably Pieter Bleeker, who would have seen and collected this ‘by-catch’. Fish collections today are still a source for undescribed cymothoids.

The Cymothoidea differ significantly from all other free-living isopod families in the large number of genera and species described before 1900 and before 1950. As Poore and Bruce (2012) showed, there was a spike in the documentation of isopod species in the period 1970–1990. The Cirolanidae are typical of free-living families with 12% and 28% of species described by 1900 and 1950, respectively. In contrast approximately 42% of Cymothoidea (depending on accepted synonymies) were described by 1900, 55% by 1950 (Fig. 1).

William Elford Leach (1813–1814, 1815, 1818) was the first significant contributor naming nine cymothoid species and establishing the family name Cymothoidea Leach, 1818. Earlier described species such as *Cymothoa ichtiola* (Brünnich, 1764), the first post-Linnaeus species to be described and *Ceratothoa imbricata* (Fabricius, 1775) predate the family and its genera. Leach achieved particular fame through naming eight genera based on the name Caroline and Carolina (after Queen Caroline of Britain, 1768–1821; see Bruce, 1995). Milne Edwards’ (1840) *Histoire naturelle des crustacés comprennent l’anatomie, la physiologie et la classification de ces animaux* can be taken as the practical start to the discovery for the Isopoda including the Cymothoidea as that publication was the first world-wide review of the Crustacea, at which point 30

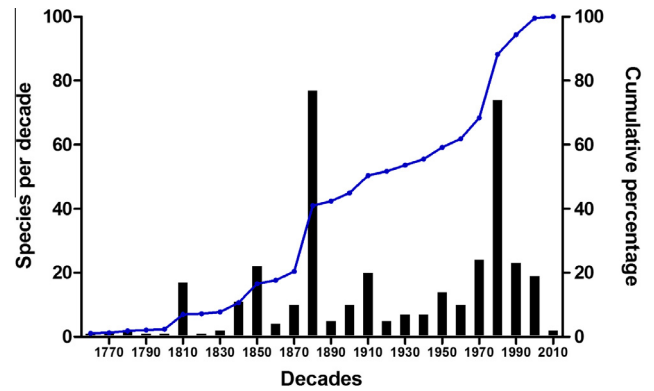


Fig. 1. Absolute numbers and cumulative percentage of species of Cymothoidea (373) published per decade since Linnaeus (1758). Data from the World List of Marine, Freshwater and Terrestrial Isopod Crustaceans hosted by the Smithsonian and at the WoRMS database (Schotte et al., 1995 onwards).

species names of Cymothoidea had been proposed. Others from that era made individual contributions such as Risso (1816), Say (1818), Otto (1828) and Perty (1833).

The period following Milne Edwards’ (1840) work saw several taxa described, but the most significant contribution was a single work by the fish taxonomist Pieter Bleeker (1857) describing 14 species; both Edward John Miers (1877, 1880) and G. Haller (1880) each described five species.

The great work of the Danish co-authors Jørgen Christian Schioedte and Frederik Vilhelm August Meinert fixed the concept of the family that stands today, and provided a largely unambiguous concept for the Cymothoidea. This work is an outstanding contribution by the standards of the day and nothing since has come close to that breadth of coverage. Schioedte and Meinert undertook a comprehensive world revision of what is now the superfamily Cymothoidea, including the families Corallanidae, Aegidae (Schioedte and Meinert 1879a,b) and Cymothoidea (Schioedte and Meinert 1881, 1883, 1884) in an age that had no ‘rapid communication’, no rapid shipping and no rapid international travel. Schioedte and Meinert borrowed specimens from the major museums of the western world of Europe and the USA. Again, ahead of their time, they specified both the provenance and the holding institutions of the specimens that they examined. Schioedte and Meinert also offered a detailed classification for the family, proposing several sub-family and tribe names. Some of these reflected perceptible differences in the morphology of the species and genera, but their classification caused some subsequent confusion, and these family group names have subsequently been largely ignored. Although the descriptions and drawings may be regarded as too brief and simple by the standards of today, this does not detract from their outstanding contribution. The completion of their body of work brought the total number of species proposed to 146 in 33 genera. The comprehensive nature of their monographs is demonstrated by the fact that of the genera accepted today 35% are attributed to Schioedte and Meinert. Since 1884 only 17 genera have been described, and 16 genera are junior synonyms or otherwise invalid.

The decades following Schioedte and Meinert’s work saw little sustained activity, the most significant contribution being the accumulated works of Carl Bovallius [1855–1887] describing seven cymothoid species (among other taxa). The early Twentieth Century in contrast saw considerable activity with contributions from the major isopod taxonomists of the period such as the Reverend Thomas Roscoe Rede Stebbing [1893–1923; two species], Harriet Richardson [1884–1914; 24 species], Hugo Frederik Nierstrasz [1915–1931; five species], and Herbert Matthew Hale

[1926–1952; three species], the last named whose work continued past World War II.

The 1970s saw the start of a period of sustained research on the family, with a number of authors working for sustained periods both regionally and globally. Slightly pre-dating this period were Thomas Elliot Bowman [1962–1983; 13 species] who published a series of detailed descriptions and redescrptions of cymothoids and Jean-Paul Trilles [1961–present; seven species] who published on diverse aspects of the Cymothoidae, and in a taxonomic context is particularly noted for his compilations of synonymies and museum holdings (Trilles, 1994). Ernest H. Williams and Lucy Bunkley-Williams [1978–2006; 27 species] were prolific in publishing on the Caribbean fauna and also that of Japan and Thailand. These authors also provided a synopsis of fish-parasitic isopods and corrected many of the problems and errors encountered in the fish-parasitic literature (Bunkley-Williams and Williams, 1998; Williams and Bunkley Williams, 2000). The late Vernon Thatcher [1988–2009; 15 species] made a huge contribution to what had been an almost unstudied region and habitat – the South American freshwaters. V.V. Avdeev [1973–1990; 15 species] and Niel L. Bruce [1982–present; 39 species] both made a significant contribution to the documentation of Indo-Pacific Cymothoidae, Bruce notably attempting to revise and restrict generic concepts within the family. Richard C. Brusca [1977–1983; 2 species] documented the Cymothoidae of the tropical East Pacific, culminating in an influential monograph (Brusca, 1981) that presented the first phylogeny and evolutionary hypothesis for the family.

Regional documentation of the Cymothoidae has been highly inconsistent on a global basis. Proximity to major population centres clearly influenced progress in this regard. The major centres of post-Linnaean taxonomy were the museums and universities (parsonage in Stebbing's case) of Europe and North America, and the Cymothoidae of those regions were consequently well documented by the Twentieth Century. The age of European expansion and empire played its part in documentation of tropical faunas, notably the Indo-Malaysian region. Since the 1970s some regions have received in-depth and specialist attention, notably the East Pacific (Brusca), the Caribbean (Williams and Bunkley-Williams), and eastern Australia (Bruce).

3. Variable morphology, generic and species synonymies – a particular challenge

A particular challenge, indeed an impediment to progress on the taxonomy of the family, is the high level of variability shown by many species. In the historic period of cymothoid taxonomy it is clear that intra-specific variation became confounded with interspecific differences. The present high level of names in synonymy attests to this difficulty. This particular difficulty is a 'two-way street'. To give just one example, the species *Mothocya melanosticta* (as *Irona melanosticta*) had become regarded as a highly variable species, indiscriminate in host preference, occupying diverse habitats from the pelagic to inshore, occurring in all oceans; in fact, this was simply due to sustained misidentifications of what proved to be a group of nine similar looking species with narrow host and habitat preferences (see Table 3 in Bruce, 1986). *M. melanosticta* was shown to occur only on flying fishes (see Bruce 1986). Conversely many spurious new names were proposed on supposed differences of what later proved to be intra-specific variation; this latter situation has been a particular issue for *Nerocila*, as the long synonymy for *Nerocila orbignyi* shows (see Bruce, 1987a).

The problem that this poses is that in many cases it is still highly uncertain which names are valid, which should be placed into synonymy and equally which species to bring out of synonymy. In many cases it is not possible to confirm or reject many

of the literature records for many species, so distribution and patterns of host preference are often, at best, uncertain.

Generic concepts remained loose, often not based on the type species, and modified as new species were discovered and placed into available genera. Genera described in the Nineteenth Century were given brief diagnoses that were evidently subsequently difficult to apply – consequently species were frequently placed incorrectly into genera, sometimes comprehensively. For example, of the approximately 60 species that had been placed in *Livoneca* up to 1990, most were relocated to *Elthusa* and *Ichthyoxenus*, with only three species now remaining in the genus (see Bruce, 1990). Similarly the name *Irona* was widely misused for what was the genus *Mothocya*.

4. Relationships and classification within the Cymothoidae

The Cymothoidae has long been recognized as a well-unified family, nested within the group of carnivorous, commensal, micro-predatory and parasitic families that now constitutes the superfamily Cymothoidea Leach, 1814.

Classification within the family dates from the work of Schioedte and Meinert (1884) who proposed five family-group names. These names were subsequently used erratically or ignored. The Anilocridae and Saophridae became subsumed by the Cymothoidae as subfamilies, while the Ceratothoinae and Livonecinae were regarded as tribes. Bruce (1990) concluded that only the Anilocrinae and Cymothoinae could be recognised. Trilles (1994) in his 1994 *Podromus* used all of these names, though without explanation, definitions or morphological justification. Earlier Avdeev (1985) also made use of these names suggesting that the Cymothoidae consisted of two subfamilies, and a further two tribes, one being a new family-group name. These names were not explicitly defined or justified, and in large part were based on homoplasious characters of body shape or site of attachment, and found little favour with most taxonomists.

As mentioned above, perception of relationships within the family was strongly driven by site of attachment – namely external or scale attaching (Fig. 2A), buccal dwelling (Figs. 2C, E, F), gill attaching (Fig. 2D) and flesh burrowing (Fig. 2B). Brusca (1981) presented a cladogram and a phylogeny of the family (Brusca, 1981, Fig 4A and B), identifying the putative ancestor as an externally attaching 'Nerocila-like' taxon. The externally attaching genera and part of the South American freshwater genera were sister groups to all remaining cymothoids. Brusca termed the two major groups the 'Nerocila lineage' and the 'Livoneca lineage'. *Livoneca* (and presumably other non-specified gill-attaching genera) was considered to be the sister group to flesh-burrowing and freshwater South American taxa, the sister group to these being 'other flesh burrowing taxa'.

Bruce (1987a,b,c, 1990) redescribed and redefined the externally attaching and gill attaching cymothoids from Australian waters. By 1997 it was apparent on morphological criteria that there was a group of related genera that approximated to the 'Nerocila lineage' of Brusca (1981) and the Anilocrinae of Schioedte and Meinert (1883). Bruce (1987b) accepted the use of the name Anilocrinae for the externally (scale attaching) genera, giving a diagnosis to the subfamily. Bruce (1990) later revised this opinion when reviewing the gill-attaching cymothoids, observing that genera and species of what were Anilocrinae by morphological criteria also occurred on the gills (*Livoneca*, *Nerocila lomatia*, *Norileca*) and in the mouth (*Smenispa*). Furthermore one species of the otherwise gill-attaching genus *Mothocya* was buccal attaching and had a general body shape similar to that of *Cymothoa* or *Ceratothoa*. Bruce (1990) concluded "there still inadequate data for many cymothoid genera, it seems preferable to avoid the use of subfamily names other than Anilocrinae and Cymothoinae." To

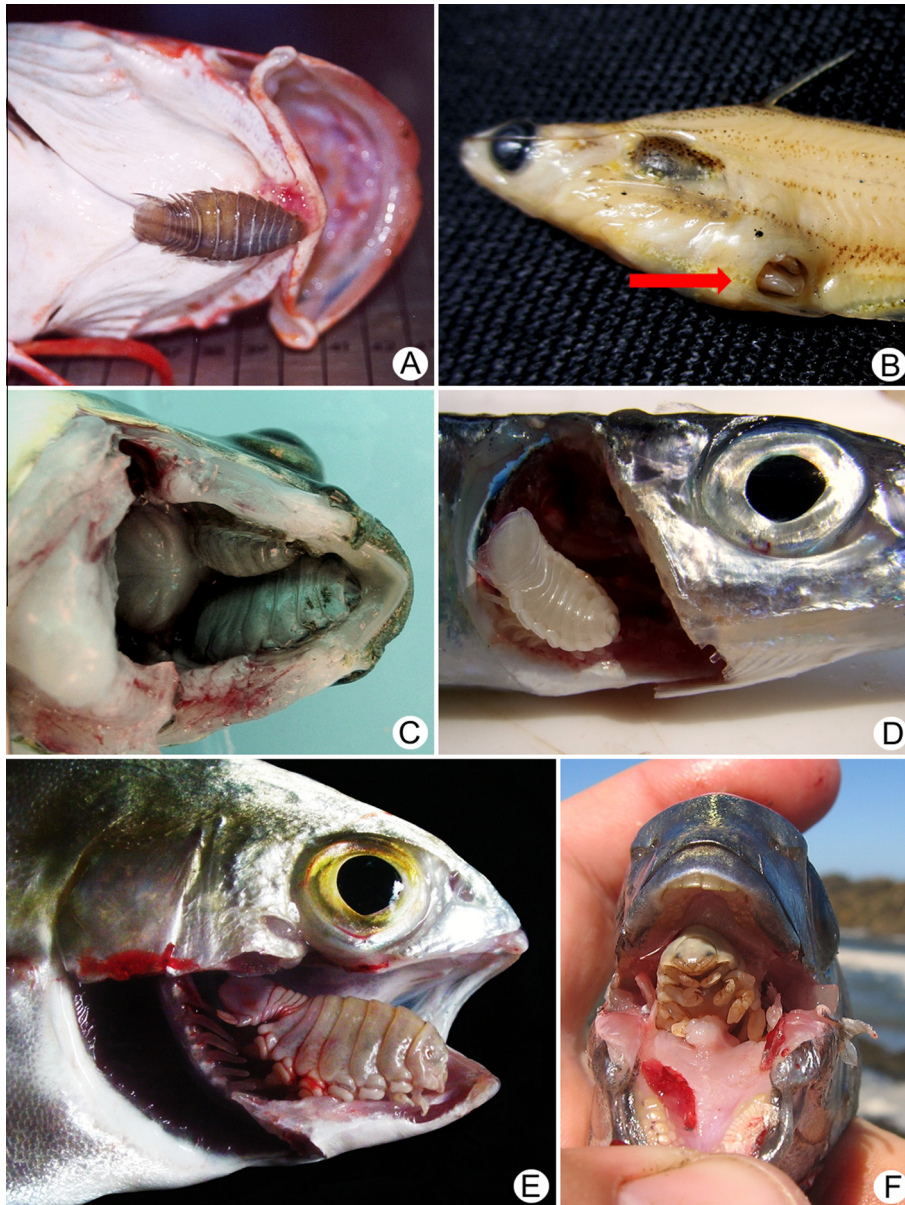


Fig. 2. Different attachment sites of cymothoids. External or scale attaching (A), flesh-burrowing (B) buccal dwelling (C, E, F) and gill attaching (D).

the present day there remains little use of subfamily categories within the family.

In the Twenty-first Century small molecular data sets, and data sets using unidentified taxa were analysed, giving inconsistent and probably unreliable results. For example Dreyer and Wägele (2002) using 18S rDNA; Ketmaier et al. (2008) using 16S rRNA and cytochrome oxidase I; and Jones et al. (2008) using 16S mtDNA. Given the small number of taxa, the unexpected pairings, such as *Nerocila* with *Ceratothoa* rather than *Anilocra* (see Ketmaier et al., 2008), should not be considered as significant. Jones et al. (2008) showed a lack of unity for a '*Nerocila* clade', with that genus forming a clade together with *Cymothoa* and *Olencira*.

Recently Hadfield (2012) reappraised the relationships of the genera of the Cymothoidae based on a morphological data set. The resultant trees revealed that the 'Anilocrinae' form a well-supported clade and are in a terminal position. The buccal attaching taxa (*Cymothoa*, *Ceratothoa*, etc.) also form a robust clade that is sister to the 'Anilocrinae clade'; the gill-attaching genera are basal and did not form a clade under any constraints. There are several

implications from this result: the long-held view that the gill attaching genera together derived from the purportedly *Nerocila*-like 'ancestor' is not upheld; the *Nerocila*-clade and *Ceratothoa* clade are more derived than the gill attaching and flesh-burrowing taxa. The question that then must, in our view, arise, is what would be the plausible ancestral isopod to the Cymothoidae? In our opinion the ancestor would most likely have been similar to a Corallanidae or Aegidae. The mouthparts of *Rocinela*, as pointed out by Dreyer and Wägele (2001) are more similar to those of the Cymothoidae than to the remaining Aegidae. *Rocinela* have the most flat body of the Aegidae, and adapting to living in the gill cavity is certainly plausible, as is becoming more permanently attached to the hosts. At least one species, *Rocinela signata*, is known to occur in the gill chamber of its host fish (Bunkley-Williams et al., 2006; Cavalcanti et al., 2012). Further more, one still has to consider that there may have been two evolutionary events leading to fish parasitism in the Cymothoidae, which within the Isopoda has occurred in several different families (e.g. Gnathiidae, Aegidae, Corallanidae, Tridentellidae and Cymothoidae).

5. Classification and relationships within the Isopoda

The Cymothoidae have been regarded as part of a “lineage” (Brusca, 1981) going from the free-living scavenging and predatory Cirolanidae, through to the families Corallanidae, Tridontellidae and Aegidae showing progressively more trophic dependency as commensals and micropredators, to the obligate fish parasites of the family Cymothoidae. The then Epicaridea (now Bopyroidea and Cryptoniscoidea) were regarded as related, indeed some analyses showing them to be the sister group to the Cymothoidae, but there was a lack of clarity as to the precise degree of relatedness. These families were placed with the suborder Flabellifera.

Wägele (1987) challenged this classification, and suggested (among other changes) the separation of the Cymothoida from the Sphaeromatidea. This view was not well received at the time, and the first cladistic analysis of the Isopoda by Brusca and Wilson (1991) did not support this separation. For a period there was at times acrimonious debate over isopod classification, which eventually succumbed through inertia and immovability of the different parties. Brandt and Poore (2003) developed a much larger data set than had previously been used, and further offered it widely for appraisal prior to publication. Their analysis strongly supported that the Flabellifera be abandoned and the Cymothoida and Sphaeromatidea be recognized as suborders, supporting Wägele’s original assessment, albeit based on different characters. The new resultant classification was immediately widely accepted (with little dissent). The Cymothoidae are sister group to the Aegidae or Bopyridae within the clade that is the superfamily Cymothoidea.

6. Fossil record

The fossil record for the Cymothoidae is extremely poor – indeed virtually non-existent. In part this is because it is not possible to place fossil isopods without appendages into an extant family with any degree of confidence. This was demonstrated for the species *Palaega lamnae*, which Bowman (1971) showed could be placed equally in the Cirolanidae or the Cymothoidae.

Conway Morris (1981) showed the bopyrid isopods were present back to the Jurassic era, their presence being indicated by the characteristic distortion of the carapace in fossil decapods (crabs and shrimps). It is equally probable therefore the Cymothoidae had also evolved at that point.

To our knowledge no fossil isopod has been specifically attributed to the family Cymothoidae.

7. Taxonomic diversity

The Cymothoidae is a large family, exceeded in the number of genera and species only by the Sphaeromatidae, Cirolanidae and Bopyridae. There are currently 40 genera with 383 species accepted (See Fig. 3 for examples of some of the different generic body forms). Sixteen genera and 83 species are in synonymy. A further seven species are regarded as *Nomina dubia*. The family, as is typical for most marine isopod families, is dominated by a relatively small number of large genera – such as *Anilocra* (49 species), *Nerocila* (42 species), *Ceratothoa* (33 species), *Cymothoa* (51 species), *Elthusa* (28 species) and *Mothocya* (29 species). The predominantly freshwater genus *Ichthyoxenus* has 24 species, while most of the remaining genera have between one and ten species, including the South American freshwater genera.

8. Hosts

Cymothoids have been described from representatives of almost every single family of marine teleosts as well as a number

of freshwater groups. In general there does not seem to be a specific host characteristic, whether morphology or behaviour, that influences the possibility of being parasitised by a cymothoid. In addition to parasitising teleosts, cymothoids have also been reported from chondrichthyan fishes, jellyfish, cephalopods, crustaceans, and amphibians (Trilles and Ökterner, 2004; Ateş et al., 2006). Although there are within the different cymothoid genera and species varying degrees of host specificity, there exists a general trend that host specificity increases with decreasing latitude. For example, high-latitude temperate species (e.g. *Anilocra phylsodes*) use more host taxa than tropical species, where tropical species of *Anilocra* typically primarily parasitize fish of a single family, possibly a single genus and in some cases a single fish species (Bruce, 1987b). This might be related to the general lower cymothoid diversity in temperate regions where the low diversity possibly results in an increased number of hosts species used. The opposite might be true for the tropics where the high cymothoid diversity possibly results in competition that leads to an increasing specialization. However, the current uncertainties in species level taxonomy within the family referred to earlier (Section 3), also impacts on our knowledge of host specificity. For example, if we accept that every host record of *Ceratothoa trigonocephala* is correct then we will conclude that it parasitises at least 18 species in 17 genera and 14 families of fish hosts. Recent work by our group actually shows that the majority of these host records are due to incorrect identification of the cymothoid and not because this species parasitises a wide range of hosts (Hadfield et al., 2014a). Incorrect host identification further confuses the matter making accurate host records scanty.

Another interesting aspect of cymothoid-host interaction is their specific site of attachment, which seems to be very consistent within species and sometimes genus specific. Bowman and Mariscal (1968) found that the attachment position of *Nerocila heterozota* on *Amphiprion akallopisos* was always on the anterior trunk region, just behind the head. Likewise, Morton (1974) showed the attachment site of *Nerocila phaeopleura* is overlying the lateral line in the posterior third of the body. Morton (1974) further suggested that site specificity is determined by the needs of the parasite and the limitations exerted by the morphology and habits of the host.

Fish infested by cymothoids have been described as suffering from localised damage or lesions, reduced growth and condition index, host behavioural problems and in extreme cases death (Romestand and Trilles, 1979; Brusca, 1981; Grabda and Rokicki, 1982; Colorni et al., 1997; Horton and Okamura, 2001; dos Santos Costa and Chellapa, 2010; Rameshkumar and Ravichandran, 2014). Impaired reproduction and a reduced lifespan in some hosts have also been observed (Adlard and Lester, 1994). Depending on the particular species and its location on the host, a number of negative effects can be observed on the fish host (Trilles, 1994), namely: buccal species cause tongue degeneration (Romestand and Trilles, 1979; Brusca and Gilligan, 1983), skull deformations (Trilles, 1994) and teeth problems (Romestand and Trilles, 1979); gill parasites cause gill and branchial filament damage (Kroger & Guthrie, 1972), pericardial cavity and heart decompression, and reduced respiratory metabolism (Trilles, 1994). External parasites can cause partly degenerating fins, particularly near the site of attachment (Bowman and Mariscal, 1968; Brusca, 1978) and damage to the scales and epidermis. Physiological modifications of the chimic composition of the fish plasma (Romestand and Trilles, 1979; Horton and Okamura, 2003) have been observed, and in many instances buccal and surface parasites have affected growth rate (Trilles, 1994). The sustained aerobic swimming speed and the swimming endurance of parasitised fish at high-water speeds was also found to be reduced due to the drag of the external isopod (Östlund-Nilsson et al., 2005).



Fig. 3. Representative cymothoid forms. *Mothocya* (A); *Olencira* (B); *Norileca* (C); *Anilocra* (D); *Nerocila* (E); *Telotha* (F); *Cymothoa* (G); *Cinusa* (H); *Ceratothoa* (I); *Agarna* (J, K). Scale bars = 5 mm.

However, there have also been a number of studies where no obvious or recordable harmful effects were observed (Brusca, 1981; Landau et al., 1995). Östlund-Nilsson et al. (2005) proposed that the apparent lack of change in the condition of infested hosts may be a result of infested hosts feeding more and more often than non-parasitised hosts, in order to compensate for the high rate of energy loss. Interestingly, it appears as if populations of the same cymothoid species can have either a negative impact or no effect at all, depending on which host they infest. This can be seen on the East Coast of the United States where *Livoneca ovalis* cause growth inhibition of young white perch, (Sadzikowski and Wallace, 1974) as well as erosion of gill filaments and flared opercula recorded from bluefish (Meyers, 1978), but have no apparent damage or effect on the growth of the young-of-the-year bluefish, *Pomatomus saltatrix*, in a nearshore environment (Landau et al., 1995).

9. Reproduction and life cycle

The life history and its cycle for most individual cymothoid species is poorly known or documented. One of the main difficulties arises from keeping these parasites in laboratory conditions and monitoring their growth, especially if the parasite resides inside

the host. Similarly, in the field there is the problem of recognising the same fish host as markings can fade and fin clips or wounds can heal. Similar to other isopods, the adult female cymothoid is known to carry the developing embryos in the marsupium. This pouch protects the young and keeps the embryos aerated with its oostegites (Varvarigos, 2003). The eggs hatch in the marsupium and undergo their first moult into the pullus stage, which are sexually non-differentiated. The first pullus (pullus I) is only found in the marsupium where it will moult into the second pullus (pullus II) which has six pairs of pereopods armed with dactyli and a strongly pigmented cuticle. Sexual differentiation occurs only after the young have left the brood pouch in search of a host. These young and active isopods (now termed manca) are well equipped for swimming with long setae on the margins of the appendages and well developed eyes. They can remain free swimming for several days feeding on yolk stores (Brusca, 1978) and are capable of leaving a host provided they have not moulted into the following stage. Mancas will seek an appropriate host on which to attach and, once found, will moult and lose their swimming setae, becoming immotile. After permanent attachment is complete, a subsequent moult follows where a seventh segment and pair of pereopods appear and the isopod is in a pre-adult form. The isopod is now referred to as a juvenile which will function as a male until

circumstances require it to transform into a female. The transformation of the male into the female is a complex process and is dependent on many factors including the presence of other individuals, especially other females which would prevent the transformation (Lincoln, 1971). Sexual transformation occurs as the male organs regress and the female reproductive apparatus develops and becomes more dominant. Once fully female, the isopod is known as an adult.

Little information is available on the duration of one cycle which can range from 62 days in *Anilocra pomacentri* (see Adlard and Lester, 1995) to one year for *Glossobius hemiramphi* (see Bakenhaster et al., 2006). To fully understand the potential impact of these parasites on aquaculture more studies are needed on the life cycles and reproduction of cymothoids.

10. Biogeography

Only when mapping the distribution of the marine cymothoids using Spalding et al.'s (2007) Marine Ecoregions of the World (MEOW) can one really appreciate their skewed global distribution (Fig. 4, data from Poore and Bruce, 2012). It is clear that the highest diversity resides within the tropical regions with the Central Indo-Pacific realm hosting almost double the number of species than any other realm. What is interesting to note is that although 41 species have been recorded from the Tropical Atlantic realm, the vast majority are from the Western Atlantic (see Williams and Williams, 1981, 1982, 1985 to cite a few) and almost nothing from the Eastern Atlantic (off Africa). Although there is no doubt that the highest biodiversity of cymothoids are indeed in the tropics, the low number of species recorded from the temperate regions might rather be a reflection of the focus of researchers that have been working on this group rather than their actual distribution. It is clear from Section 2 that the main focus of the researchers

that contributed the most to species descriptions was on the tropical fauna. For example Poore and Bruce (2012) reported only two species from the Temperate South African realm, but recent focused research by Kerry Hadfield and colleagues from this region showed that this number have the potential to increase fivefold (Hadfield et al., 2010, 2011, 2013, 2014a,b).

No clear distribution pattern is apparent for the freshwater cymothoids where the majority (approximately 13 species) are known from the Amazon region of South America (Thatcher et al., 2003, 2009) followed by six species distributed from various localities in Asia and only four from central Africa (Brusca, 1981).

11. Human issues

The occurrence of cymothoids in natural populations is often irregular and the levels of prevalence and distribution extremely variable (Brusca, 1981). Infestations prevalence of up to 73% by *Ceratothoa* spp. and *Cymothoa* spp. in natural populations (see Horton and Okamura, 2002; Horton et al., 2005; Hadfield et al., 2013) can be considered as very high, however it can increase to 98% on fish kept in farming facilities (Sievers et al., 1996). Other occurrences of cymothoids in aquaculture are also very high, causing mass mortalities in cultured fish (Horton and Okamura, 2001, 2003; Mladineo, 2002, 2003; Rajkumar et al., 2005a,b). In the majority of cases, fishes infested by cymothoids in aquaculture are not those traditionally recorded as the natural host. Papapanagiotou et al. (1999) therefore, proposed that the cultured fishes are only parasitised due to infested wild fish (which are the natural hosts) coming in close contact with the cultured fish and transferring their parasites. Horton and Okamura (2001) further supported this idea as none of the cymothoid isopods they reported from aquaculture conditions are known to parasitise the same species in the wild.

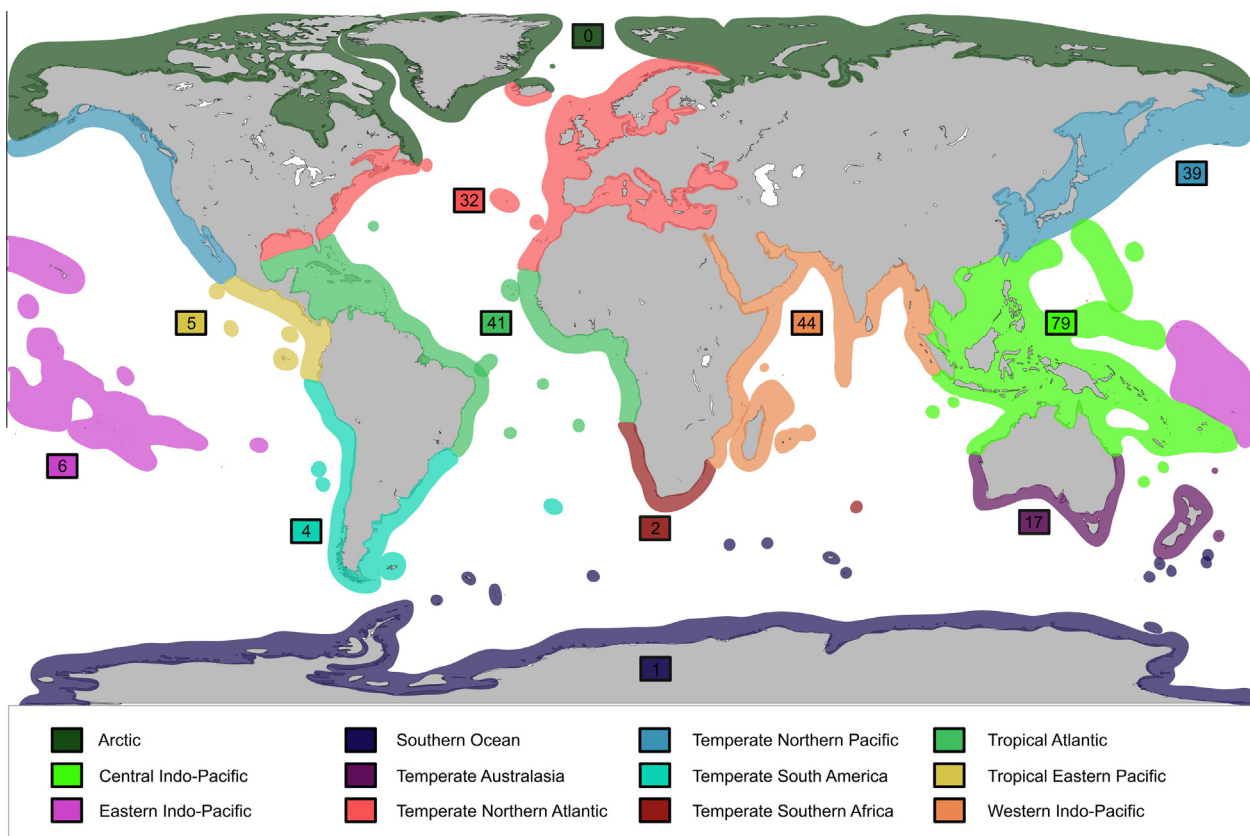


Fig. 4. Number of marine Cymothoidae in biogeographic regions (Marine Ecoregions of the World). Data from Poore and Bruce (2012).

Crustacean fish parasites are very difficult to remove from fish culture facilities. However, transmission of the parasite could be prevented by using small-sized mesh nets around the cages to hinder the swimming larvae from getting to the fish (Rajkumar et al., 2005a). Other management practices include changing fouled nets, placing the cages in stronger currents, lowering the water temperatures and placing them in greater depths to discourage the isopods who seem to thrive with the opposites of these conditions (Papapanagiotou et al., 1999; Papapanagiotou and Trilles, 2001). The use of a large variety of chemical treatments against cymothoids in aquaculture has also been tested with successful treatments having little or no adverse effects on the fish hosts and no reinfections. Certain insecticides (Sievers et al., 1995; Athanassopoulou et al., 2001) and formalin baths (Williams, 1974) are among those treatments on specific cymothoid and host species and at specific concentrations. However, these chemical treatments are not always effective and occasionally the adult stages seem to be little affected by the chemical treatments (Papapanagiotou and Trilles, 2001), or conversely attempts to eliminate the parasite will often result in damage to the host fish (Sievers et al., 1995).

12. Conclusion

Sampling for cymothoids presents unique problems. Unlike free-living isopods, where specific taxa can be targeted with reasonable expectation of success, it is simply not possible to acquire a broad range of cymothoid genera in a single survey through direct collecting. Use of micro-spears with SCUBA adequately targets the externally attaching genera only. Cymothoidae, other than the scale-attaching taxa, can be obtained directly in small numbers and on an opportunistic basis, or indirectly via museum collections, fishers and fishing organisations or by joining fish trawlers, research or commercial, and examining the by-catch. Infestation rates are often low, and discovery of sites where there infestation rates are in the 5–10% category is rare, and usually opportunistic, such as checking fish landing sites. Combining all these methods can produce good material for morphological systematics, but the range of taxa that can be used for molecular analysis is inevitably very limited.

Three or four regions can be considered as well known or moderately well-known from the taxonomic perspective. These are the Central Indo-Pacific, the overlapping region of eastern Australia, the Caribbean and the South American freshwater taxa of the Amazon River and its tributaries. Typically these well-known regions are those that have received attention from specialist taxonomists focused on the Cymothoidae.

Cymothoids decrease rapidly in diversity from the tropics to temperate and cold waters. While some of these areas such as the North Atlantic, New Zealand or northern East Pacific have relatively low diversity, the isopod faunas of these areas are well known. In contrast there are several major regions where documentation remains minimal, these regions are both seaboard of South Atlantic, the Eastern and Western Indian Ocean and the Eastern Indo-Pacific.

Tropical coral reefs, that is living reef, are by their nature difficult to sample by mass collecting methods. Photographs from amateur and professional photographers suggests that a great diversity of small fish species will have associated cymothoids, but these specimens have yet to find their way into collections or to taxonomists.

Brusca (1981) noted that the Cymothoidae is “taxonomically the least understood family within the suborder Flabellifera and is one of the most troublesome of all isopod taxa with which to work”. The many challenging aspects of the family, from collection to identification, account for the Cymothoidae being rarely studied,

with only a handful of cymothoid specialists worldwide. Brusca's (1981) statement is still relevant more than 30 years later and future studies regarding their ecology, taxonomy, lifecycle and molecular studies are still required in order to present a complete understanding of this economic and ecological important taxon.

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References

- Adlard, R.D., Lester, R.J.G., 1994. Dynamics of the interaction between the parasitic isopod, *Anilocra pomacentri*, and the coral reef fish, *Chromis nitida*. *Parasitology* 109, 311–324.
- Adlard, R.D., Lester, R.J.G., 1995. The life cycle and biology of *Anilocra pomacentri* (Isopoda: Cymothoidae), an ectoparasitic isopod of the coral reef fish, *Chromis nitida* (Perciformes: Pomacentridae). *Aust. J. Zool.* 43, 271–281.
- Ahyong, S.T., Lowry, J.K., Alonso, M., Bamber, R.N., Boxshall, G.A., Castro, P., Gerken, S., Karaman, G.S., Goy, J.W., Jones, D.S., Meland, K., Rogers, D.C., Svavarsson, J., 2011. Subphylum Crustacea Brönnich, 1772. In: Zhang, Z.-Q. (Ed.), *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness*. *Zootaxa*, 3148, pp. 165–191.
- Ateş, A.S., Trilles, J.P., İşmen, A., Yiğın, C.C., 2006. New unusual associations involving parasitic isopods. *Crustaceana* 79, 375–380.
- Athanassopoulou, F., Bouboulis, D., Martinsen, B., 2001. In vitro treatments of deltamethrin against the isopod parasite *Ceratothoa oestroides*, a pathogen of sea bass *Dicentrarchus labrax* L. *Bull. Eur. Assoc. Fish Pathol.* 21, 26–29.
- Avdeev, V.V., 1985. On the system of parasitic isopods of the suborder Flabellifera. *Zool. Zh.* 64, 217–225.
- Bakenhaster, M.D., McBride, R.S., Price, W.W., 2006. Life history of *Glossobius hermiramphi* (Isopoda: Cymothoidae): development, reproduction, and symbiosis with its host *Hemiramphus brasiliensis* (Pisces: Hemiramphidae). *J. Crustacean Biol.* 26, 283–294.
- Bleeker, P., 1857. Recherches sur les Crustacés de L'Inde Archipelagique II. Sur les Isopodes Cymothoadiens de L'Archipel Indien. *Natuurkundige vereniging in Nederlandsche-Indie, Batavia, Verhandelingen* 2, 20–40.
- Bowman, T.E., Mariscal, R.N., 1968. *Renocila heterozota*, a new cymothoid isopod, with notes on its host, the anemone fish *Amphiprion akalopsis*, in the Seychelles. *Crustaceana* 14, 97–104.
- Bowman, T.E., 1971. *Palaega lamnae*, new species (Crustacea: Isopoda) from the upper Cretaceous of Texas. *J. Paleontol.* 45, 540–541.
- Brandt, A., Poore, G.C.B., 2003. Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships. *Invert. Syst.* 17, 893–923.
- Bruce, N.L., 1986. Revision of the isopod crustacean genus *Mothocya* Costa, in Hope, 1851 (Cymothoidae: Flabellifera), parasitic on marine fishes. *J. Nat. Hist.* 20, 1089–1192.
- Bruce, N.L., 1987a. Australian species of *Nerocila* Leach, 1818, and *Creniola* n. gen. (Isopoda: Cymothoidae), crustacean parasites of marine fishes. *Rec. Aust. Mus.* 39, 355–412.
- Bruce, N.L., 1987b. Australian *Pleopodias* Richardson, 1910, and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. *Rec. Aust. Mus.* 39, 85–130.
- Bruce, N.L., 1987c. Australian *Renocila* Miers, 1880 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. *Rec. Aust. Mus.* 39, 169–182.
- Bruce, N.L., 1990. The genera *Catoessa*, *Elthusa*, *Ichthyoxenus*, *Idusa*, *Livoneca* and *Norileca* n. gen. (Isopoda, Cymothoidae), crustacean parasites of marine fishes, with descriptions of eastern Australian species. *Rec. Aust. Mus.* 42, 247–300.
- Bruce, N.L., 1995. Comment on the proposed conservation of *Lironeca* Leach, 1818 (Crustacea, Isopoda) as the correct original spelling. *Bull. Zool. Nomencl.* 52, 69.
- Brusca, R.C., Gilligan, M.R., 1983. Tongue replacement in a marine fish (*Lutjanus guttatus*) by a parasitic isopod (Crustacea: Isopoda). *Copeia* 1983, 813–816.
- Brusca, R.C., Wilson, G.D.F., 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations. *Mem. Queensl. Mus.* 31, 143–204.
- Brusca, R.C., 1978. Studies on the cymothoid fish symbionts of the eastern Pacific (Crustacea: Isopoda: Cymothoidae) I. Biology of *Nerocila californica*. *Crustaceana* 34, 141–154.
- Brusca, R.C., 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. *Zool. J. Linn. Soc.* 73, 117–199.
- Bunkley-Williams, L., Williams Jr., E.H., 1998. Isopods associated with fishes: a synopsis and corrections. *J. Parasitol.* 84, 893–896.
- Bunkley-Williams, L., Williams Jr., E.H., Bashirullah, A.K.M., 2006. Isopods (Isopoda: Aegidae, Cymothoidae, Gnathiidae) associated with Venezuelan marine fishes (Elasmobranchii, Actinopterygii). *Rev. Biol. Trop.* 54 (Suppl. 3), 175–188.

- Cavalcanti, W.T.S., Silva do Nascimento, S.K., Barros, C.H.N., Chelappa, S., 2012. Occurrence of the isopod parasite *Rocinela signata* (Isopoda: Aegidae) on marine fish *Sparisoma frondosum* (Osteichthyes: Scaridae). *Mar. Biodivers. Rec.* 5, 1–4.
- Colomi, A., Trilles, J.-P., Golani, D., 1997. *Livoneca* sp. (Flabellifera: Cymothoidae), an isopod parasite in the oral and branchial cavities of the Red Sea silverside *Atherinomorus lacunosus* (Perciformes, Atherinidae). *Dis. Aquat. Org.* 31, 65–71.
- Conway Morris, S., 1981. Parasites and the fossil record. *Parasitology* 82, 489–509.
- dos Santos Costa, E.F., Chelappa, S., 2010. New host record for *Livoneca redmanni* (Leach, 1818) (Isopoda: Cymothoidae) in the Brazilian coastal water with aspects of host–parasite interaction. *Braz. J. Oceanogr.* 58 (4), 73–77.
- Dreyer, H., Wägele, J.W., 2001. Parasites of crustaceans (Isopoda: Bopyridae) evolved from fish parasites: Molecular and morphological evidence. *Zoology* 103, 157–178.
- Dreyer, H., Wägele, J.W., 2002. The Scutocoxifera tax nov and the information content of nuclear ssu rDNA sequences for reconstruction of isopod phylogeny (Peracarida: Isopoda). *J. Crust. Biol.* 22, 217–234.
- Grabda, J., Rokicki, J., 1982. Crustacean parasites of marine fishes. *Wiad. Parazytol.* 28, 183–186.
- Hadfield, K.A., Bruce, N.L., Smit, N.J., 2010. Redescription of the monotypic genus *Cinusa* Schioedte and Meinert, 1884 (Isopoda, Cymothoidae), a buccal-cavity isopod from South Africa. *Zootaxa* 2437, 51–68.
- Hadfield, K.A., Bruce, N.L., Smit, N.J., 2011. *Cymothoa hermani* sp. nov. (Isopoda, Cymothoidae, Crustacea), a parasitic isopod, collected off the Zanzibar coast, Tanzania from the mouth of a parrotfish (Scaridae). *Zootaxa* 2876, 57–68.
- Hadfield, K.A., Bruce, N.L., Smit, N.J., 2013. Review of the fish-parasitic genus *Cymothoa* Fabricius, 1783 (Isopoda, Cymothoidae, Crustacea) from the south-western Indian Ocean, including a new species from South Africa. *Zootaxa* 3640, 152–176.
- Hadfield, K.A., Bruce, N.L., Smit, N.J., 2014a. Review of the fish parasitic genus *Ceratothoa* Dana, 1852 (Crustacea, Isopoda, Cymothoidae) from South Africa, including the description of two new species. *Zookeys* 400, 1–42.
- Hadfield, K.A., Bruce, N.L., Szinétár, C., Smit, N.J., 2014b. *Ceratothoa retusa* (Schioedte & Meinert, 1883), a variable species of fish parasitic marine isopod (Isopoda, Cymothoidae) from the Indian Ocean. *Crustaceana* (in press).
- Hadfield, K.A., 2012. The Biodiversity and Systematics of Marine fish Parasitic Isopods of the Family Cymothoidae from Southern Africa. (Ph.D. thesis), University of Johannesburg, Johannesburg, South Africa: pp. 445.
- Von Haller, G., 1880. Ueber einige neue Cymothöinen. *Arch. Nat.* 46, 375–395 (pl. 18).
- Horton, T., Okamura, B., 2001. Cymothoid isopod parasites in aquaculture: a review and case study of a Turkish sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus auratus*) farm. *Dis. Aquat. Org.* 46, 181–187.
- Horton, T., Okamura, B., 2002. The distribution of *Ceratothoa steindachneri* (Crustacea: Isopoda: Cymothoidae) parasitic in *Echiichthys vipera* in the north-east Atlantic. *J. Mar. Biol. Assoc.* 82, 415–417.
- Horton, T., Okamura, B., 2003. Post-haemorrhagic anaemia in sea bass, *Dicentrarchus labrax* (L.), caused by blood feeding of *Ceratothoa oestroides* (Isopoda: Cymothoidae). *J. Fish Dis.* 26, 401–406.
- Horton, T., Diamant, A., Galil, B.S., 2005. *Ceratothoa steindachneri* (Isopoda, Cymothoidae): an unusual record from the Mediterranean. *Crustaceana* 77, 1145–1148.
- Jones, C.M., Miller, T.L., Grutter, A.S., Cribb, T.H., 2008. Natatory-stage cymothoid isopods: description, molecular identification and evolution of attachment. *Int. J. Parasitol.* 38, 477–491.
- Ketmaier, V., Joyce, D.A., Horton, T., Mariani, S., 2008. A molecular phylogenetic framework for the evolution of parasitic strategies in cymothoid isopods (Crustacea). *J. Zool. Syst. Evol. Res.* 46, 19–23.
- Landau, M., Danko, M.J., Slocum, C., 1995. The effect of the parasitic cymothoid isopod *Lironeca ovalis* (Say, 1818) on growth of young-of-the-year bluefish, *Pomatomus saltatrix* (Linnaeus, 1766). *Crustaceana* 68, 397–400.
- Leach, W.E., 1813–1814. *Crustaceology*. In: Brewster, D. (Ed.), *The Edinburgh Encyclopaedia*. Baldwin, London, pp. 383–437.
- Leach, W.E., 1815. A tabular view of the external characters of four classes of animals, which Linne arranged under Insecta: with the description of the genera comprising three of these classes into order, etc., and descriptions of several new genera and species. *Trans. Linn. Soc. Lond.* 11, 306–400.
- Leach, W.E., 1818. Cymothoadées, Cymothoadés. (Crust.). In: Cuvier, F. (ed.) *Dictionnaire des Sciences Naturelles, dans lequel on traite Méthodiquement des Différens êtres de la Nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la Médecine, l'Agriculture, le Commerce et les Arts. Suivi d'une biographie des plus Célèbres Naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçans, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères génériques et spécifiques, leur lieu natal, leurs propriétés et leurs usages*. Vol. 12. Strasbourg et Paris: F.G. Levrault et Le Normant. pp 337–354.
- Lincoln, R.J., 1971. Isopod fish parasites. *Mar. Obs.* 41 (234), 184–186 (page opposite 186 and 187).
- Linnaeus, C., 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Laurentius Salvius: Holmiae. ii, pp. 824.
- Meyers, T.R., 1978. Prevalence of fish parasitism in Raritan Bay, New Jersey. *Proc. Helm. Soc. Wash.* 45, 120–128.
- Miers, E.J., 1877. On a collection of Crustacea, Decapoda and Isopoda, chiefly from South America, with descriptions of new genera and species. *Proc. Zool. Soc. Lond.* 43, 653–679 (pls 66–69).
- Miers, E.J., 1880. On a collection of Crustacea from the Malaysian Region Part 4. Penaeidae, Stomatopoda, Isopoda, Suctorina and Xiphosura. *Ann. Mag. Nat. Hist.* 5, 457–467.
- Milne Edwards, H., 1840. *Histoire Naturelle des Crustacés Comprendent l'anatomie, la physiologie et la classification de ces animaux*. Roret, Paris 3 (i–ii), 1–638.
- Mladineo, I., 2002. Prevalence of *Ceratothoa oestroides* (Risso, 1826), a cymothoid isopode parasite, in cultured sea bass *Dicentrarchus labrax* L. on two farms in middle Adriatic Sea. *Acta Adriat.* 43, 97–102.
- Mladineo, I., 2003. Life cycle of *Ceratothoa oestroides*, a cymothoid isopod parasite from sea bass *Dicentrarchus labrax* and sea bream *Sparus aurata*. *Dis. Aquat. Org.* 57, 97–101.
- Morton, B., 1974. Host specificity and position on the host in *Nerocila phaeopleura* Bleeker (Isopoda, Cymothoidae). *Crustaceana* 26, 143–148.
- Östlund-Nilsson, S., Curtis, L., Nilsson, G.E., Grutter, A.S., 2005. Parasitic isopod *Anilocra apogonae*, a drag for the cardinal fish *Cheilodipterus quinquelineatus*. *Mar. Ecol. Prog. Ser.* 287, 209–216.
- Otto, A.W., 1828. Beschreibung einiger neuen, in den Jahren 1818 und 1819, im Mittel-ländischen Meere gefundener Crustaceen. *Nova Acta Acad. Caes. Leop. Carol.* 14, 331–354.
- Papapanagiotou, E.P., Trilles, J.P., 2001. Cymothoid parasite *Ceratothoa parallela* inflicts great losses on cultured gilthead sea bream *Sparus aurata* in Greece. *Mar. Ecol. Prog. Ser.* 45, 237–239.
- Papapanagiotou, E.P., Trilles, J.P., Photis, G., 1999. First record of *Emetha audouini*, a cymothoid isopod parasite, from cultured sea bass *Dicentrarchus labrax* in Greece. *Dis. Aquat. Org.* 38, 235–237.
- Perty, M., 1833. *Crustacea Brasiliensia*. In: *Delectus animalium articulatum quae in itinere per Brasiliam annis MDCCCXXVII–MDCCCXXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi peracto collegerunt Dr. J. B. de Spix et Dr. C. F. Ph. de Martius*, 44 + 224 pp., 40 pls Monachii (= München), “1830–1834”. 211–212, pl. XL.
- Poore, G.C.B., Bruce, N.L., 2012. Global Diversity of Marine Isopods (Except Asellota and Crustacean Symbionts). *PLoS One* 7, e43529.
- Rajkumar, M., Vasagam, K.P.K., Perumal, P., Trilles, J.P., 2005a. First record of *Cymothoa indica* (Crustacea, Isopoda, Cymothoidae) infecting the cultured catfish *Mystus gulio* in India. *Dis. Aquat. Org.* 65, 269–272.
- Rajkumar, M., Perumal, P., Trilles, J.-P., 2005b. *Cymothoa indica* (Crustacea, Isopoda, Cymothoidae) parasitizes the cultured larvae of the Asian seabass *Lates calcarifer* under laboratory conditions. *Dis. Aquat. Org.* 66, 87–90.
- Rameshkumar, G., Ravichandran, S., 2014. Problems caused by isopod parasites in commercial fishes. *J. Parasit.* 138, 138–141.
- Risso, A., 1816. *Histoire naturelle des Crustacés des environs de Nice*. Librairie Grecque-Latine-Allemande, Paris, 1–175 (pls. 1–3).
- Romestand, B., Trilles, J.-P., 1979. Influences des Cymothodiens *Meinertia oestroides*, *Meinertia parallela* et *Anilocra physodes* (Crustacés, Isopodes; parasites de poissons) sur la croissance des poissons hôtes *Boops boops* et *Pagellus erythrinus* (Sparidés). *Z. Parasitenk.* 59, 195–202.
- Sadzikowski, M.R., Wallace, D.C., 1974. The incidence of *Livoneca ovalis* (Say) (Crustacea, Isopoda) and its effects on the growth of white perch, *Morone americana* (Gmelin), in the Delaware River near Artificial Island. *Chesap. Sci.* 15, 163–165.
- Say, T., 1818. An account of the Crustacea of the United States, part 7. *J. Acad. Nat. Sci. Philadelphia* 1, 374–401.
- Schioedte, J.C., Meinert, F., 1879. De cirolanis Aegas simulantibus commentatio brevis. *Naturh. Tidsskr. Kjøbenhavn*. 12, 279–302.
- Schioedte, J.C., Meinert, F., 1879b. Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiae. I. Aegidae. *Naturh. Tidsskr. Kjøbenhavn*. 12, 321–414 (pls 7–13).
- Schioedte, J.C., Meinert, F., 1881. Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiae. Anilocridæ. *Naturh. Tidsskr. Kjøbenhavn*. 12, 1–166.
- Schioedte, J.C., Meinert, F., 1883. Symbolæ ad monographium Cymothoarum crustaceorum familiae. III. Saophridae. IV. Ceratothoinæ. *Naturh. Tidsskr., Kjøbenhavn*. 13, 281–378, pls. 11–6.
- Schioedte, J.C., Meinert, F., 1884. Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiae. IV. Cymothoidæ Trib. II. Cymothoinæ. Trib. III: Lironecinæ. *Naturh. Tidsskr., Kjøbenhavn*. 14, 221–454, pls. 6–13.
- Schotte, M., Kensley, B.F., Shilling, S., 1995 onwards. World list of Marine, Freshwater and Terrestrial Crustacea Isopoda. National Museum of Natural History Smithsonian Institution: Washington D.C., USA. Available online at: <http://invertebrates.si.edu/isopod> (accessed 4 February 2014).
- Sievers, G., Palacios, P., Inostroza, R., Dölz, H., 1995. Evaluation of the toxicity of 8 insecticides in *Salmo salar* and the in vitro effects against the isopode parasite *Ceratothoa gaudichaudii*. *Aquaculture* 134, 9–16.
- Sievers, G., Lobos, C., Inostroza, R., Ernst, S., 1996. The effect of the isopod parasite *Ceratothoa gaudichaudii* on the body weight of farmed *Salmo salar* in southern Chile. *Aquaculture* 143, 1–6.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., Mcmanus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a biogeographical analysis of coastal and shelf areas. *Bioscience* 57, 573–583.
- Thatcher, V.E., De Conceição, L.P., Froehlich, O., 2003. *Riggia cryptocularis* sp. nov. (Isopoda, Cymothoidae) from the body cavity of a freshwater fish of Mato Grosso do Sul State, Brazil. *Rev. Bras. Zool.* 20, 285–289.
- Thatcher, V.E., De Oliveira, A.A.N., Garcia, A.M., 2009. *Braga cigarra* comb. nov. for *Philostomella cigarra* (Crustacea: Isopoda: Cymothoidae) with a redescription of

- the species based on specimens from *Galeocharax kneri*, a freshwater fish of Minas Gerais State, Brazil. *Zoologia (Curitiba)* 26, 155–160.
- Trilles, J.-P., Ökter, A., 2004. *Livoneca sinuata* (Crustacea; Isopoda; Cymothoidae) on *Loligo vulgaris* from Turkey, and unusual cymothoid associations. *Dis. Aquat. Org.* 61, 235–240.
- Trilles, J.-P., 1994. Les Cymothoidae (Crustacea, Isopoda) du Monde. Podrome pour une faune. *Stud. Mar.* 21/22, 1–288. [for 1991].
- Varvarigos, P., 2003. Parasitic isopods (suborder Flabellifera) affecting the farmed marine fish in Greece, with special reference to *Ceratothoa oestroides* (family Cymothoidae). *Vet Care*, Athens, Greece. Available online at: http://www.vetcare.gr/ARTPRES/Pathogenic_isopoda.htm (accessed 4 February 2014).
- Wägele, J.W., 1987. Evolution und phylogenetisches System der Isopoda: Stand der Forschung und neue Erkenntnisse. Universität Oldenburg, pp. 399.
- Williams, L.B., Williams Jr., E.H., 1981. Nine new species of *Anilocra* (Crustacea: Isopoda: Cymothoidae) external parasites of West Indian coral reef fishes. *Proc. Biol. Soc. Wash.* 94, 1005–1047.
- Williams Jr., E.H., Williams, L.B., 1982. *Mothocya bohlkeorum*, new species (Isopoda: Cymothoidae) from West Indian cardinalfishes (Apogonidae). *J. Crust. Biol.* 2, 570–577.
- Williams Jr., E.H., Williams, L.B., 1985. *Cuna insularis* n. gen. and n. sp. (Isopoda: Cymothoidae) from the gill chamber of the sergeant major, *Abedudefduf saxatilis* (Linnaeus), (Osteichthyes) in the West Indies. *J. Parasitol.* 71, 209–214.
- Williams Jr., E.H., Bunkley-Williams, L., et al., 2000. On the generic placement of 'Livoneca sp.': a critique of Colomi et al. (1997). *Dis. Aquat. Org.* 40, 233–234.
- Williams Jr., E.H., 1974. Treatments employed for control of parasites of selected fishes stocked in mariculture experiments (1969–1972). *Proc. World Maricult. Soc.* 5, 291–295.