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New host-parasite records of siphonostomatoid copepods infesting elasmobranch fishes in Tunisian waters

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Abstract

Between 2013 and 2015, 2092 chondrichthyan fish belonging to eight species were collected along the Tunisian coast and examined for parasitic copepods. Eleven different species of copepods representing five families, Caligidae, Eudactylinidae, Kroyeriidae, Lernaeopodidae and Pandaridae, were collected. Three of these species are reported for the first time in Tunisia (*Pseudocharopinus malleus, Perissopus dentatus* and *Nesippus orientalis*) and one new species of *Kroyeria* was found. In addition, we identified a number of new host records including: the presence of *Eudactylinella alba* on *Bathytoshia centroura*, *Dasyatis pastinaca*, *Mustelus mustelus* and *Scyliorhinus canicula*. This is the first record of *Nemesis* sp. on *B. centroura* in Tunisia. We report here for the first time the presence of *Pseudocharopinus bicaudatus* and *Pseudocharopinus concavus* on *Bathytoshia centroura* and *Lernaeopoda galei* on *Raja clavata*.

Introduction

Copepods parasitic on fishes belong to two orders, the Siphonostomatoida and the Cyclopoida which now includes the Poecilostomatoida (Khodami *et al.*, 2017).

The order Siphonostomatoida Thorell, 1859 currently consists of 39 families that are mostly marine and infect invertebrate as well as vertebrate hosts (Walter & Boxshall, 2018). Most of the copepods using teleost and elasmobranch fishes as hosts are members of the Siphonostomatoida (Dippenaar, 2004). Ten siphonostomatoid families have been reported as parasites of elasmobranchs (Kabata, 1979; Benz, 1994; Boxshall & Halsey, 2004; Dippenaar, 2016).

Chondrichthyan fishes are considered one of the most ancient and successful vertebrate lineages dating back about 400 million years, near the Devonian–Silurian boundary (Corrigan & Beheregaray, 2009). Their lineage has survived four mass extinction events (Raup & Sepkoski, 1982). Therefore, the elasmobranchs are of particular interest with regards to host-parasite co-evolutionary relationships (Henderson *et al.*, 2013). Despite the large amount of literature that exists on the copepod parasites of teleost fishes, studies of parasites of elasmobranchs are scarcer and geographically patchy: little is known of the diversity of parasitic copepods of chondrichthyan fishes (Henderson *et al.*, 2013).

Tunisia has a rich diversity of elasmobranchs, with more than 61 reported species (Bradaï *et al.*, 2012). However, investigations into their parasites in Tunisian waters are rare (Essafi, 1975; Youssef *et al.*, 2016) and our understanding of species distributions and host-parasite specificity is incomplete. Thus, knowledge of the host-parasite associations will enhance our future understanding of the dynamics between siphonostomatoids and their hosts and of their co-evolutionary history. The aim of this study is to provide new data on the parasitic copepod species that infect chondrichthyan fishes off the Tunisian coast, as well as to provide data on the host associations of these species.

Materials and methods

Between 2013 and 2015, 2092 fish belonging to eight species of chondrichthyan fishes were examined for parasitic copepods. Samples were collected along the Tunisian coast, focusing especially on the Bay of Bizerte, the Gulf of Tunis, the Gulf of Hammamet and the Gulf of Gabes (Figure 1).

The collected fish were immediately transported to the laboratory for analysis. For each fish, the total length and the standard length were measured and the weight was taken using a digital balance. The host species were identified using Fischer *et al.* (1987) and Séret (2006). Host nomenclature is according to Froese & Pauly (2018).

All body parts (skin, fins, gills, mouth, cloaca) were carefully examined. Gills were removed and placed in Petri dishes containing seawater. Each holobranch was individually examined. Copepods were removed from the hosts and preserved in 70% ethanol. The date, sampling area, name and size of host fish and the microhabitat of the parasite were noted. Subsequently, specimens were cleared in lactic acid for 2 h prior to examination by stereo

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Fig. 1. Sampling sites, indicated by black stars.

and light microscopy. Specimens were dissected on glass slides and mounted as temporary preparations in lactophenol. Parasite species identification was done at the Natural History Museum of London and based on morphological features following Kabata (1964, 1979), Cressey (1967), Deets (1994) and Boxshall & Halsey (2004).

Rates of infestation were evaluated using prevalence and mean intensity as defined by Margolis *et al.* (1982) and modified by Bush *et al.* (1997).

Three indices (specific richness (SR), the Shannon–Weaver index (H') and Simpson index (D)) were calculated using Microsoft Excel 2007 software to explore copepod diversity on the different hosts.

Results

Eleven different species of copepods were collected, namely: Eudactylinella alba Wilson, 1932, Nemesis sp., Pseudocharopinus concavus (Wilson, 1913), Pseudocharopinus malleus (Rudolphi in Nordmann, 1832), Pseudocharopinus bicaudatus (Krøyer, 1837), Kroyeria sp., Kroyeria lineata Van Beneden, 1853, Perissopus dentatus Steenstrup & Lütken, 1861, Nesippus orientalis Heller, 1865, Lernaeopoda galei Krøyer, 1837 and Caligus sp.

Parasitological indices of the collected siphonostomatoids

Our analysis shows that prevalence is low for most species studied. *Nemesis* sp. on *Bathytoshia centroura* (Mitchill, 1815) has the highest prevalence recorded (P = 16.27%). *Pseudocharopinus malleus* found on *Dasyatis pastinaca* (Linnaeus, 1758) also showed a relatively high prevalence (P = 6.06%) (Table 1).

Caligus sp. found on *Raja clavata* Linnaeus, 1758 has the lowest prevalence recorded during this survey (P = 0.20%) (Table 1).

The mean intensity of the different species was relatively low and did not exceed 1.61 except for *Caligus* sp. on *R. clavata* with the highest mean intensity in our study (MI = 6) (Table 1).

Eudactylinella alba was collected from four different host species (*B. centroura*, *D. pastinaca*, *Mustelus mustelus* (Linnaeus, 1758) and *Scyliorhinus canicula* (Linnaeus, 1758)). This copepod exhibits a higher prevalence on host species from the family Dasyatidae (P = 3.10%), compared with its prevalence on *M. mustelus* (P = 1.45%) and *S. canicula* (P = 1.04%) (Table 1).

Lernaeopoda galei was also found on multiple hosts (*Mustelus punctulatus* (Risso, 1826), *M. mustelus* and *Raja clavata*). The highest prevalence of this parasite was recorded on *M. punctulatus* (P = 3.24%), whereas it showed a low prevalence on *M. mustelus* (P = 2.50%) and on *R. clavata* (P = 0.83%) (Table 1).

Parasitic richness per host species

Among the eight different species of elasmobranchs, seven species were infested by parasitic copepods. *Mustelus mustelus* had the highest richness (SR) with six different species of copepods (Table 2). *Bathytoshia centroura* displayed the second highest specific richness (SR) with four different species (Table 2). *Dasyatis pastinaca* and *R. clavata* were each infested by two species of copepods. *Mustelus punctulatus*, *S. canicula* and *Torpedo marmorata* (Risso, 1810) each hosted a single copepod (Table 2). While *Torpedo torpedo* (Linnaeus, 1758) was the only species in our survey that was not parasitized by any copepod species (RS = 0) (Table 2).

The Simpson index (D) varied between 0.00 and 0.76. *Mustelus mustelus* presented the highest value (D = 0.76), while the lowest value was noted for three different hosts (*M. punctulatus*, *S. canicula* and *T. marmorata*) (D = 0.00) (Table 2).

The highest value of the Shannon–Weaver index (H') was observed for the parasite community of *M. mustelus* (H' = 1.55) followed by the parasitic community of *B. centroura* (H' = 1.06). The Shannon–Weaver indices of *D. pastinaca* (H'=0.68) and *R. clavata* (H' = 0.67) were almost identical (Table 2). The value of the Shannon-Weaver index was 0.00 for *M. punctulatus, S. canicula* and *T. marmorata* (Table 2).

Parasitic richness per family

The 11 species collected during our survey belong to five families Caligidae, Eudactylinidae, Kroyeriidae, Lernaeopodidae and Pandaridae (Table 1).

Two copepod species belong to the family Eudactylinidae (*E. alba* and *Nemesis* sp.) and two are Kroyeriidae species (*Kroyeria* sp. and *K. lineata*). The Pandaridae is also represented by two species, *Perissopus dentatus* and *Nesippus orientalis*. The highest diversity was for the Lernaeopodidae with four species (*Pseudocharopinus bicaudatus*, *P. concavus*, *P. malleus* and *Lernaeopoda galei*). The Caligidae has the lowest richness and was only represented by a single species (*Caligus* sp.).

Microhabitat of the collected parasites

The copepods occupied several different microhabitats (Table 1). The majority were found on the gills of their hosts, but some species were exclusively gathered from the cloaca (*Pseudocharopinus malleus* and *Lerneaeopoda galei*), while others were found on the external surface of the host, such as *Caligus* sp. and *Perissopus dentatus*. Nesippus orientalis was the only species found in the mouth of its host, *Mustelus mustelus*.

Host	NEF	NIF	Parasitic copepods	Family	Microhabitat	P (%)	МІ
Bathytoshia centroura	129	4	Eudactylinella alba	Eudactylinidae	Gills	3.10	1
		21	Nemesis sp.	Eudactylinidae	Gills	16.27	1.6
		3	Pseudocharopinus bicaudatus	Lernaeopodidae	Spiracles and gills	2.32	1
		6	Pseudocharopinus concavus	Lernaeopodidae	Gills	4.65	1
Dasyatis pastinaca	132	6	Eudactylinella alba	Eudactylinidae	Gills	4.54	1.5
		8	Pseudocharopinus malleus	Lernaeopodidae	Gills	6.06	1
Mustelus mustelus	480	7	Eudactylinella alba	Eudactylinidae	Gills	1.45	1.1
		19	Kroyeria lineata	Kroyeriidae	Gills	3.95	1
		5	Kroyeria sp.	Kroyeriidae	Gills	1.04	1
		12	Lernaeopoda galei	Lernaeopodidae	Cloacae cavity	2.50	1.2
		2	Nesippus orientalis	Pandaridae	Mouth	0.41	1
		4	Perissopus dentatus	Pandaridae	Dorsal fin	0.83	1
Mustelus punctulatus	216	7	Lernaeopoda galei	Lernaeopodidae	Cloacae cavity	3.24	1
Raja clavata	480	1	Caligus sp.	Caligidae	Flanc	0.20	6
		4	Lernaeopoda galei	Lernaeopodidae	Cloacae cavity	0.83	1
Scyliorhinus canicula	480	5	Eudactylinella alba	Eudactylinidae	Gills	1.04	1
Torpedo marmorata	63	1	Pseudocharopinus malleus	Lernaeopodidae	Cloacae cavity	1.58	1
Torpedo torpedo	112	-	-	-	-	-	-

Table 1. List of siphonostomatoid parasites and their hosts

NEF, Number of Examined Fishes; NIF, Number of Infested Fishes; P (%), Prevalence; MI, Mean Intensity; -, Absent.

 Table 2. Measures of the parasites biodiversity for the different host species

	Index		
Host	Species richness (SR)	Simpson's (D)	Shannon– Weaver (H')
Bathytoshia centroura	4	0.58	1.06
Dasyatis pastinaca	2	0.52	0.68
Mustelus mustelus	6	0.76	1.55
Mustelus punctulatus	1	0.00	0.00
Raja clavata	2	0.53	0.67
Scyliorhinus canicula	1	0.00	0.00
Torpedo marmorata	1	0.00	0.00
Torpedo torpedo	0	-	-

Discussion

Among the eight fish species examined, only *Torpedo torpedo* was not parasitized by any copepod. In the Mediterranean Sea, only *Pseudocharopinus malleus* was reported from this fish (Raibaut *et al.*, 1998; Benkirane *et al.*, 1999). This suggests that *T. torpedo* presents low parasitic copepod richness.

Analysis of the three calculated indexes of copepod diversity (the specific richness (SR), Shannon-Weaver index (H') and Simpson index (D)) shows that *Mustelus mustelus* has the highest specific richness among the different host species studied in Tunisian waters. This may be due to the difference in the life traits of the host species. *Mustelus mustelus* is an active, strongswimming epibenthic shark (Smale & Compagno, 1997). Trawl catches often revealed individuals of similar size in the same net which suggests some schooling, or at least aggregations, for at least some of the time (Smale & Compagno, 1997). This behaviour would ease the transmission of parasites and increase the specific richness (Combes, 1995). Indeed, the size of the parasite community (parasite species richness) may increase because aggregated hosts provide a collectively larger habitat for parasites through effects analogous to island biogeography (Morand, 2000). Moreover, it is worth considering specific richness on the host on a geographic scale (Poulin *et al.*, 2011). According to Raibaut *et al.* (1998), Carcharhinidae (*Prionace glauca* (Linnaeus, 1758)) and Triakidae (*Mustelus mustelus* and *M. punctulatus*) show the highest richness among elasmobranch species in the Mediterranean.

Mustelus mustelus and M. punctulatus are demersal species that have the same diet (teleosts and cephalopods) (Compagno, 1984). According to Bradaï (2000), Mustelus punctulatus is common along the Tunisian coasts, however it still rarer than M. mustelus. Indeed, during this study, we were able to examine 216 specimens of M. punctulatus over a three-year period while M. mustelus was more abundant and 480 fish were examined in just one year. Mustelus mustelus has the highest parasitic richness with six species, while M. punctulatus was host to only Lernaeopoda galei. These results may be induced by the low population density of this host species. Indeed, Kamiya et al. (2014) identified host population density as one of the key universal determinants of interspecific variation in parasite species richness.

The family Lernaeopodidae has the highest diversity with four different species (Table 1). These results are consistent with the findings of Raibaut *et al.* (1998) on elasmobranch species in the Mediterranean.

Lernaeopoda galei was found on three hosts (Mustelus mustelus, M. punctulatus and Raja clavata). It is a common parasite of elasmobranchs and has been reported from several host species (Raibaut et al., 1998; Henderson et al., 2003; Dippenaar, 2004; Karaytug et al., 2004; Gaevskaya, 2012), although it seems to display a preference for Triakidae since it was reported by Raibaut et al. (1998), Dippenaar (2004) and Karaytug et al. (2004) from *M. mustelus* and by Raibaut *et al.* (1998) from *M. punctulatus*. We collected this parasite on *Raja clavata*, and this is a new host record.

Three different species belonging to the genus *Pseudocharopi*nus (Kabata, 1964) were collected. *P. bicaudatus* seems to prefer members of the Squalidae as hosts. In fact, this copepod has been collected on *Squalus acanthias* (Linnaeus, 1758) (Raibaut *et al.*, 1998; Benkirane *et al.*, 1999; Henderson *et al.*, 2002), *S. acutipinnis* (Regan, 1908) (Dippenaar, 2004) and *S. megalops* (Macleay, 1881) (Dippenaar & Molele, 2015). We found *P. bicaudatus* on *Bathytoshia centroura* and this is the first report on this host and on any Dasyatidae species.

We, also, report for the first time *Pseudocharopinus concavus* from *Bathytoshia centroura*. The relatively high prevalence (P = 4.65%) suggests that its presence on this host is neither accidental nor opportunistic.

We collected *Pseudocharopinus malleus* on two hosts (*Dasyatis pastinaca* and *Torpedo marmorata*). Raibaut *et al.* (1998) reported this parasite on a variety of hosts in the Mediterranean namely *D. pastinaca, Myliobatis aquila* (Linnaeus, 1758), *Rhinoptera marginata* (Geoffroy Saint-Hilaire, 1817), *T. marmorata* and *Torpedo torpedo*. We note that this species had the second highest prevalence on *D. pastinaca* (P = 6.06%). In contrast, its prevalence on *T. marmorata* is relatively low (P = 1.58%) which may suggest that the preferred host in Tunisian waters is *D. pastinaca*.

A single species of the family Caligidae was found on *Raja clavata*. This host was sampled for three years, but *Caligus* sp. was found only during the summer season and it had the lowest prevalence recorded during this study (P = 0.20%). Only adult males of a *Caligus* sp. were found. This host is known to harbour two caligids, *Caligus coryphaenae* (Steenstrup & Lütken, 1861) and *Lepeophtheirus pectoralis* (O.F. Müller, 1776) (Kabata, 1979). However, morphological features of the collected *Caligus* are different from those two species.

Two species of the Family Eudactylinidae were recovered from the gills of four species of Tunisian elasmobranchs.

Eudactylinella alba exhibited the highest host diversity. It was found on *B. centroura*, *D. pastinaca*, *M. mustelus* and *S. canicula*. This parasite seems to prefer members of the Dasyatidae as hosts and has higher prevalence on *D. pastinaca* (P = 3.30%) and on *B. centroura* (P = 3.10%).

Eudactylinella alba has previously been reported from two Japanese dasyatid rays, *Taeniura meyeni* (Müller & Henle, 1841) and *Dayastis akajei* (Müller & Henle, 1841) (Izawa, 2011). However, this is the first record on *B. centroura*, *D. pastinaca*, *M. mustelus* and *S. canicula*.

Two Nemesis species (Nemesis lamna Risso, 1826 and N. robusta (Van Beneden, 1851)) were found on numerous hosts in the Mediterranean (Raibaut *et al.*, 1998). During our survey, we found Nemesis sp. only on *B. centroura*. It was attached to the gills of its host and showed the highest prevalence recorded in our study (P = 16.27%). This is the first record of Nemesis sp. on *B. centroura* from Tunisia.

We collected two Kroyeriidae species, *Kroyeria lineata* and *Kroyeria* sp. Both were found on the gills of *M. mustelus*. *Kroyeria lineata* was previously reported on *M. mustelus* by Deets (1994) and Raibaut *et al.* (1998). The other *Kroyeria* sp. appears to be a new species.

Kroyeria species are considered to have a high parasite load on their hosts, similar to *Nemesis* (Risso, 1826) species and in contrast to *Eudactylina* (Van Beneden, 1853) species (both Eudactylinidae) (Deets, 1994). However, in the present work *Kroyeria* species display relatively low prevalence. Indeed, the prevalence of *K. lineata* is 3.12% which is slightly higher than the prevalence of *Kroyeria* sp. (P = 1.04%). In contrast we note that *Nemesis* sp. exhibits the highest prevalence (P = 16.27%)

recorded in our study. Furthermore, species of *Kroyeria* and *Eudactylina*, like many other parasitic copepods, typically exhibit a high degree of host specificity (Deets, 1994). However, we found *Kroyeria lineata* on *M. mustelus* and *Eudactylinella alba* on *B. centroura*, *D. pastinaca*, *M. mustelus* and *S. canicula*.

Copepods of the Pandaridae are typically ectoparasites of elasmobranchs and, less commonly, species of Actinopterygian fishes (Bernot & Boxshall, 2017). Two species belonging to this family were found, both on *M. mustelus* with a fairly low prevalence. *Nesippus orientalis* was attached in the mouth of its host and *Perissopus dentatus* on the dorsal fin.

Nesippus orientalis is very common, having been reported from a number of sharks, but appears to be restricted to inshore species and is usually found in the mouth and on the gill arches of the host (Cressey, 1967, 1970). In the South African coasts, Dippenaar & Jordaan (2012) reported this species on 12 different host species (*Carcharodon carcharias* (Linnaeus, 1758); *Isurus* oxyrinchus Rafinesque, 1810; Alopias vulpinus (Bonnaterre, 1788); *Carcharias taurus* Rafinesque, 1810; *Carcharhinus brevipinna* (Müller & Henle, 1839); *C. brachyurus* (Günther, 1870); *C. leucas* (Müller & Henle, 1839); *C. limbatus* (Müller & Henle, 1839); *C. obscurus* (Lesueur, 1818); *Sphyrna lewini* (Griffith & Smith, 1834); *S. mokarran* (Rüppell, 1837) and *S. zygaena* (Linnaeus, 1758)). In the Mediterranean, Raibaut et al. (1998) reported *N. orientalis* on *M. mustelus*.

Perissopus dentatus was found on *M. mustelus* in the Mediterranean (Raibaut *et al.*, 1998) and on *Carcharhinus limbatus, C. sealei* (Pietschmann, 1916), *C. leucas, C. obscurus, Mustelus mosis* Hemprich & Ehrenberg, 1899 and *M. mustelus* off the South African coast (Dippenaar & Jordaan, 2007). This is the first record of these two parasites in Tunisian waters where *M. mustelus* seems to be their preferred host.

Host and microhabitat or site selection is exhibited to a varying degree between parasite species and groups (Rohde, 1979; Kabata, 1981). The morphological and physiological factors that determine the selection of a specific site by a specific copepod are still unknown for most species (Kabata, 1981). Siphonostomatoids are found attached to virtually all external body surfaces of their hosts (Benz *et al.*, 2000). In general, all copepods exhibit a high degree of host and attachment site specificity (Kabata, 1979; Benmansour, 2001). We note that the majority of the parasites collected were found on the gills of their hosts. This is probably due to the richness of this habitat as a food source (the host's blood), ease of access and the relative protection that gills offer from the external environment.

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References

- Benkirane O, Coste F and Raibaut A (1999) On the morphological variability of the attachment organ of Lernaeopodidae (Copepoda: Siphonostomatoida). *Folia Parasitologica* **46**, 67–75.
- Benmansour B. (2001) Biodiversité et bioécologie des copépodes parasites des poissons téléostéens. Thèse de doctorat. Université de Tunis El Manar Tunis II, Tunisia.
- **Benz GW** (1994) Evolutionary biology of Siphonostomatoida (Copepoda) parasitic on vertebrates. PhD thesis. University of British Columbia, Vancouver, Canada.

- Benz GW, Kabata Z and Bullard SA (2000) Margolisius abditus n. gen., n. sp. (Copepoda: Lernaeopodidae) from gill lamellae of a remora (*Remora remora*) collected in the Gulf of California. Journal of Parasitology 86, 241–244.
- Bernot JP and Boxshall GA (2017) A new species of *Pseudopandarus* kirtisinghe, 1950 (Copepoda: Siphonostomatoida: Pandaridae) from sharks of the genus *Squalus* L. in New Caledonian waters. *Systematic Parasitology* 94, 275–291.
- **Boxshall GA and Halsey SH** (2004) An Introduction to Copepod Diversity. London: The Ray Society.
- **Bradaï MN** (2000) Diversité du peuplement ichtyque et contribution à la connaissance des sparidés du Golfe de Gabès. PhD thesis, University of Sfax, Tunisia.
- Bradaï MN, Saiidi B and Enajjar S (2012) Elasmobranchs of the Mediterranean and Black Sea: Status, Ecology and Biology. Bibliographic Analysis. Studies and Reviews. General Fisheries Commission for the Mediterranean. No. 91. FAO: Rome, pp. 1–103.
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis *et al.*, revisited. *Journal of Parasitology* 83, 575–583.
- **Combes C.** (1995). *Interaction Durables: ecologie et Évolution du Parasitisme*. Paris: Masson, 524 pp.
- Compagno LJV (1984) FAO Species Catalogue. Vol. 4: Sharks of the World, Part 2 – Carcharhiniformes. FAO Fisheries Synopsis 125, Vol. 4. FAO: Rome, pp. 251–633.
- **Corrigan S and Beheregaray LB** (2009) A recent shark radiation: molecular phylogeny, biogeography and speciation of Wobbegong sharks (family: Orectolobidae). *Molecular Phylogenetics and Evolution* **52**, 205–216.
- **Cressey RF** (1967) Revision of the family Pandaridae (Copepoda, Caligoida). Proceedings of the United States National Museum **121**, 1–133.
- Cressey RF (1970) Copepods parasitic on sharks from the west coast of Florida. Smithsonian Contributions to Zoology 38, 1–30.
- **Deets GB** (1994) Copepod-Chondrichthyan coevolution: A cladistic consideration. PhD thesis. University of British Columbia. Canada.
- Dippenaar SM (2004) Reported siphonostomatoid copepods parasitic on marine fishes of southern Africa. *Crustaceana* 77, 1281–1328.
- Dippenaar SM (2016) Biodiversity and studies of marine symbiotic siphonostomatoids off South Africa. African Journal of Marine Science 38, 1–5.
- Dippenaar SM and Jordaan BP (2007) New host and geographical records of siphonostomatoid copepods associated with elasmobranchs off the KwaZulu-Natal coast, South Africa. Onderstepoort Journal of Veterinary Research 74, 169–175.
- Dippenaar SM and Jordaan BP (2012) Notes on the morphology and ecology of the adult females of *Nesippus* species (Siphonostomatoida: Pandaridae) with a key for identification. *Zootaxa* 3170, 18–30.
- Dippenaar SM and Molele RA (2015) Siphonostomatoid copepods infecting Squalus acutipinnis Regan, 1908 off South Africa. African Journal of Marine Science 37, 605–608.
- **Essafi K** (1975) Contribution à l'étude des copépodes parasites des sélaciens de *Tunisie.* Thèse de Doctorat. Université Tunis El Manar. Tunis II. Tunisia.
- Fischer W, Bauchot ML and Schneider M (1987) Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et Mer Noire. Zone de Pêche 37. Rome: FAO, 761–1529.
- Froese R and Pauly D (eds) (2018) FishBase. http://www.fishbase.org.
- Gaevskaya AV (2012) Parasites and diseases of fishes in the Black Sea and the Sea of Azov: I. Sevastopol. *EKOSI Gidrofizika*.

- Henderson AC, Flannery K and Dunne J (2002) An investigation into the metazoan parasites of the spiny dog fish (*Squalus acanthias* L.), off the west coast of Ireland. *Journal of Natural History* **36**, 1747–1760.
- Henderson AC, Flannery K and Dunne J (2003) Biological observations on shark species taken in commercial fisheries to the west of Ireland. *Biology* and Environment: Proceedings of the Royal Irish Academy **103B**, 1–7.
- Henderson AC, Reeve AJ and Tang D (2013) Parasitic copepods from some northern Indian Ocean elasmobranchs. *Marine Biodiversity Records* 6, 1–3.
- Izawa K (2011) Dangoka japonica nov. gen. nov. sp. and Eudactylinella alba Wilson, 1932 (Copepoda, Siphonostomatoida, Eudactylinidae) infesting Japanese elasmobranchs. Crustaceana 84, 1269–1277.
- Kabata Z (1964) Revision of the genus Charopinus Kroyer 1863 (Copepoda: Lernaeopodidae). Videnskabelige Meddelelser Dansk Naturhistorisk Forening 127, 28–112.
- Kabata Z (1979) Parasitic Copepods of British Fishes. London: The Ray Society, i-xii, 1–468.
- Kabata Z (1981) Copepoda (Crustacea) parasitic on fishes: problems and perspectives. Advances in Parasitology 19, 1–71.
- Kamiya T, O'Dwyer K, Nakagawa S and Poulin R (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews* 89, 123–134.
- Karaytug S, Sak S and Alper A (2004) Parasitic copepod Lernaeopoda galei Kroyer, 1837 (Copepoda: Siphonostomatoida): a first record from Turkish seas. Turkish Journal of Zoology 28, 123–128.
- Khodami S, McArthur JV, Blanco-Bercial L and Martinez Arbizu P (2017) Molecular phylogeny and revision of copepod orders (Crustacea: Copepoda). *Scientific Reports* 7, 9164.
- Margolis L, Esche GW, Holmes JC, Kuris AM and Schrad GA (1982) The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology* 68, 131–133.
- **Morand S** (2000) Wormy world: comparative tests of theoretical hypotheses on parasite species richness. In Poulin R, Morand S and Skorping A (eds), *Evolutionary Biology of Host–Parasite Relationships*. Amsterdam: Elsevier, pp. 63–79.
- Poulin R, Krasnov BR and Mouillot D (2011) Host specificity in phylogenetic and geographic space. *Trends in Parasitology* 27, 355–361.
- Raibaut A, Combes C and Benoit F (1998) Analysis of the parasitic copepod species richness among Mediterranean fish. *Journal of Marine Systems* 15, 185–206.
- Raup D and Sepkoski J (1982) Mass extinctions in the marine fossil record. Science 215, 1501–1503.
- Rohde K (1979) A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. American Naturalist 114, 648–671.
- Séret B (2006) Guide d'identification des principales espèces de requins et de raies de l'Atlantique oriental tropical, à l'usage des enquêteurs et biologistes des pêches. FIBA, PRCM & IUCN.
- Smale MJ and Compagno LJV (1997) Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* Smith, 1957 (Pisces: Triakidae). South African Journal of Marine Science 18, 229–248.
- Walter TC and Boxshall G (2018) World of Copepods Database. Available via World Register of Marine Species. http://www.marinespecies.org/aphia.php? p=taxdetails&id=135531.
- Youssef F, Benmansour B, Ben Hassine OK and Zouari-Tlig S (2016) Some parasitic copepods of selected teleost and chondrichthyan fishes from the Tunisian Gulfs. *African Journal of Microbiology Research* **10**, 1467–1476.