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Alebion carchariae (Copepod: Caligidae) host plasticity and distribution: a new host and locality record from Ascension Island

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Abstract

The first record of the parasite *Alebion carchariae* in the waters of Ascension Island collected from Galapagos sharks, *Carcharhinus galapagensis* (Carcharhinidae), is described. No previous record of this parasite exists for Ascension Island, nor have Galapagos sharks previously been listed as a host. Specimens of *A. carchariae* were identified using morphological techniques and DNA barcoding of the cytochrome *c* oxidase I subunit (COI) gene. This study provides the first COI barcodes for this species and a brief review of known hosts. We recommend further research to understand the life cycle of this parasite, its plasticity in terms of host/habitat selection, and to determine the implications of its presence on the hosts it inhabits.

Introduction

Copepods are the most abundant metazoan animals in the ocean, with over 14,500 accepted species of parasitic copepods recorded to date (Walter & Boxshall, 2022). Despite their abundance, the distribution of these species is patchily recorded across ocean basins, with their occurrence in remote locations poorly understood. Adding to patchily known species distributions can be useful in identifying stepping-stones of transport and colonisation, which facilitate widespread animal distributions. The order Siphonostomatoida contains 2233 species, of which an estimated 69% feed on the epidermal tissue, mucus or blood of marine fishes, ranging from small bait fish to large elasmobranchs (Austin *et al.*, 2014; Ohtsuka *et al.*, 2020). This order contains ~550 genera and nearly 40 families (Austin *et al.*, 2014), including the genus *Alebion* which is contained within the family Caligidae. Kabata (1979) placed *Alebion* in the family Euryphoridae; however, Boxshall & Halsey (2004) recognise *Alebion* and other former euryphorid genera as members of the Caligidae. The caligids are a diverse group of copepods that predominantly parasitise marine fishes (Dojiri & Ho, 2013). The adults exhibit highly modified body forms. The adult female caligid body is dorso-ventrally flattened to allow the cephalothorax to serve as a suction cup to attach to the host (Dojiri & Ho, 2013 and sources therein). Since the first description of the genus *Alebion* by Krøyer in 1863, nine species have been described (formerly 14, later redescribed as 9; Cressey, 1972; Dippenaar, 2018).

Alebion carchariae has been recorded on at least 16 shark and one fish species (Table 1), with three records in the South Atlantic Ocean spanning from the eastern USA (listed hosts include smooth hammerhead, *Sphyrna zygaena*; scalloped hammerhead, *Sphyrna lewini*, see Rokicki & Bychawska, 1991), São Paulo (unspecified host, reviewed in Luque & Tavares, 2007) and off the coast of Senegal, West Africa (Vaissière, 1959). Here we describe the occurrence of this species in the nearshore waters of Ascension Island, a remote island located in the South Atlantic Ocean. Thereafter we provide the first DNA barcode sequence for this species.

Materials and methods

Six specimens of *Alebion carchariae* were collected off the north-west coast of Ascension Island in the South Atlantic Ocean (7.9467°S 14.3559°W). On 27 January 2021, one specimen was removed from the snout region of a juvenile (~90 cm TL) Galapagos shark (*Carcharhinus galapagensis*) at Comfortless Cove (7.9104°S 14.4030°W). On 17 April 2021, an additional five specimens were removed from the face of a juvenile (<100 cm TL) Galapagos shark (*Carcharhinus galapagensis*) at English Bay (7.8933°S 14.3849°W). Hosts were caught unintentionally using light or medium-action fishing rods in both incidences and released promptly after manually removing the copepod/s from the host. Copepods were preserved in 70% ethanol and stored temporarily in the Ascension Island Government Conservation Centre on Ascension Island.

The copepod specimens were sent to the College of Fisheries and Ocean Sciences at the University of Alaska, Fairbanks (USA) and examined with a Leica M205C stereomicroscope, and photographed using a Leica DMC4500 camera. Two specimens were dissected to examine the legs and genital complex in further detail. The specimens were identified as *Alebion carchariae*

Table 1. The diversity of recorded *Alelion carchariae* hosts

Host species	Water type	Depth range (preferred)	Habitat	Paper	Locale
Bull shark (<i>Carcharhinus leucas</i>)	Marine, freshwater	1–164 (1–30)	Reef-associated, amphidromous	Henderson <i>et al.</i> (2013)	Oman, Northern Indian Ocean
				Cressey (1970)	West Coast of Florida
Blacktip shark (<i>Carcharhinus limbatus</i>)	Marine, brackish	0–140 (0–30)	Reef-associated, amphidromous	Henderson <i>et al.</i> (2013)	Oman, Northern Indian Ocean
				Cressey (1970)	West Coast of Florida
Dusky shark (<i>Carcharhinus obscurus</i>)	Marine brackish	0–400 (200–400)	Reef-associated, oceanodromous	Lesueur (1818)	Southern Africa
				Cressey (1970)	West Coast of Florida
				Vaissière (1959)	Off the coast of Senegal, West Africa
Great hammerhead (<i>Sphyrna mokarran</i>)	Marine, brackish	1–300 (1–100)	Pelagic-oceanic, oceanodromous	Cressey (1970)	West Coast of Florida
Lemon shark (<i>Negaprion brevirostris</i>)	Marine, brackish	0–92	Reef-associated, oceanodromous	Cressey (1970)	West Coast of Florida
Oceanic whitetip shark (<i>Carcharhinus longimanus</i>)	Marine	0–1082 (0–152)	Pelagic-oceanic, oceanodromous	Cressey (1970)	West Coast of Florida
Pigeye shark (<i>Carcharhinus amboinensis</i>)	Marine, brackish	0–150	Reef-associated	Henderson <i>et al.</i> (2013)	Oman, Northern Indian Ocean
Sandbar shark (<i>Carcharhinus plumbeus</i>)	Marine, brackish	0–500 (20–65)	Benthopelagic, oceanodromous	Cressey (1970)	West Coast of Florida
Sand tiger shark (<i>Carcharias taurus</i>)	Marine	1–191 (15–25)	Reef-associated, oceanodromous	Oldewage & Smale (1993)	18–20 miles south of Cape Recife, South Africa
Scalloped hammerhead (<i>Sphyrna lewini</i>)	Marine, brackish	0–1000 (0–25)	Pelagic-oceanic, oceanodromous	Cressey (1970)	West Coast of Florida
				Rokicki & Bychawska (1991)	Off east coast of the USA, Atlantic Ocean
				Vaissière (1959)	Off the coast of Senegal, West Africa
Shortfin mako shark (<i>Isurus oxyrinchus</i>)	Marine	0–750 (100–150)	Pelagic-oceanic, oceanodromous	Oldewage (1995)	Cape Recife coast, South Africa
Silky shark (<i>Carcharhinus falciformis</i>)	Marine	0–4000 (0–500)	Reef-associated, oceanodromous	Henderson <i>et al.</i> (2013)	Oman, Northern Indian Ocean
Small eye hammerhead (<i>Sphyrna tudes</i>)	Marine	>12	Benthopelagic	Vaissière (1959)	Off the coast of Senegal, West Africa
Smooth hammerhead (<i>Sphyrna zygaena</i>)	Marine, brackish	0–200 (0–20)	Pelagic-oceanic, oceanodromous	Rokicki & Bychawska (1991)	Off the East Coast of the USA, Atlantic Ocean
Spinner shark (<i>Carcharhinus brevipinna</i>)	Marine	0–100	Reef-associated, oceanodromous	Cressey (1970)	West coast of Florida
				Vaissière (1959)	Off the coast of Senegal, West Africa
Tiger shark (<i>Galeocerdo cuvieri</i>)	Marine, brackish	0–800 (0–140)	Benthopelagic, oceanodromous	Cressey (1970)	West coast of Florida
Pompano dolphinfish (<i>Coryphaena equisetis</i>)	Marine	0–400	Pelagic-oceanic, oceanodromous	Vaissière (1959)	Off the coast of Senegal, West Africa

Data on the host species ecology (water type, depth range, habitat) were extracted from <https://fishbase.se>.

based on the taxonomic descriptors of Cressey (1972), Boxshall & Halsey (2004), Dojiri & Ho (2013) and Dippenaar (2018). After dissection, specimens were stored in ethanol at -20°C . Subsequent DNA extraction and amplicon sequencing was conducted on two individual specimens.

DNA extraction, PCR amplification and sequencing

Prior to DNA extraction, individually selected and identified female *A. carchariae* were rinsed in sterile Milli-Q® water to

remove all traces of ethanol to enable successful DNA extraction. Genomic DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit with a final elution volume of 200 μl elution buffer. A 658 base-pair (bp) region of the mitochondrial cytochrome oxidase I (COI) gene (i.e. the barcode region) was targeted for species identification (Bucklin *et al.*, 2011). Polymerase Chain Reaction (PCR) was carried out using 12.5 μl Q5® Hot Start High-Fidelity 2X Master Mix (New England Biolabs Inc.), 1.25 μl of each forward and reverse primer (10 μM), 3–5 μl DNA template, and PCR grade water for a final reaction volume of 25 μl . COI was

amplified with the universal primer pair LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.*, 1994). PCR thermal cycle protocol consisted of 35 cycles of 98°C for 10 s, 62°C for 20 s, 72°C for 20 s and a final extension at 72°C for 2 min. PCR products were run on a 1.5% agarose TBE buffer gel stained with GelRed. Amplicons from successful PCR reactions were purified using ExoSAP-IT™ Express PCR cleanup, combined with either the forward or reverse primer for bi-directional sequencing, and sequenced by Azenta Life Sciences (<http://www.azenta.com>).

Bi-directional COI sequences were assembled to create contiguous reads and checked for ambiguous base calling using Geneious Prime (Ver. R10). COI sequences for copepods in the family Caligidae with species-level identifications were retrieved from the NCBI GenBank public repository (www.ncbi.nlm.nih.gov/genbank) and analysed with COI data for *A. carchariae* obtained in this study. COI reads were aligned using the MUSCLE algorithm (Edgar 2004) and trimmed to uniform lengths. Neighbour-joining (NJ) gene trees were analysed after 10,000 coalescence simulations using a bootstrap test of 1000 replicates. The COI sequence for *Demoleus heptapus* (MH242722) represents the out-group. Pairwise proportional nucleotide distances (p-distance) within and between Caligidae species were calculated in MEGA X (Kumar *et al.*, 2018).

Results

Morphological identification

The body was dorso-ventrally flattened (Figure 1) with genital complex bearing elongated posterior processes extending slightly beyond the caudal rami. Lateral processes of the first abdominal somite reached the distal margin of the second abdominal somite. The genital complex had a slight bulge in the centre and margin armed with spinules, with legs 1–3 biramous, and leg 1 possessing 2 segmented rami (Figure 2A). Importantly, the specimen's exopodal spines of legs 1–3 were modified into large paddle-like structures (Figure 2B), characteristic of the genus *Alebion*. Additionally, legs 2 and 3 possessed 3-segmented rami (Figure 2C, D, E), while leg 4 was reduced and uniramous (Figure 2F). Leg 5 was represented by the elongated posterior processes extending from genital segment. Both female specimens

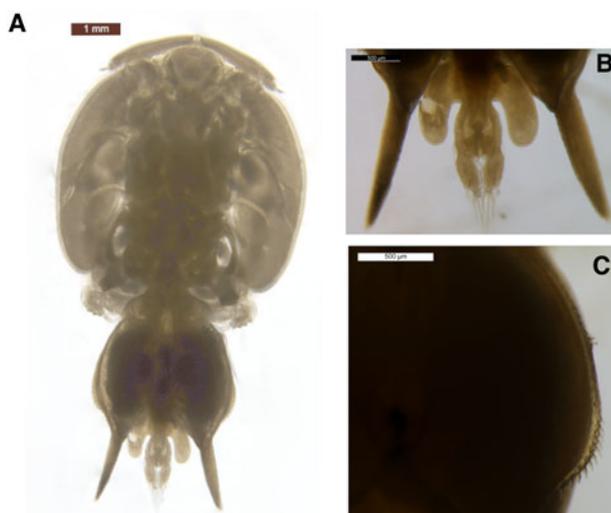


Fig. 1. *Alebion carchariae* female. (A) Body, dorsal view; (B) abdomen and caudal rami; posterior processes of genital segment, dorsal view; (C) spinules on margin of genital complex.

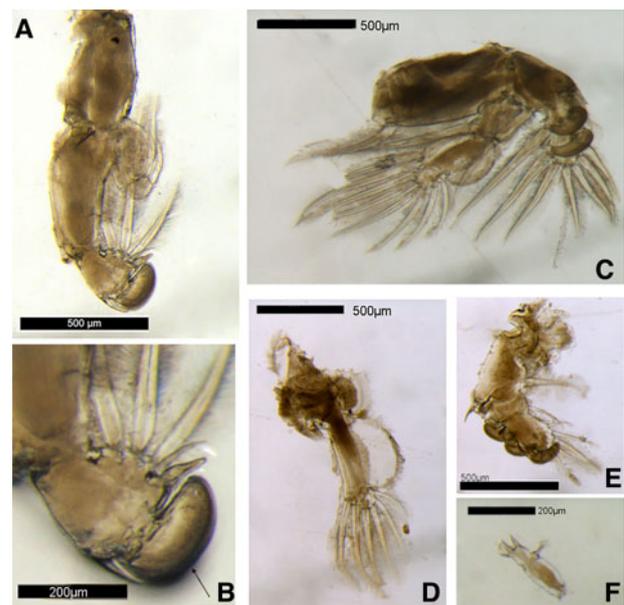


Fig. 2. *Alebion carchariae* female. (A) Leg 1; (B) Distal portion of exopod of leg 1; arrow indicates modified paddle-like exopodal spine; (C) Leg 2; (D) Leg 3 endopod; (E) Leg 3 exopod; (F) Leg 4.

were 8.6 mm in total length. The cephalothorax lengths of the individuals were 5.1 and 5.3 mm.

Analysis of COI sequences

Two COI sequences of 557 base-pairs (bp) in length were sequenced for *A. carchariae* (GenBank accession nos ON807358 and ON807359). These data represent the first publicly available COI barcodes for *A. carchariae* and the first species-level COI data for the genus *Alebion*. Low pairwise distances (p-distances) were observed within individual *A. carchariae* (0.36%; N = 2) with high between-species distances observed when compared with *Caligus* spp. (18.0–28.1%; N = 9; Table 2). The high interspecific genetic variability for the COI barcode region is consistent with metazoan species (10–25%; Hebert *et al.*, 2003). However, phylogenetic trees based on COI variation for species in the family Caligidae (Figure 3) revealed a bifurcating pattern with *A. carchariae* clustering separately from the other Caligidae species (100% bootstrap support). These data suggest *A. carchariae* and *Caligus* spp. may not belong in the same family, but additional COI data for species across multiple families in the order Siphonostomatoida are needed to resolve phylogenetic lineages.

Discussion

Alebion carchariae (Krøyer, 1863)

New record. Ascension Island (7.9467°S 14.3559°W)

The recorded diversity of *A. carchariae* hosts suggests this parasite has plasticity in terms of the hosts it infects and the conditions it can tolerate, given the variety of habitats and depths utilised by these hosts. Documented hosts include sharks and fishes commonly distributed across reef habitats, benthic and pelagic to oceanic realms, with preferred depths ranging between 0–500 m. Current knowledge regarding the life cycle of caligids is based on studies of sea lice genera, including *Caligus* and *Lepeophtheirus*, which have been relatively well studied due to their economic impact on aquaculture (Boxaspen, 2006; Hemmingsen *et al.*, 2020). The generalised caligid life cycle consists of two naupliar stages and one infective copepodid stage (Hamre *et al.*, 2013). However, the number of stages between

Table 2. Pairwise genetic distances (p-distance) within and between eight species in the family Caligidae based on COI sequence variation. GenBank accession numbers for *Caligus* spp. are in parentheses

	<i>A. carchariae</i> (Alcr01COI)	<i>A. carchariae</i> (Alcr02COI)	<i>C. diaphanus</i> (EF065616)	<i>C. fugu</i> (KR049056)	<i>C. punctatus</i> (KR049057)	<i>C. hoplognathi</i> (KR049058)	<i>C. quadratus</i> (KR049059)	<i>C. elongatus</i> (KT20840)	<i>C. curtus</i> (KT209233)
<i>A. carchariae</i> (Alcr01COI)	–								
<i>A. carchariae</i> (Alcr02COI)	0.012	–							
<i>C. diaphanus</i> (EF065616)	0.226	0.214	–						
<i>C. fugu</i> (KR049056)	0.274	0.269	0.266	–					
<i>C. punctatus</i> (KR049057)	0.276	0.276	0.251	0.196	–				
<i>C. hoplognathi</i> (KR049058)	0.238	0.233	0.225	0.264	0.236	–			
<i>C. quadratus</i> (KR049059)	0.246	0.241	0.190	0.213	0.187	0.191	–		
<i>C. elongatus</i> (KT20840)	0.284	0.282	0.238	0.227	0.250	0.234	0.224	–	
<i>C. curtus</i> (KT209233)	0.227	0.225	0.238	0.239	0.282	0.201	0.196	0.248	–

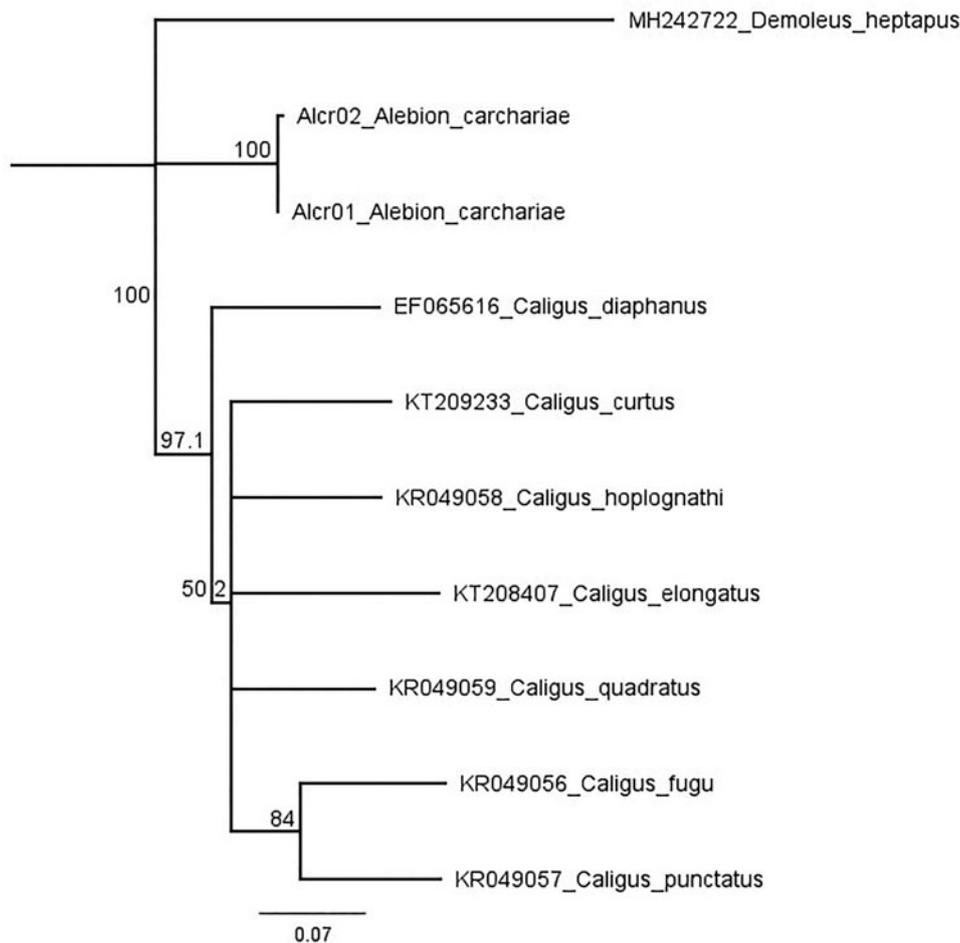


Fig. 3. COI gene tree for copepods in the family Caligidae based on COI reads for *Alebion carchariae* generated in this study and species-level data available in GenBank (www.ncbi.nlm.nih.gov/genbank). *Demoleus heptapus* (MH242722) represents the outgroup. Neighbour-joining tree with Tamura & Nei (1993) substitution model; 1000× bootstrap values are indicated at nodes; values >50 are shown; scale bar indicates genetic distance.

the copepodid and adult stage reported to vary between four chalimus stages (*Pseudocaligus* and *Caligus* species; Kim, 1993; Piasecki, 1996; Ohtsuka *et al.*, 2009) to four chalimus plus two preadult stages (*Lepeophtheirus* species; Lewis, 1963; Voth, 1972; Boxshall, 1974; Johnson & Albright, 1991). The copepodid stage of caligids is infective, and the subsequent chalimus stages bear a frontal filament used to attach to the host. Wilson (1907) reported that *Alebion glaber* does not possess a frontal filament, but instead attaches to the host with prehensile antennae. It should also be noted that there are no published studies regarding the life cycle of caligid genera formerly included in the Euryphoridae, including *Alebion*. Experimental studies show the infective stage of a salmon louse (*Lepeophtheirus salmonis*) will aggregate in the upper water column to increase the probability of encountering potential hosts (Heuch *et al.*, 1995). The lifespan of the infective stage of sea lice has been reported as lasting between 1–9 days (Johnson & Albright, 1991), and only upon attachment to a host can the lice fully develop and sexually reproduce. Life cycle estimates have ranged from less than two weeks (in controlled trials at 20 and 30°C; Khoa *et al.*, 2019) to <210 days under laboratory conditions (Mustafa *et al.*, 2001). The potential longevity of these species may enable them to hitchhike onto migratory species and facilitate their distribution (Boxaspen, 2006). For example, previous records of *Alebion carchariae* closest to Ascension Island include South America and West Africa, and longevity could facilitate its widespread distribution via hitchhiking on hosts traversing ocean basins or transport via ocean currents (enabling subsequent host

infection). The described position of attachment of *A. carchariae* includes shark pectoral fins (*C. obscurus*, Vaissière, 1959) and the underside of the head (*Sphyrna lewini*, Vaissière, 1959), and fish gills (*Coryphaena equisetis*, Vaissière, 1959). *Alebion* has also been reported to wander the body surface of hosts (Cressey, 1972). Dorso-ventral flattening likely facilitates its successful adhesion by reducing drag when situated on the face (as observed in *Nerocila*, Nagler & Haug, 2016), and the versatility of its attachment location may increase its chance of success.

Further sampling of the parasitic assemblage around Ascension Island through opportunistic sampling, e.g. during fisheries surveys to collect mature individuals, and water sampling for pre-adult stages, could provide insight into the ecology and life cycle of this poorly studied genus and identify susceptible hosts. For example, data are required to determine the mechanisms that support its widespread distribution and its potential tolerance to a range of conditions (i.e. depths) that may facilitate its association with diverse hosts. Additionally, sampling this parasite may offer a minimally invasive technique to explore parasite-host interactions and/or the genetic structure of host populations such as *C. galapagensis* sharks around Ascension Island (following Meekan *et al.*, 2017). While only seven *A. carchariae* were collected from two sharks it was noted that one individual hosted numerous other *A. carchariae* that were not collected. The implications of the presence of this parasitic copepod on host health and fitness remain unknown and warrants further research.

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Author contributions. DLO collected the specimens. The specimens were photographed by CS and sequenced by JQ. TS provided logistical support on Ascension Island. DLO wrote the manuscript with support from NEH, JQ, CS, TS. All authors discussed the results and contributed to the final manuscript.

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Conflict of interest. The authors declare none.

References

- Austin CM, Tan MH, Lee YP, Croft LJ, Meekan MG, Pierce SJ and Gan HM (2014) The complete mitogenome of the whale shark parasitic copepod *Pandarus rhincodonicus* Norman, Newbound & Knott (Crustacea; Siphonostomatoida; Pandaridae) – a new gene order for the copepoda. *Mitochondrial DNA* **27**, 694–695.
- Boxaspen K (2006) A review of the biology and genetics of sea lice. *ICES Journal of Marine Science* **63**, 1304–1316.
- Boxshall GA (1974) Developmental stages of *Lepeophtheirus pectoralis* (Muller, 1776) (Copepoda-Caligidae). *Journal of Natural History* **8**, 681–700.
- Boxshall GA and Halsey SH (2004) *An Introduction to Copepod Diversity*. Andover: Ray Society.
- Bucklin A, Steinke D and Blanco-Bercial L (2011) DNA Barcoding of Marine Metaxoa. *Annual Review of Marine Science* **3**, 471–508.
- Cressey RF (1970) Copepods parasites on sharks from the west coast of Florida. *Smithsonian Contributions to Zoology* **38**, 1–30.
- Cressey RF (1972) Revision of the genus *Alebion* (Copepoda: Caligoida). *Smithsonian Contributions to Zoology* **123**, 1–29.
- Dippenaar SM (2018) Resurrection of *Alebion difficile* (van Beneden, 1892) (Copepoda: Siphonostomatoida: Caligidae) with notes on other species of *Alebion* Krøyer, 1863 collected from elasmobranchs off South Africa and an updated key of the adult females. *Systematic Parasitology* **95**, 881–891.
- Dojiri M and Ho J-S (2013) *Systematics of the Caligidae, Copepods Parasitic on Marine Fishes*. Leiden: Brill.
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**(5), 1792–1797. doi: 10.1093/nar/gkh340.
- Folmer O, Black M, Hoeh W, Lutz R and Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.
- Hamre Lars A, Eichner Christiane, Caipang Christopher Marlowe A, Dalvin Rasmie T, Bron James E, Nilsen Frank, Boxshall Geoff, Skern-Mauritzen Rasmus and Krkosek Martin (2013) The Salmon Louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) Life Cycle Has Only Two Chalimus Stages. *PLoS ONE* **8**(9), e73539. doi: 10.1371/journal.pone.0073539.
- Hebert PDN, Ratnasingham S and deWaard JR (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B: Biological Sciences* **270**, S96–S99.
- Hemmingsen W, MacKenzie K, Sagerup K, Remen M, Bloch-Hansen K and Dagbjartarson Imsland AK (2020) *Caligus elongatus* and other sea lice of the genus *Caligus* as parasites of farmed salmonids: a review. *Aquaculture* **522**, 735160.
- Henderson AC, Reeve AJ and Tang D (2013) Parasitic copepods from some northern Indian Ocean elasmobranchs. *Marine Biodiversity Records* **6**, e44.
- Heuch PA, Parsons A and Boxaspen K (1995) Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 681–689.
- Johnson SC and Albricht LJ (1991) Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. *Journal of the Marine Biological Association of the United Kingdom* **71**, 425–436.
- Kabata Z (1979) *Parasitic Copepoda of British Fishes*. London: Ray Society.
- Khoa TND, Malazan S, Muda S and Shaharom-Harrison F (2019) The life cycle of *Caligus minimus* on seabass (*Lates calcarifer*) from floating cage culture. *Thalassas* **35**, 77–85.
- Kim IH (1993) Developmental stages of *Caligus punctatus* Shiino, 1955 (Copepoda: Caligidae). In *Pathogens of Wild and Farmed Fish: Sea Lice*. Chichester: Ellis Horwood, pp. 16–29.
- Krøyer H (1863) Bidrag til Kundskab om Snyltekrebsene. *Naturhistorisk Tidsskrift Ser III* **2**, 75–320.
- Kumar S, Stecher G, Li M, Knyaz C and Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35**, 1547–1549.
- Lesueur CA (1818) Description of several new species of North American fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1**, 222–235.
- Lewis AG (1963) Life history of the caligid copepod *Lepeophtheirus dissimulatus*. *Pacific Science* **17**, 195–242.
- Luque J and Tavares L (2007) Checklist of Copepoda associated with fishes from Brazil. *Zootaxa* **1579**, 1–39.
- Meekan M, Austin CM, Tan MH, Wei N-WV, Miller A, Pierce SJ, Rowat D, Stevens G, Davies TK, Ponzo A and Gan HM (2017) IDNA at sea: recovery of whale shark (*Rhincodon typus*) mitochondrial DNA sequences from the whale shark copepod (*Pandarus rhincodonicus*) confirms global population structure. *Frontiers in Marine Science* **4**(420). doi: 10.3389/fmars.2017.00420.
- Mustafa A, Conboy GA and Burka JF (2001) Life-span and reproductive capacity of sea lice, *Lepeophtheirus salmonis*, under laboratory conditions. *Special Publication Aquaculture Association of Canada* **4**, 113–114.
- Nagler C and Haug JT (2016) Functional morphology of parasitic isopods: understanding morphological adaptations of attachment and feeding structures in *Nerocila* as a pre-requisite for reconstructing the evolution of Cymothoidae. *PeerJ* **4**, e2188.
- Ohtsuka S, Nawata M, Nishida Y, Nitta M, Hirano K, Adachi K, Kondo Y, Venmathi Maran BA and Suárez-Morales E (2020) Discovery of the fish host of the ‘planktonic’ caligid *Caligus undulatus* Shen & Li, 1959 (Crustacea: Copepoda: Siphonostomatoida). *Biodiversity Data Journal* **8**, e52271.
- Ohtsuka Susumu, Takami Ikuo, Venmathi Maran BA, Ogawa Kazuo, Shimono Takaki, Fujita Yusuke, Asakawa Manabu and Boxshall Geoffrey A (2009) Developmental stages and growth of *Pseudocaligus fugu* Yamaguti, 1936 (Copepoda: Siphonostomatoida: Caligidae) host-specific to Puffer. *Journal of Natural History* **43**(29–30), 1779–1804. doi: 10.1080/00222930902993757.
- Oldewage WH (1995) Redescription of *Alebion carchariae* Krøyer, 1863 (Copepoda, Siphonostomatoida) from *Isurus oxyrinchus* in South Africa. *Crustaceana* **68**, 38–42.
- Oldewage WH and Smale MJ (1993) Occurrence of piscine parasitic copepods (Crustacea) on sharks taken mainly off Cape Recife, South Africa. *South African Journal of Marine Science* **13**, 309–312.
- Piasecki W (1996) The developmental stages of *Caligus elongatus* von Nordmann, 1832 (Copepoda: Caligidae). *Canadian Journal of Zoology* **74**, 1459–1478.
- Rokicki J and Bychawska D (1991) Parasitic copepods of Carcharhinidae and Sphyridae (Elasmobranchia) from the Atlantic Ocean. *Journal of Natural History* **25**, 1439–1448.
- Tamura K and Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzee. *Molecular Biology and Evolution* **10**, 512–526.
- Vaissière R (1959) Parasites de poissons de mer ouest-africains récoltés par J. Cadenat. II. Copépodes. Copépodes caligides. Première note: Les Euryphorinae. *Bulletin de l'Institut français d'Afrique noire. Série A* **21**, 543–553.
- Voth DR (1972) Life history of the caligid copepod *Lepeophtheirus hospitalis* Fraser, 1920 (Crustacea: Caligoida). Doctoral thesis, Oregon State University.
- Walter TC and Boxshall G (2022) *World of Copepods Database*. Available at <https://www.marinespecies.org/copepoda> (accessed 26 October 2022). doi: 10.14284/356.
- Wilson CB (1907) North American parasitic copepods belonging to the family Caligidae. Part 2. *Proceedings of the National Academy of Sciences USA* **31**, 669–720.