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Parasite loss or parasite gain? Story of *Contracaecum* nematodes in antipodean waters

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A B S T R A C T

Contracaecum spp. are parasitic nematodes belonging to the family Anisakidae. They are known to be able to have highly pathogenic impacts on both wildlife (fish, birds, marine mammals) and humans. Despite having the most numerous species of any genus of Anisakidae, and despite a wide range of publications on various aspects of their pathogenicity, biology and ecology, there are no recent comprehensive reviews of these important parasites, particularly in the Southern Hemisphere. In this article, the diversity of *Contracaecum* parasites in Australian waters is reviewed and possible anthropological impacts on their populations are discussed. The abundance and diversity of these parasites may have been under-reported due to the inadequacy of common methods used to find them. Populations of *Contracaecum* parasites may be increasing due to anthropogenic factors. To minimise the risk these parasites pose to public health, preventive education of stakeholders is essential. There are still many unknown aspects of the parasites, such as detailed information on life cycles and host switching, that will be interesting directions for future studies.

Contents

1. Introduction

The genus *Contracaecum* Railliet & Henry, 1912 are parasitic nematodes belonging to the family Anisakidae Railliet & Henry, 1912 and have a global distribution (Anderson, 2000). If humans are excluded from their host list, *Contracaecum* is the only member of the Anisakidae that, throughout its life cycle, is able to infect both terrestrial and aquatic animals (freshwater and marine), which include a wide range of vertebrates and invertebrates. It also has zoonotic significance. With over 100 species assigned to this genus (Bezerra et al., 2019), it is the most numerous and diverse genus of the Anisakidae. Members of this genus are significant due to their number of species, the wide range of host species involved in their life cycles, and their adverse health impacts

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on hosts. Despite this, there has been no comprehensive literature review of these parasites. In particular, there is limited knowledge of these parasites in Australian waters. The aim of this article is to review the diversity of *Contracaecum* in Australian waters and provide insights into potential anthropological impacts on them.

2. Morphological characteristics of *Contracaecum*

As the genus' name suggests, these nematodes have two oppositely-directed caecae as part of their digestive system (Fig. 1). They also have an excretory pore located at their anterior end. These should be considered the most significant morphological characteristics when differentiating *Contracaecum* species from the rest of the anisakid nematodes because they are the most consistent at all developmental stages. Other important features with taxonomic significance in adult *Contracaecum* species include the presence of interlabia and labia, the absence of labial denticulation, rounded eggs with smooth shells, the presence of two spicules, conical tails in both male and females (which are shorter in males) and the presence of post- and pre-cloacal papillae in males (Fig. 1). Species within the genus can be differentiated based on variations in these features (Mozgovoi, 1953; Hartwich, 1964a).

3. How many *Contracaecum* species?

Deardorff and Overstreet (1981) placed the members of *Contracaecum* with excretory pore located close to the nerve ring, or below it, in the genus *Hysterothylacium* Ward & Magath, 1917 (Family Raphidascarididae Hartwich, 1954). This was later supported by molecular (Nadler et al., 2005) and other morphological and ecological data; e.g., *Hysterothylacium* become adults in fish whereas *Contracaecum* become adults in marine mammals and birds (Fagerholm, 1991). This resulted in the reclassification

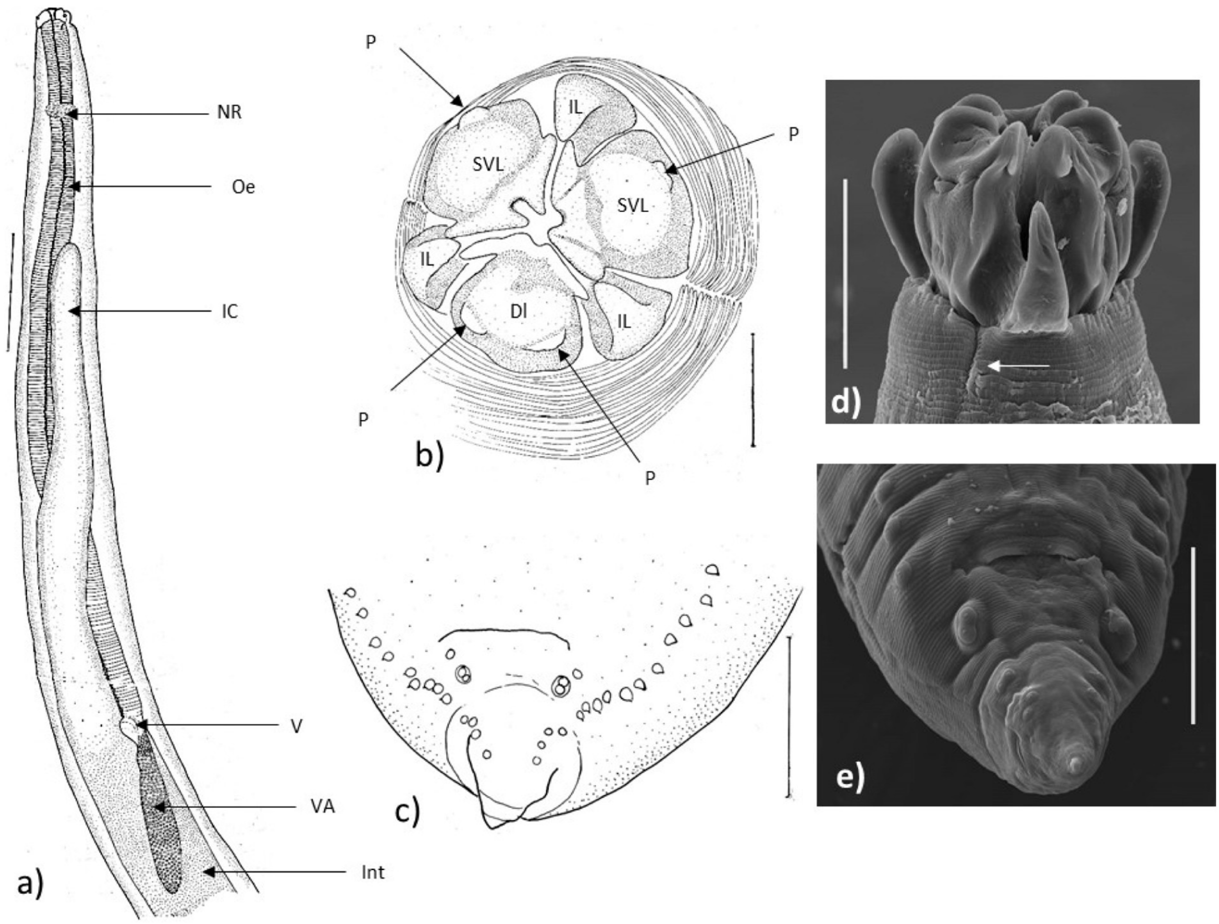

Fig. 1. Morphology of *Contracaecum* nematodes: (a) anterior end of *C. bancrofti* showing oesophagus, ventricular appendix and intestinal caecum (scale-bar = 0.65 mm); (b) apical view of lips in *C. bancrofti* (scale-bar = 0.17 mm); (c) posterior end of male (*C. pyripapillatum*), ventral view showing cloacal papillae (scale-bar = 0.17 mm); (d & e) scanning electron micrographs of *C. bancrofti*, c, showing folded interlabium. Arrow indicating lateral interruption in annulation of collar (scale-bar = 0.1 mm); (e) ventral view of male tail with three double pairs of post-cloacal papillae (scale-bar = 0.1 mm). Abbreviations: NR: nerve ring, Oe: oesophagus, IC: intestinal caecum, V: ventriculus, VA: ventricular appendix, Int: intestine, IL: interlabium, SVL: subventral labium, DL, dorsal labium, P: papillum. Modified from: Shamsi et al., 2008.

of over 70 species from *Contracaecum* to *Hysterothylacium*; however, there are still many species assigned as *Contracaecum*. Yamaguti (1961) alone recorded 63 species of *Contracaecum* in birds in his monograph and there are many more that infect marine mammals (e.g., Fagerholm, 1991). Moreover, molecular studies based on approaches such as multilocus enzyme electrophoresis (Nascetti et al., 1993; Orecchia et al., 1994) and DNA-based methods (Li et al., 2005; Shamsi et al., 2009a) have shown that some single species classifications actually comprise several distinct species with different host preferences and geographical distributions. Therefore, it can be estimated that, globally, there are still over one hundred species within the genus *Contracaecum*.

Shamsi (2014) listed 15 species of *Contracaecum* in Australia with valid taxonomic statuses, including *C. bancrofti* Johnston & Mawson, 1941, *C. eudyptulae* Johnston & Mawson, 1942, *C. heardi* Mawson, 1953, *C. magnipapillatum* Chapin, 1925, *C. microcephalum* (Rudolphi, 1809), *C. multipapillatum* (Drasche, 1882) Lucker, 1941, *C. ogmorhini* sensu stricto Johnston & Mawson, 1941, *C. osculatum* sensu *lato* (Rudolphi, 1802) Baylis, 1920, *C. pelagicum* Johnston & Mawson, 1942, *C. podicipitis* Johnston and Mawson, 1949, *C. pyripapillatum* Shamsi, Beveridge and Gasser, 2008, *C. radiatum* (Linstow, 1907) Baylis, 1920, *C. rudolphii* sensu *lato* Hartwich, 1964, *C. sinulabiatum* Johnston & Mawson, 1941 and *C. variegatum* (Rudolphi, 1809). Both in Australia and elsewhere, it is difficult to calculate the exact number of species within the genus due to issues with the validity of numerous species, particularly those described before the mid-20th century. Although the contributions of the earlier researchers to our knowledge of *Contracaecum* nematodes in Australia and elsewhere are significant, some of these early reports of the species have been poorly described and, as a result, differentiation between closely-related species is not possible. In addition, some of these species are unidentifiable by current standards, as their descriptions are brief and sometimes unillustrated. For example, *C. nycticoracis* Johnston & Mawson, 1941 was reported as a new species (Johnston and Mawson, 1941d) from *Nycticorax caledonicus* in Australia, based on only one male specimen with a brief description, unknown spicule length and no details of the post-cloacal papillae. The latter characteristics are the main features used to differentiate *Contracaecum* spp. Additionally, there are no details of the lips, size, or number of caudal papillae in the description of the new species. Therefore, this species is not differentiable from many other *Contracaecum* spp., including *C. microcephalum*. Another issue with early descriptions is that for many of the new species, such as *C. bancrofti*, *C. clelandi*, *C. sinulabiatum* and *C. magnicollare*, there is no information on the location of the type material in the original paper (Johnston and Mawson, 1941c). Some of these species have only been reported from Australia, such as *C. clelandi*, *C. eudyptes*, *C. heardi*, *C. magnicollare*, *C. nycticoracis*, *C. podicipitis* and *C. sinulabiatum*, and doubts have been raised concerning their validity (Hartwich, 1964a, b).

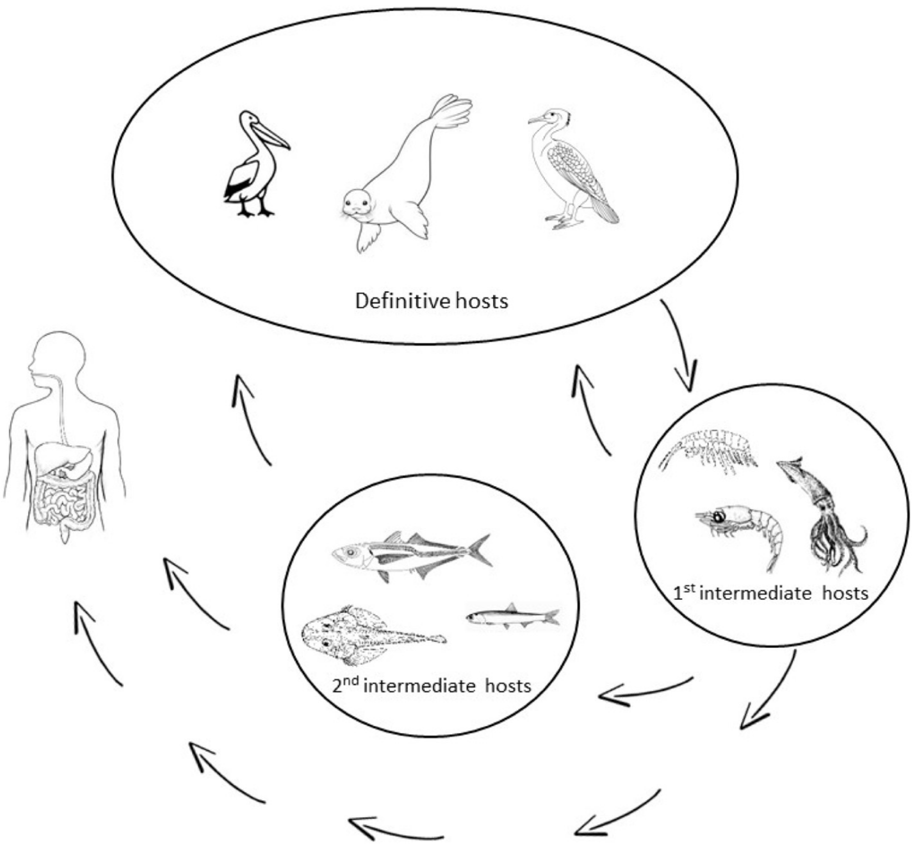

Fig. 2. Genera life cycle of *Contracaecum* spp.

4. Life cycle of *Contracaecum*: how much do we know?

The general life cycle pattern for the genus *Contracaecum* is summarised in Fig. 2. Eggs pass out in the faeces of the definitive host and enter the water, where they embryonate into first-stage larvae within the egg (L1). They then develop further and moult to the second stage (L2). Eggs or larvae can be ingested by first intermediate hosts and then grow in their haemocoel. A broad range of invertebrates, including coelenterates, ctenophores, gastropods, cephalopods, polychaetes, copepods, mysids, amphipods, euphausiids, decapods, echinoderms and chaetognaths can act as first intermediate hosts (Mozgovoi et al., 1965; Semenova, 1971; Norris and Overstreet, 1976; Semenova, 1979), although their roles in the natural transmission of the larvae to fish intermediate hosts are not completely clear (Anderson, 2000). When infected copepods are eaten by second intermediate hosts, larvae reach the third larval stage (L3). A great variety of teleost fishes can play the role of second intermediate or paratenic hosts. Various species of piscivorous birds and mammals associated with freshwater, brackish and marine environments (such as cormorants, pelicans and seals) become infected by predating upon infected fish and are definitive hosts of *Contracaecum*. It is highly likely that this general life history pattern is variable and there may be differences in the types of intermediate/definitive hosts among different species of *Contracaecum* (Shamsi, 2007).

In Australia, definitive hosts for *Contracaecum* include at least seven species of marine mammals (*Arctocephalus pusillus doriferus* Wood Jones, 1925, *Hydrurga leptonyx* (Blainville, 1820), *Leptonychotes weddelli* (Lesson, 1826), *Lobodon carcinophaga* (Hombrot & Jacquinot, 1842), *Mirounga leonina* (Linnaeus, 1758), *Neophoca cinerea* (Péron, 1816) and *Phocarctos hookeri* (Gray, 1844)) (Linstow, 1907; Johnston, 1938; Johnston and Mawson, 1941b, 1945, 1952; Mawson, 1953; Shamsi et al., 2009b) and 36 species of birds (*Anas superciliosa* Gmelin, 1789, *Anhinga melanogaster* Pennant, 1769, *Anous minutus* Boie, 1844, *A. stolidus* (Linnaeus, 1758), *Aptenodytes pataginica* Miller, 1778, *Ardea alba* Linnaeus, 1758 (reported as *Egretta alba*), *A. pacifica* Latham, 1801, (reported as *Notophoyx pacifica*), *Botaurus poeciloptilus* (Wagler, 1827), *Chlidonias leucopareia* (Temminck, 1815), *Daption capense* (Linnaeus, 1758), *Diomedea exulans* Linnaeus, 1758, *Egretta novaehollandiae* (Latham, 1790) (reported as *Ardea novaehollandiae*), *Ephippiorhynchus asiaticus* (Latham, 1790) (reported as *Xenorhynchus asiaticus*), *Eudyptes chrysolophus* (von Brandt, 1837), *E. cristatus* (J. F. Miller, 1784) accepted as *E. chrysocome* (Forster, 1781), *Eudyptula minor* (Forster, JR, 1781), *Macronectes giganteus* (Gmelin, JF, 1789), *Microcarbo melanoleucos* (Vieillot, 1817), *Morus serrator* (Gray, 1843) (reported as *Sula serrator*), *Notothenia coriiceps* Richardson, 1844, *Nycticorax caledonicus* (Gmelin, JF, 1789), *Pelecanus conspicillatus* Temminck, 1824, *Phalacrocorax carbo* (Linnaeus, 1758), *P. fuscescens* (Vieillot, 1817), *P. sulcirostris* (von Brandt, 1837), *P. varius* (Gmelin, JF, 1789), *Podiceps cristatus* (Linnaeus, 1758), *Poliocephalus poliocephalus* (Jardine & Selby, 1827), *Puffinus griseus* (Gmelin, 1789), *P. tenuirostris* (Temminck, 1835), *Pygoscelis papua* (Forster, JR, 1781), *Tachybaptus novaehollandiae* (Stephens, 1826), *Thalassarche cauta* steadi Falla, 1933 (reported as *Diomedea cauta*), *T. chlororhynchos* (Gmelin, 1789) (reported as *D. chlororhyncha*), *T. chrysostoma* (Forster, 1785) (reported as *D. chrysostoma*), *Thalassarche melanophris* (Temminck, 1828) reported as *D. melanophris*, (Johnston and Mawson, 1941a, d, 1942a, b, 1947, 1949; Mawson, 1953, 1969; McOrist, 1989; Shamsi et al., 2008; Shamsi et al., 2009a, b).

To date, nothing is known about the specific identity of first intermediate host(s) in Australian waters, but a broad variety of fish, including *Acanthopagrus butcheri* (Munro, 1949), *Aldrichetta forsteri* (Valenciennes, 1836), *Bidyanus bidyanus* (Mitchell, 1838) (reported as *Therapon bidyana*), *Carassius auratus* (Linnaeus, 1758), *Chironemus maculosus* (Richardson, 1850) (reported as *Threpterius maculosus*), *Cyprinus carpio* Linnaeus, 1758, *Galaxias maculatus* (Jenyns, 1842) (reported as *G. attenuates*), *G. olidus* Günther, 1866, *Gambusia holbrooki* Girard, 1859, *Hypseleotris klunzingeri* (Ogilby, 1898) (reported as *Carassiops klunzingeri*), *Hypseleotris* sp., *Maccullochella macquariensis* (Cuvier, 1829), *Macquaria ambigua* (Richardson, 1845), *M. colonorum* (Günther, 1863) (reported as *Percolates colonorum*), *Melanotaenia fluviatilis* (Castelnau, 1878), *Misgurnus anguillicaudatus* (Cantor, 1842), *Mogurnda adspersa* (reported as *M. adspersus*), *Mugil cephalus* Valenciennes, 1836, *Nannoperca australis* Günther, 1861, *Nematalosa erebi* (Günther, 1868), *Osteomugil cunnesius* (Valenciennes, 1836) (reported as *Mugil strongylocephalus*), *Ostorhinchus fasciatus* (White, 1790) (reported as *Apogon fasciata*), *Philypnodon grandiceps* (Krefft, 1864), *Planiliza subviridis* (Valenciennes, 1836) (reported as *Mugil dussumieri*), *Platycephalus endrachtensis* Castelnau, 1872 (reported as *P. arenarius*), *P. laevigatus* Cuvier, 1829, *Pseudocaranx dentex* (Bloch & Schneider, 1801), *Pseudogobius olorum* (Sauvage, 1880) (reported as *Mugilogobius galwayi*), *Pseudaphritis urvillii* (Valenciennes, 1832), *Pseudorhombus arsius* (Hamilton, 1822), *P. jenynsii* (Bleeker, 1855), *Retropinna semoni* (Weber, 1895), *Scomber australasicus* Cuvier, 1832, *Seriola lalandi* Valenciennes, 1833, *Sillaginodes punctatus* (Cuvier, 1829) (reported as *S. punctate*), *Tandanus tandanus* (Mitchell, 1838), *Tripodichthys angustifrons* (Hollard, 1854), *Upeneichthys lineatus* (Bloch & Schneider, 1801) (reported as *U. porosus*) and an unknown fish species belonging to family Atherinidae Risso, 1827 (hardy-head) have been reported as the second intermediate/paratenic host for *Contracaecum* larval types (Johnston and Mawson, 1940, 1944, 1947, 1951; Cannon, 1977; Lymbery et al., 2002; Shamsi et al., 2011; Jabbar et al., 2013; Shamsi et al., 2017; Shamsi et al., 2018a, b). It is believed that the occurrence and abundance of *Contracaecum* larvae in Australian fish have been significantly underestimated (Shamsi and Suthar, 2016) as most published studies have relied on visual examination of fish. Shamsi et al. (2017) showed that some *Contracaecum* larvae can be minute and deeply embedded within the gastrointestinal tissue of fish, and can only be observed by removing the gastrointestinal tissue and keeping it warm for several hours, which causes the larvae to emerge. The response of *Contracaecum* larvae in fish (exothermal animals) to slight increases in temperature in a laboratory environment, is perhaps similar to what happens in the stomachs of their natural definitive hosts, all being endothermal animals. Based on this experiment, it has been shown that combined visual examination and incubation of tissue is the most efficient method of detecting internal parasites in fish. For example, in a study of infection with anisakid larvae, including *Contracaecum*, the mean parasite abundance in flathead and mackerel, was about 7 and 14 times higher (respectively) using the method recommended by Shamsi and Suthar (2016). Since previous reports of *Contracaecum* larvae in Australian fish have all been based on visual examination, it is highly likely that many more fish are involved in the life cycle and are infected with higher numbers of *Contracaecum* larvae than previously thought.

5. *Contracaecum* and human health

Anisakidosis is a disease caused by infection with anisakid nematodes, including *Contracaecum* larvae in humans. Several reports from the Baltic region (Schaum and Müller, 1967), France (Dei-Cas et al., 1986), the Republic of Korea (Im et al., 1995), Australia (Shamsi and Butcher, 2011) and Japan (Nagasawa, 2012) have shown that *Contracaecum* larvae cause a severe and painful condition in humans following ingestion of raw or under-cooked fish carrying third-stage larvae. *Contracaecum* larvae cannot be identified to species level without the aid of molecular tools and in all the human cases mentioned above, morphological identification was to genus level only. A review of the abovementioned literature suggests that the common assumption among most authors is that the zoonotic species are those occurring in marine mammals, and in particular *C. osculatum*, while those occurring in birds are not considered zoonotic. However, there is not yet any evidence supporting this belief and, to-date, there has been no specific identification of *Contracaecum* larvae isolated from humans using molecular tools.

Therefore, identification of parasites to species level in clinical cases is highly valuable, as it can provide essential information on zoonotic species and for the prevention and control of diseases caused by seafood-borne helminths. This is particularly important in the case of new and emerging diseases such as anisakidosis. With the increased popularity of eating raw or lightly cooked seafood dishes, as well as changes in social, dietary and cultural behaviours and environmental conditions, the number of cases of seafood-borne parasitic diseases, particularly anisakidosis, is increasing. However, many questions are yet to be addressed. For example: Why have *Contracaecum* larva in Australian human cases not penetrated any tissue yet caused severe illnesses and a broad range of symptoms, whereas in other countries, *Contracaecum* larvae are reported to penetrate the tissues of various organs? Could this be because the only *Contracaecum* species in seals in Australian waters is *C. ogmorhini*, which is absent in the northern hemisphere where human *Contracaecum* cases have a different clinical presentation? If this hypothesis is true, then it leads to a new question: Are avian *Contracaecum* also of zoonotic significance? The latter question is relevant, since Fagerholm and Gibson (1987) argued that *C. ogmorhini* is an avian form which has been only recently established in marine mammals, i.e., pinnipeds.

6. Impacts of human activities

Some Australian populations of aquatic-associated birds and marine mammals—the definitive hosts of *Contracaecum*—have recovered after being severely depleted (http://www.environment.gov.au/node/16447; http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=21; http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=20). These animals harbour the adult stage of *Contracaecum* and provide it with a suitable habitat to mate, breed and produce eggs, which are then passed to the environment through faeces.

The literature suggests that recent reports of human infection with parasites acquired from marine fish in Australia are extremely scarce, with only two cases in the last 50 years (see the critical review by Shamsi and Shorey, 2018). One case was due to infection with *Contracaecum* larva (Shamsi and Butcher, 2011) and the other was due to infection with the tapeworm *Adenocephalus pacificus*, previously known as *Diphyllobothrium latum* (Moore et al., 2016). There are some interesting common factors in both cases: both parasites have seals as their definitive hosts, both occurred recently after increases in seal populations, and both occurred in South Australia, where seals migrate seasonally. These factors raise a number of critical questions: Are fish in south Australian waters becoming more infected with seal parasites? Is aquaculture industry in the region affected with seal parasites such as *C. ogmorhini* and *A. pacificus*?

Interestingly, in the northern hemisphere, Zuo et al. (2017) showed that a marked increase in the population of the Baltic gray seal in recent years was associated with 100% prevalence and a mean intensity of *Contracaecum osculatum* larvae (>80 worms per fish) in Baltic cod, compared to a low prevalence and intensity reported during the 1980s and 1990s when the seal population was smaller. A significant increase in the number of *Contracaecum* larvae (identified as *C. osculatum*) in cod has been directly related to increased risk for consumers.

In Australia, the number of human cases is too low to confidently relate them to seal populations. Although, there is no standard diagnostic test for anisakidosis in Australia, such that the number of actual cases may be underestimated.

In Australia and Antarctic region, ten species of seals and sea lions can be found. Similar to the Baltic region, despite a dramatic decline in populations of seals due to colonial-era sealing, today all seals are protected in Australian waters and populations of some species are recovering. Three species, the Australian sea lion, Australian fur seal and New Zealand fur seal, commonly occur in southern Australian waters where the abovementioned human cases were reported. One interesting area for future study would be to investigate the prevalence and abundance of seal parasites in fish in South Australian waters. Although fish stocks in Australian waters are reported to have declined by one-third in the past decade, surprisingly, no study has comprehensively investigated the roles that parasites, including *Contracaecum* larvae, may play in fish health and population size. In other countries, declines in fish populations have been attributed to increases in the mortality of large fish heavily infected with *Contracaecum* larvae (Horbowy et al., 2016). These authors also showed that the body condition of infected fish (e.g., Baltic cod) was lower than that of non-infected fish, and declined with the intensity of infection.

7. Conclusions

Populations of *Contracaecum* parasites may be increasing due to anthropogenic factors. To minimise the risk these parasites pose to public health, education of all stakeholders is essential. The abundance and diversity of these parasites may also have been under-reported due to inadequacies in the common methods used to find them. There are still many unknown aspects, such as detailed information on life cycles and host switching, which will be interesting directions for future studies.

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