YALE JOURNAL OF BIOLOGY AND MEDICINE 91 (2018), pp.361-374.

ORIGINAL CONTRIBUTION

Host Specificity and Ecology of Digenean Parasites of Nassariid Gastropods in Central Queensland, Australia, with Comments on Host-Parasite Associations of the Nassariidae

Leonie J. Barnett[a,*] and Terrence L. Miller[b,c]

[a]*Central Queensland University, School of Access Education, Bruce Highway, North Rockhampton, Queensland, Australia;* [b]*Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Cairns, Queensland, Australia;* [c]*Aquatic Animal Health Laboratories, Department of Primary Industries and Regional Development, Perth, Western Australia, Australia*

Nassariid gastropods are well represented in Australia, and *Nassarius dorsatus* (Röding), *Nassarius olivaceus* (Bruguière), and *Nassarius pullus* (Linnaeus) are common in the intertidal mangroves of the Capricornia region in Central Queensland. A survey of the digenean trematode fauna of nassariids of the region revealed cercariae of 12 species from six trematode families associated with these gastropods. Six species of Acanthocolpidae were found, including three putative species of the genus *Stephanostomum*. Additionally, two species of Himasthlidae and one species each of Microphallidae, Opecoelidae, Zoogonidae, and Lepocreadiidae were identified. The majority of the trematode species identified were found in only one host species; only four infected more than one species of nassariid. Sixteen new host-parasite combinations were added to the fauna known to infect the Nassariidae. Broader examination of host-parasite associations shows that families using nassariids commonly as first intermediate host are the Acanthocolpidae, Lepocreadiidae, and Zoogonidae, as well as *Himasthla* spp. from the Himasthlidae. Nassariid gastropods are also the dominant marine first intermediate hosts for the Acanthocolpidae, Lepocreadiidae, and Zoogonidae and one of the three most common first intermediate host families for marine *Himasthla* spp.

INTRODUCTION

The Nassariidae Iredale, 1916 (1835) is a large family of marine gastropods containing approximately 442 valid extant species [1] in the Superfamily Buccinoidea Rafinesque, 1815 of the Order Neogastropoda [2]. Nassariids are primarily carnivorous scavengers and are found predominantly in estuarine or shallow marine soft substrates [3].

Digenean trematode parasites typically have a three host life cycle, involving a vertebrate definitive host and two intermediate hosts; the first intermediate host is most often a mollusk [4]. The parasite fauna of only

*To whom all correspondence should be addressed: Leonie J. Barnett, School of Access Education, Central Queensland University, North Rockhampton Q 4702; Tel: 61 7 49309975, Email: l.barnett@cqu.edu.au.

Keywords: cercaria, Nassariidae, Digenea, Lepocreadiidae, Zoogonidae, Acanthocolpidae

Author Contributions: Leonie Barnett did the research and wrote the draft document. Terrence Miller provided guidance during the project and worked on the final draft. This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

a relatively small number of the 442 species of nassariid gastropods has been thoroughly studied (see Table 1); these gastropods include *Tritia obsoleta* (Say) [syn. *Ilyanassa obsoleta* (Say); *Nassarius obsoletus* (Say)], an intertidal gastropod found along the east and west coasts of North America [5], and *Tritia reticulata* (Linnaeus) [syn. *Nassarius reticulatus* (Linnaeus)], common to the north-eastern Atlantic and the Mediterranean, Black, and Azov Seas [6].

The Nassariidae is well represented in Australia [7], with *Nassarius dorsatus* (Röding), *Nassarius olivaceus* (Bruguière), and *Nassarius pullus* (Linnaeus) common inhabitants in the intertidal mangroves of the Capricornia region in Central Queensland, Australia. Knowledge of larval digenean fauna infecting gastropods in Australian marine environments is broadly lacking. To date, few surveys of the digenean fauna in marine gastropods have been conducted in Australia, and only one comprehensive taxonomic survey of the cercariae of a gastropod species has been undertaken. A study of *Clypeomorus batillariaeformis* Habe and Kosuge reported infections with cercariae of eleven species in eight families [8]. This study aimed to document and characterize the trematode fauna infecting *N. dorsatus*, *N. olivaceus,* and *N. pullus* in mangroves in Central Queensland, Australia.

MATERIALS AND METHODS

Host gastropod and parasite collection. Gastropods were collected by hand from mudflats at Sandy Point, Corio Bay (22°58′ S, 150°46′ E), Ross Creek, Yeppoon (23°8′ S, 150°45′ E), and the mouth of Cawarral Creek, Keppel Sands (23°19′ S, 150°47′ E) in Central Queensland, Australia. Totals of 1766 *N. dorsatus*, 1908 *N. olivaceus,* and 1614 *N. pullus* were collected between August 2004 and May 2006. For the first twelve months, up to approximately 100 individuals of each species were collected every three months from each locality. The numbers of nassariids at Ross Creek were lower than at the other two localities due to the small area and limited habitat available. This collection was continued for a further twelve months at Sandy Point, whereas at Ross Creek and Cawarral Creek, only *N. olivaceus* and reduced numbers of *N. dorsatus* were collected (no *N. pullus* were collected from Ross Creek or Cawarral Creek in the second twelve months).

Gastropods were held in filtered seawater at room temperature (20–28°C) and examined for naturally emerged cercariae every 1–3 days for up to one month. Freshly emerged cercariae were transferred to a cavity block in a small volume of seawater and heat-killed by pouring several volumes of near boiling seawater into the dish. Specimens for morphological analysis were fixed in 5% formalin and identified to family using Schell [9]. A subset of infected gastropods was dissected to determine the nature of intramolluskan stages.

A subset of gastropods from which cercariae did not emerge was also dissected to check infection status. Totals of 720 *N. dorsatus* (40.8% of 1766), 877 *N. olivaceus* (46.0% of 1908), and 70 *N. pullus* (4.3% of 1614) were dissected.

Morphological analysis. Fixed cercariae were examined as temporary wet mounts without flattening. Live specimens and rediae were also observed as temporary wet mounts as per Barnett, Smales [10].

Literature review. Previous reports in the literature were collated to provide a list of cercariae reported from nassariid gastropods (see Table 1) and to derive a matrix of families reported from nassariids (see Table 2).

RESULTS

Cercariae of 12 species from six families were found from *N. olivaceus*, *N. dorsatus,* and *N. pullus* (Table 3). Of these, six were attributed to the family Acanthocolpidae Lühe, 1906 and comprised three unusual cercariae and three similar to known *Stephanostomum* spp. cercariae. Of the others, there was one species of each of the families Lepocreadiidae Odhner, 1905, Opecoelidae Ozaki, 1925, Zoogonidae Odhner, 1902, and Microphallidae Ward, 1901 and two of the family Himasthlidae Odhner, 1910 (both were morphologically similar to reported *Himasthla* spp.). The cercariae from the Lepocreadiidae, Microphallidae, and Himasthlidae and one of the *Stephanostomum* sp. cercaria are yet to be formally described.

A total of 115 infections were identified by cercarial emergence from the 5288 gastropods observed, and a further eleven were identified by dissection. Of the 1667 gastropods dissected, 16 infections were found, four in *N. dorsatus* and 12 in *N. olivaceus*. Of these, 11 were able to be identified as the opecoelid cercaria, whereas the four infections in *N. dorsatus* and one in *N. olivaceus* could not be identified by dissection as the cercariae were too immature and the rediae were not sufficiently distinctive.

Cercariae of eight species were found only in a single gastropod species and only four infected more than one host species (Table 3). No cercaria infected all three species studied. Of the four infections with two host species, three involved *N. olivaceus* and *N. dorsatus* (the acanthocolpids *Cercaria capricornia* III and *Cercaria capricornia* VII (a *Stephanostomum* sp.), and the lepocreadiid cercaria) and the other involved *N. olivaceus* and *N. pullus* (one himasthlid cercaria). For the two-host species, there was generally a higher prevalence of infection in one nassariid species than in the other. For the acanthocolpid *C. capricornia* III, infection was more prevalent in *N. olivaceus* (0.4%) than in *N. dorsatus* (<0.1%). Similarly, the lepocreadiid cercaria was more

Table 1. Digenean parasites (cercariae) reported from nassariid gastropods.

Host species	Parasite family	Parasite species	Region	Sources
Family Nassariidae				
Subfamily Buccinanopsinae				
Buccinanops cochlidium (Dillwyn)	Lepocreadiidae	*Opechona* sp.	South America	[44]
Buccinanops globulosus (Kiener)	Zoogonidae	*Diphterostomum* sp.	South America	[45]
Buccinanops monilifer (Kiener)	Lepocreadiidae	*Opechona* sp.	South America	[44,46]
Subfamily Bullinae				
Bullia digitalis (Dillwyn)	Microphallidae Zoogonidae	*Cercaria hastata* Webb, 1991 *Cercaria hapax* Brown & Webb, 1994 [probable *Zoogonoides* sp.] *Cercaria bulliae* Brown & Webb, 1994 [uncertain placement, tailless cercaria]	South Africa, Atlantic & Indian Oceans	[47,48]
Subfamily Nassariinae				
Nassarius arcularia plicatus (Röding)	Cyathocotylidae Opecoelidae	Longifurcate-pharyngeate cercaria [Cyathocotylidae] Cotylomicrocercous cercaria 1 [Opecoelidae]	Indian Ocean	[49]
Nassarius circumcinctus (A. Adams)	Lepocreadiidae	*Cercaria levantina* 2 Lengy & Shchory, 1970	Indian Ocean & Mediterranean Sea	[30]
Nassarius dorsatus (Röding)	Acanthocolpidae	*Cercaria capricornia* III Barnett, Smales & Cribb, 2008 *Cercaria capricornia* VI Barnett, Smales & Cribb, 2008 *Cercaria capricornia* VII Barnett, Miller & Cribb, 2010 [probable *Stephanostomum* sp.] *Cercaria capricornia* VIII Barnett, Miller & Cribb, 2010 [probable *Stephanostomum* sp.]	Pacific Ocean	[10,31]
Nassarius olivaceus (Bruguière)	Acanthocolpidae	*Cercaria capricornia* I Barnett, Smales & Cribb, 2008 *Cercaria capricornia* III Barnett, Smales & Cribb, 2008 *Cercaria capricornia* VII Barnett, Miller & Cribb, 2010 [probable *Stephanostomum* sp.]	Pacific Ocean	[10,31,33,43]
	Opecoelidae Zoogonidae	*Cercaria capricornia* XII Barnett & Miller, 2014 *Cercaria capricornia* XI Barnett & Miller, 2014		
Nassarius orissaensis (Preston)	Acanthocolpidae	*Stephanostomum cloacum* (Srivastava, 1938) Manter & Van Cleave, 1951	Indian Ocean	[50,51]
	Zoogonidae	*Cercaria chilkaensis* II, Madhavi & Shameem, 1991		

Table 1. cont'd

Nassarius protrusidens (Melvill)	Opecoelidae	Cotylomicrocercous cercaria 1	Indian Ocean	[49]
Nassarius stolatus (Gmelin)	Acanthocolpidae	*Cercaria bengalensis* VII Gnana Mani, 1994 [similar to *Stephanostomum* spp.]	Indian Ocean	[52]
Phrontis vibex (Say) [syn. *Nassarius vibex* (Say)]	Himasthlidae	*Himasthla quissetensis* (Miller & Northup, 1926) Stunkard, 1938 *Cercaria criolissima* II Nasir, 1976 [similar to *Himasthla* spp.] *Cercaria criolissima* IV Nasir, 1976 [similar to *Himasthla* spp.]	Caribbean Sea	[34,53,54]
	Lepocreadiidae	*Cercaria caribbea* LXVI Cable, 1963		
Tritia corniculum (Olivi) [syn. *Nassarius corniculum* (Olivi)]	Lepocreadiidae	*Lepocreadium album* (Stossich, 1890) Stossich, 1903 *Lepocreadium pegorchis* (Stossich, 1901) Stossich, 1903	North Atlantic	[44,55-58]
	Strigeidae	*Cardiocephalus longicollis* Szidat, 1928 [syn. *Cercaria nassae* Dolgikh, 1965]		
Tritia mutabilis (Linnaeus) [syn. *Nassarius mutabilis* (Linnaeus)]	Lepocreadiidae	*Lepocreadium album* (Stossich, 1890) Stossich, 1903 *Lepocreadium pegorchis* (Stossich, 1901) Stossich, 1903	North Atlantic	[55,56,58-61]
	Zoogonidae	*Diphterostomum brusinae* (Stossich, 1888) Stossich, 1903 [syn. *Diphtherostomum brusinae* (Stossich, 1888) Stossich, 1903; *Distomum brusinae* Stossich, 1888; *Cercaria crispata* Pelseneer, 1906; *Cercaria inconstans* Sinitsin, 1911] *Zoogonus lasius* (Leidy, 1891) Stunkard, 1940 [syn. *Cercaria lintoni* Miller & Northup, 1926; *Distomum lasium* Leidy, 1891; *Zoogonus rubellus* (Olsson, 1868) of Stunkard (1938) in part]		
Tritia obsoleta (Say) [syn. *Ilyanassa obsoleta* (Say); *Nassarius obsoletus* (Say)]	Acanthocolpidae	*Stephanostomum tenue* (Linton, 1898) Linton, 1934 *Stephanostomum dentatum* (Linton, 1900) Linton, 1940 [syn. *Cercaria dipterocerca* Miller & Northup, 1926]	North Atlantic	[62-68]
	Diplostomidae	*Diplostomum nassa* (Martin, 1945) Stunkard, 1973		
	Himasthlidae	*Himasthla quissetensis* (Miller & Northup, 1926) Stunkard, 1938		
	Lepocreadiidae	*Lepocreadium setiferoides* (Miller & Northup, 1926) Martin, 1938		
	Microphallidae	*Gynaecotyla adunca* (Linton, 1905) Yamaguti, 1939		
	Pronocephalidae	*Pleurogonius malaclemys* Hunter, 1961		
	Schistosomatidae	*Austrobilharzia variglandis* (Miller and Northup, 1926) Penner, 1953		
	Zoogonidae	*Zoogonus lasius* (Leidy, 1891) Stunkard, 1940 [syn. *Cercaria lintoni* Miller & Northup, 1926; *Distomum lasium* Leidy, 1891; *Zoogonus rubellus* (Olsson, 1868) of Stunkard (1938) in part]		
Tritia pellucida (Risso) [syn. *Cyclope pellucida* Risso; *Cyclope donavania* Risso; *Cyclonassa kamyschiensis* Chenu]	Zoogonidae	*Diphterostomum brusinae* (Stossich, 1888) Stossich, 1903 [syn. *Diphtherostomum brusinae* (Stossich, 1888) Stossich, 1903; *Distomum brusinae* Stossich, 1888; *Cercaria crispata* Pelseneer, 1906; *Cercaria inconstans* Sinitsin, 1911]	North Atlantic	[58,69,70]

Table 1. cont'd

Tritia pygmaea (Lamarck) [syn. *Nassarius pygmaeus* (Lamarck)]	Lepocreadiidae	*Opechona bacillaris* (Molin, 1859) Dollfus, 1927	North Atlantic	[71]
Tritia reticulata (Linnaeus) [syn. *Nassarius reticulatus* (Linnaeus)]	Acanthocolpidae	*Cercaria pontica* Dolgikh, 1965 [similar to *Stephanostomum* spp.]	North Atlantic	[6,14,44, 47,57,60, 61,70-73]
	Himasthlidae	*Himasthla quissetensis* (Miller & Northup, 1926) Stunkard, 1938		
	Lepocreadiidae	*Lepocreadium album* (Stossich, 1890) Stossich, 1903 *Cercaria fascicularis* Villot, 1875 *Cercaria sebastopoli* Dolgikh, 1965 [similar to *Lepocreadium* sp.]		
	Microphallidae	*Gynaecotyla longiintestinata* Leonov, 1958 [syn. *Cercaria sevillana* Russell-Pinto & Bartoli, 2002; *Cercaria misenensis* Dolgikh, 1965]		
	Strigeidae	*Cardiocephalus longicollis* Szidat, 1928 [syn. *Cercaria nassae* Dolgikh, 1965]		
	Zoogonidae	*Diphterostomum brusinae* (Stossich, 1888) Stossich, 1903 [syn. *Diphtherostomum brusinae* (Stossich, 1888) Stossich, 1903; *Distomum brusinae* Stossich, 1888; *Cercaria crispata* Pelseneer, 1906; *Cercaria inconstans* Sinitsin, 1911] *Zoogonus rubellus* (Olsson, 1868) Odhner, 1902 [syn. *Cercaria reticulatum* Stunkard, 1932; *Zoogonus mirus* Looss, 1901] An unidentified zoogonid cercaria		
Tritia trivittata (Say) [syn. *Ilyanassa trivittata* (Say); *Nassarius trivittatus* (Say)]	Hemiuridae	*Tubulovesicula pinguis* (Linton, 1940) Manter, 1947	North Atlantic	[74,75]
	Lepocreadiidae	*Lepocreadium areolatum* (Linton, 1900) Stunkard, 1969		

prevalent in *N. olivaceus* (0.7%) than in *N. dorsatus* (<0.1%), whereas *C. capricornia* VII was more prevalent in *N. dorsatus* (0.6%) than in *N. olivaceus* (0.3%). The himasthlid cercaria was more prevalent in *N. olivaceus* (1.0%) than in *N. pullus* (0.2%).

There were four rare infections with an overall prevalence of infection of ≤0.1%. These were the acanthocolpids *Cercaria capricornia* VI and one *Stephanostomum* sp., and the zoogonid *Cercaria capricornia* XI, which each had only a single infection, and the *Stephanostomum* sp. *Cercaria capricornia* VIII, which had two infections. No species occurred at a prevalence of more than 1.4% overall. The most common species were the acanthocolpid *Cercaria capricornia* I (27 infections; 1.4%), the *Stephanostomum* sp. *C. capricornia* VII (15 in two host species), the lepocreadiid cercaria (14 in two host species), the opecoelid *Cercaria capricornia* XII (20; 1.0%), and one himasthlid cercaria (24 in two host species).

Some cercarial species were collected only from a single locality (Table 4). For rare infections, this is unlikely to indicate specificity for the locality, but for the two himasthlid and the microphallid cercariae, all infections were restricted to Sandy Point and occurred at locality prevalences of 2.4% (*N. olivaceus*) and 0.4% (*N. pullus*) for one himasthlid, 0.6% for the other himasthlid and 1.0% for the microphallid. Species that were found at all localities included the acanthocolpids *C. capricornia* I and *C. capricornia* III, the *Stephanostomum* sp. *C. capricornia* VII, the lepocreadiid cercaria and the opecoelid *C. capricornia* XII, although for the opecoelid, there were more infections at Cawarral Creek than at the other two localities.

The prevalence of infection varied among localities (Table 4). At Cawarral Creek, only the acanthocolpid *C. capricornia* I and the opecoelid cercaria were present at prevalences higher than 1.0%. At Sandy Point, *C. capricornia* I and one himasthlid cercaria had prevalences greater than 1.0%. Most parasitized gastropods collected at Ross Creek were infected at prevalences greater than 1.0%, but this was a small area and this may be a result of bias towards collection of larger, older gastropods at that locality. Morphotypes rarely found were *C. capricornia* I, *C. capricornia* V, *C. capricornia* VI, *C. capricornia* VIII, one *Stephanostomum* sp., *C. capricornia* XI, and one of the two himasthlid cercariae.

Overall, *N. olivaceus* had the greatest species richness (8 species from 6 families), followed by *N. dorsatus* (7 species from 3 families), and *N. pullus* (1 species only). *Nassarius olivaceus* also had the highest frequency of infection (102 of 1908; 5.3%), followed by *N. dorsatus* (20 of 1766; 1.1%), and *N. pullus* (4 of 1614; 0.2%).

DISCUSSION

One interesting feature of the pattern of infection in the three species of *Nassarius* in the present system is the overall low prevalence of infection. Several parasite species had prevalences well under 1% and the highest, *C. capricornia* I, was only 4.3% at Ross Creek. The highest overall prevalence of infection was 5.3% in *N. olivaceus*. These data contrast strikingly with the well-studied nassariid *T. obsoleta,* reported to be generally uninfected until sexual maturity at around three years, incidence of infection then rising exponentially from 5 to 30% at 3 years to 90 to 100% in older individuals [11]. However, the longevity of *T. obsoleta* is remarkable, estimated at 30 to 40 years and, in one population, at 70 years of age [12,13]. Tallmark and Norrgren [14] also found 100% parasitism in older *T. reticulata*, reported to live to 11 years in Portugal [15] and 15 years in Sweden [16]. In addition, spatial heterogeneity of parasitism is seen in *T. obsoleta*, and highly variable results between sample populations were reported from a single sand-flat (infection frequencies of less than 10% as well as 100%) [11]. Similar spatial heterogeneity has been reported in other studies of *T. obsoleta* [13,17]. Curtis [17] admitted that there was considerable variation between sites and that the Delaware regional trematode community had a higher frequency of infection than other studies. In North Carolina, *T. obsoleta* was infected at 6.49% [18] and 4.07% [19], results similar to those seen in *N. olivaceus* in Capricornia.

Also, the longevity of the infected nassariids in Capricornia was much shorter than that of *T. obsoleta* and *T. reticulatus*; *N. olivaceus* survived for up to ~4.5 years, *N. dorsatus* for up to ~0.8 years and *N. pullus* for only ~0.3 years after collection. Most infected *N. olivaceus* died within the first year (53%), 26% in the second year, 9% in the third and fourth years, and only 3% survived into the fifth year. Although a few infected *N. dorsatus* survived into the second six months after collection, the majority died within the first six months. The longevity of *N. dorsatus* and *N. olivaceus* is unknown. McKillup and McKillup [20] reported that *N. dorsatus* at Cawarral Creek appeared to have a very short life cycle, growing rapidly and surviving for only about 2 months following settlement. They also reported that laboratory maintained specimens of *N. dorsatus* displayed a similar rapid growth [20]. Puturuhu [21] suggested that growth was faster in warm tropical than cool temperate regions, with reduced longevity. A review of published data on 54 species of gastropods found that prevalence was positively correlated with trematode species richness, but found no evidence that longevity was associated with prevalence [22]. However, they warned that their study did not include data from tropical latitudes. A comparison of

Table 2. Matrix of host-parasite records for nassariid gastropods by parasite family (numbers within matrix indicate number of species recorded for each family).

Host species	L	Z	A	Hi	M	O	St	P	D	Sc	He	C	Total families in host	Total species in host
Subfamily Bullinae														
Bullia digitalis		2			1								**2**	**3**
Subfamily Buccinanopsinae														
Buccinanops cochlidium	1												**1**	**1**
Buccinanops globulosus		1											**1**	**1**
Buccinanops monilifer	1												**1**	**1**
Subfamily Nassariinae														
Nassarius arcularia plicatus						1						1	**2**	**2**
Nassarius circumcinctus	1												**1**	**1**
Nassarius dorsatus	1		5	1									**3**	**7**
Nassarius mutabilis	2	2											**2**	**4**
Nassarius olivaceus	1	1	3	1	1	1							**6**	**8**
Nassarius orissaensis		1	1										**2**	**2**
Nassarius protrusidens						1							**1**	**1**
Nassarius pullus				1									**1**	**1**
Nassarius pygmaeus	1												**1**	**1**
Nassarius stolatus			1										**1**	**1**
Phrontis vibex	1			3									**2**	**4**
Tritia corniculum	2						1						**2**	**3**
Tritia obsoleta	1	1	2	1	1			1	1	1			**8**	**9**
Tritia pellucida		1											**1**	**1**
Tritia reticulata	3	3	1	1	1		1						**6**	**10**
Tritia trivittata	1										1		**2**	**2**
Total host records (families)	**12**	**8**	**6**	**6**	**4**	**3**	**2**	**1**	**1**	**1**	**1**	**1**		
Total host records (species)	**16**	**12**	**13**	**8**	**4**	**3**	**2**	**1**	**1**	**1**	**1**	**1**		

L: Lepocreadiidae, Z: Zoogonidae, A: Acanthocolpidae, Hi: Himasthlidae, M: Microphallidae, O: Opecoelidae, St: Strigeidae, P: Pronocephalidae, D: Diplostomatidae, Sc: Schistosomatidae, He: Hemiuridae, C: Cyathocotylidae

parasite prevalence in horn snails that included tropical regions reported that prevalence increased with latitude, and they suggested that higher mortality rates at lower latitudes may be one contributor to this [23]. The low prevalence of infections observed in the tropical nassariids in Capricornia relative to the cold-water inhabiting species discussed above may be due to their shorter life span resulting in less overall potential exposure to infectious stages of the trematode parasites in the system.

Host Specificity

The majority of the cercariae were found in only one host species; only four (the acanthocolpids *C. capricornia* III and *C. capricornia* VII (*Stephanostomum* sp.), the lepocreadiid cercaria and one himasthlid cercaria) infected two species. All three *Stephanostomum* spp. cercariae infected *N. dorsatus*, whereas only one infected *N. olivaceus*, and at a lower prevalence. All other cercariae that infected two host species were more prevalent in *N. olivaceus.* More cercarial species used both *N. olivaceus* and *N. dorsatus* as dual hosts than *N. olivaceus* and *N.*

Table 3. Parasite species and first intermediate and definitive hosts for cercariae found in nassariid gastropods in Central Queensland, showing prevalence of infection (%).

Digenean species	Likely placement	Host species	Likely definitive host[a]	Number infected and percentage (%)
Acanthocolpidae				
Cercaria capricornia I	Acanthocolpidae	*Nassarius olivaceus*	Fishes	27 (1.4%)
Cercaria capricornia III	Acanthocolpidae	*Nassarius olivaceus* *Nassarius dorsatus*	Fishes	8 (0.4%) 1 (<0.1%)
Cercaria capricornia VI	Acanthocolpidae	*Nassarius dorsatus*	Fishes	1 (<0.1%)
Cercaria capricornia VII	*Stephanostomum* sp.	*Nassarius dorsatus* *Nassarius olivaceus*	Fishes	10 (0.6%) 5 (0.3%)
Cercaria capricornia VIII	*Stephanostomum* sp.	*Nassarius dorsatus*	Fishes	2 (0.1%)
acanthocolpid cercaria 9	*Stephanostomum* sp.	*Nassarius dorsatus*	Fishes	1 (<0.1%)
Lepocreadiidae				
lepocreadiid cercaria	*Prodistomum* sp.	*Nassarius olivaceus* *Nassarius dorsatus*	Fishes	13 (0.7%) 1 (<0.1%)
Zoogonidae				
Cercaria capricornia XI	Zoogonidae	*Nassarius olivaceus*	Fishes	1 (<0.1%)
Opecoelidae				
Cercaria capricornia XII	Opecoelidae	*Nassarius olivaceus*	Fishes	20 (1.0%)
Himasthlidae				
himasthlid cercaria 1	*Himasthla* sp.	*Nassarius olivaceus* *Nassarius pullus*	Birds	20 (1.0%) 4 (0.2%)
himasthlid cercaria 2	*Himasthla* sp.	*Nassarius dorsatus*	Birds	4 (0.2%)
Microphallidae				
microphallid cercaria	Microphallidae	*Nassarius olivaceus*	Birds	8 (0.4%)
Uncertain family		*Nassarius dorsatus* *Nassarius olivaceus*		4 (0.2%) 1 (<0.1%)

[a]final host details can be obtained from the Keys to the Trematoda Volumes 2 and 3: [76,77].

pullus. Both of these gastropods were historically included in the now invalid subgenus *Zeuxis*, whereas *N. pullus* was in the subgenus *Plicarcularia*. This may indicate that more closely related gastropod species may have more shared parasite species than more distantly related species. Further examination of other closely related and sympatric nassariids is needed to test this.

Nassarius olivaceus was observed with the highest overall prevalence of infection and the greatest species richness (eight species from all six families) (Table 3). The three gastropod species were closely located at each locality but displayed a degree of zonation. *Nassarius olivaceus* was generally found in shaded pools amongst mangrove trees and in pools adjacent to the trees; and occurred slightly higher in the intertidal zone than *N. dorsatus* and *N. pullus*. There was also some overlap, as all three species were found in the pools along the seaward boundary of the mangroves at Sandy Point, and *N. dorsatus* and *N. pullus* were found together in some areas. Mollusks living in areas with habitat attractive to birds (*e.g.*, roosting trees or longer tidal exposure) are suggested to have an increased likelihood of infection by bird parasites and a higher diversity [24] or prevalence of infection [24-28]. In Capricornia, bird species infected all three nassariid species, but the diversity and prevalence were highest in *N. olivaceus*. There were two bird parasites in *N. olivaceus*, a himasthlid and a microphallid. Both *N. dorsatus* and *N. pullus* were each infected by a himasthlid but at lower prevalences. Gastropods higher in the intertidal incline potentially emerge earlier and submerge later than those lower in the incline, resulting in longer periods of exposure to infection from birds.

The reason for the depauperate parasite fauna in *N. pullus* is unknown. This nassariid was present at Sandy Point in very high numbers, but was infected by only a single cercaria. This may be linked to the apparent shorter life span of infected *N. pullus* in Capricornia. Although the longevity of *N. pullus* was estimated at 3.85 years in

Table 4. Distribution of infections of each parasite species for each host species at the localities sampled (the percentage of gastropods infected at each locality for each species is shown in brackets).

	Cawarral Creek			Ross Creek			Sandy Point		
	N. dorsatus (n = 815)	*N. olivaceus* (n = 903)	*N. pullus* (n = 452)	*N. dorsatus* (n = 241)	*N. olivaceus* (n = 185)	*N. pullus* (n = 198)	*N. dorsatus* (n = 710)	*N. olivaceus* (n= 820)	*N. pullus* (n = 964)
C. capricornia I	–	10 (1.1%)	–	–	8 (4.3%)	–	–	9 (1.1%)	–
C. capricornia III	1 (0.1%)	1 (0.1%)	–	–	4 (2.2%)	–	–	3 (0.4%)	–
C. capricornia VI	–	–	–	–	–	–	1 (0.1%)	–	–
C. capricornia VII	1 (0.1%)	1 (0.1%)	–	3 (1.2%)	1 (0.5%)	–	6 (0.8%)	3 (0.4%)	–
C. capricornia VIII	2 (0.2%)	–	–	–	–	–	–	–	–
acanthocolpid cercaria 9	–	–	–	1 (0.4%)	–	–	–	–	–
lepocreadiid cercaria	–	4 (0.4%)	–	–	3 (1.6%)	–	1 (0.1%)	6 (0.7%)	–
C. capricornia XI	–	1 (0.1%)	–	–	–	–	–	–	–
C. capricornia XII	–	17 (1.9%)	–	–	2 (1.1%)	–	–	1 (0.1%)	–
himasthlid cercaria 1	–	–	–	–	–	–	–	20 (2.4%)	4 (0.4%)
himasthlid cercaria 2	–	–	–	–	–	–	4 (0.6%)	–	–
microphallid cercaria	–	–	–	–	–	–	–	8 (1.0%)	–
unknown cercariae	2 (0.2%)	–	–	–	1 (0.5%)	–	2 (0.3%)	–	–
Total	4	34	0	4	18	0	12	50	4

Indonesia [21], its longevity in the field here is unknown (the longest surviving infected *N. pullus* lived for only ~0.3 years after collection). If the species lives for a much shorter period in this region, the risk of exposure to infection is reduced. Conversely, if infection markedly reduces longevity, infected *N. pullus* may not survive for long in the field and would therefore not be available for collection.

Geographic Specificity

As the distribution of infection in first intermediate hosts is expected to reflect the distribution of final hosts, results were examined to see if there was any specificity of infections at these localities. Although these sites flow into Keppel Bay, the localities are geographically separate, and each is part of a discrete coastal wetland habitat.

Species that use fish as their definitive host were distributed across all localities, except for the rare infections, which were present in numbers too low to determine their distribution. The most commonly observed cercariae were the acanthocolpids *C. capricornia* I, *C. capricornia* III, and *C. capricornia* VII, and the lepocreadiid and opecoelid cercariae, although there were many more opecoelid infections collected at Cawarral Creek than at the other two localities. This indicates that the fish hosts of these cercariae visit all three localities. As all three localities connect with the same bay, many adult fish species are expected to move between them.

Both himasthlid and the single microphallid species were found only at Sandy Point. Digeneans of both families generally infect birds as their final hosts, and Sandy Point is listed as important habitat for both domestic and migratory birds. Sandy Point is in the eastern estuaries of the Shoalwater and Corio Bays Ramsar wetland (designated as a site of significant international importance under the Ramsar Convention), an area that provides important roosting sites for local and migratory birds, and the mud and sandflats are feeding sites for a diversity of shorebirds [29]. The Ramsar wetland was reported to have 226 species of birds, representing 32 percent of Australia's bird fauna [29]. The other localities are of lower importance as bird habitats and have much smaller and less diverse bird populations. These results reflect the relative significance of Sandy Point as an important bird habitat, which has resulted in a higher diversity and prevalence of parasites that use birds as definitive hosts.

Trematode Fauna of Nassariid Gastropods

Sixteen new host-parasite records can now be added for the Nassariidae. No infections were found in *N. olivaceus*, *N. dorsatus,* or *N. pullus* by families that had not been previously reported from other nassariids, although there were six previously reported families that were not found (Table 1).

The Nassariidae contains the subfamilies Buccinanopsinae, Photinae, Cylleninae, Bullinae, Anentominae, Dorsaninae, and Nassariinae [2]. Of these, no parasites have yet been reported from gastropods of the Dorsaninae, Anentominae, Cylleninae or Photinae. Parasites are reported from gastropods in the Nassariinae (from *Nassarius* spp., *Phrontis vibex* and *Tritia* spp.), the Bullinae (*Bullia digitalis*) and the Buccinanopsinae (*Buccinanops* spp.). Digenean families commonly reported to use nassariids as first intermediate hosts include the Acanthocolpidae, Himasthlidae, Lepocreadiidae, Microphallidae, and Zoogonidae (Tables 1 and 2).

The nassariid reported with the highest number of infecting parasite families is *T. obsoleta*. *Tritia obsoleta* is indigenous to the Atlantic coast of North America, but was also introduced to the west coast unintentionally via attempted oyster transplantation in the early 1900s [5]. The invasive west coast population was reported to have lost three parasites in the new range, and had not gained any new native west coast parasites [5]. *Tritia* spp. are generally found in the North Atlantic and West Africa, with two isolated species from Australia and New Zealand [1]. Of the other nassariids that have been reported as hosts, their distribution is geographically restricted: *Buccinanops* spp. are found in South America, *Bullia* spp. from the Indian Ocean, *Phrontis* spp. from the Caribbean Sea and both coasts of the Isthmus of Panama, and *Nassarius* spp. from the Indo-Pacific Ocean and the coast of Israel on the Mediterranean Sea [1,30].

Of the nassariid hosts that have been studied, the most common family using them as first intermediate host is the Lepocreadiidae (12 host-family records for 16 parasite species), followed by the Zoogonidae (8 for 12), Acanthocolpidae (6 for 13), Himasthlidae (6 for 8), Microphallidae (4 for 4), Opecoelidae (3 for 3), Strigeidae (2 for 2), and the rest with single records (Table 2). Nassariid gastropods were also found to be the dominant marine first intermediate hosts for the Acanthocolpidae, Lepocreadiidae, and Zoogonidae.

Gastropods from the superfamily Buccinoidea were the most commonly reported first intermediate hosts for the Acanthocolpidae, with parasites reported from the Buccinidae, Columbellidae, Fasciolariidae and Nassariidae [31]. The majority of infections were in gastropods from the Nassariidae, all in the subfamily Nassariinae. Eight cercariae are now reported from *Nassarius* spp. and include five *Stephanostomum* or *Stephanostomum*-like and three non-*Stephanostomum* species, compared to only three in *Tritia* spp., all suggested to be *Stephanostomum* or *Stephanostomum*-like.

Huston *et al*. [32] reviewed the first intermediate hosts for the Lepocreadioidea and remarked that, apart from a single exception, the Lepocreadiidae used the Nassariidae, Columbellidae, or Conidae as first hosts. Their study found that the Nassariidae was the most common family reported. They included a number of cercariae of uncertain status, also mostly from the Nassariidae or Columbellidae, and noted that these may also be lepocreadiid cercariae. In Tables 1 and 2, these uncertain cercariae have been placed as Lepocreadiidae as they closely resemble other lepocreadiid cercariae. Lepocreadiids have been reported from all three nassariid subfamilies.

For the Zoogonidae, gastropods from the Buccinidae, Columbellidae, Fasciolariidae and Nassariidae, Naticidae (Naticoidea), and Trochidae and Turbinidae (Trochoidea) were the first intermediate hosts for cercariae [33]. The dominant host group for zoogonids was the Buccinoidea, and within that superfamily, the Nassariidae was the most frequently infected family, harboring at least seven species of zoogonid (of 15 described cercariae reported as belonging to the Zoogonidae). Zoogonids are also reported from all three nassariid subfamilies.

Nassariids are also one of the most common first intermediate host families for species of marine *Himasthla* spp. (Himasthlidae) (5 in 6 species of nassariid). Other families hosting marine *Himasthla* or *Himasthla*-like cercariae are the Melongenidae (2 in 1) [34], the Littorinidae of superfamily Littorinoidea (5 in 3) [35-39] and a single cercaria is reported to infect the Potamididae (1 from 1) [40]. From the Himasthlidae, only *Himasthla* and *Himasthla*-like cercariae have been reported from nassariids to date, all in the subfamily Nassariinae.

Microphallid cercariae have been found in only a small number of nassariid gastropods, three from the Nassariinae and one from Bullinae; these are *N. olivaceus*, *T. obsolete* and *T. reticulata*, and *B. digitalis*. Adult microphallids infect a variety of vertebrates, mainly birds [41]. Most reports of cercariae are from littorinid and hydrobid gastropods [42] and the Nassariidae does not appear to be an important intermediate host for this family.

Opecoelid parasites are reported from a broad range of gastropods. Over 70 cercariae have been reported from at least ten superfamilies of molluskan first intermediate hosts, but only two have been reported from nassariids [43]. These both involved species of *Nassarius*, and no opecoelid cercariae have been reported from other nassariid genera. Other buccinoid hosts of opecoelids include gastropods from the Buccinidae and Columbellidae. The Opecoelidae has four subfamilies: the Opecoelinae Ozaki, 1925, the Plagioporinae, Manter, 1947, the Stenakrinae Yamaguti, 1970, and the Opecoelininae Gibson & Bray, 1984. The cercaria found here was placed in the Opecoelinae, and the dominant hosts for opecoeline cercariae are columbellids [43].

The most ancient genus of nassariids with reported host-parasite associations was suggested to be *Buccinanops* [1]; only lepocreadiids and zoogonids are reported from this genus (and from all nassariid subfamilies, as well as from related buccinoid families). This indicates a long-standing relationship between the family and these two parasite families that has potentially co-evolved with the divergence of the Nassariidae from other buccinoids.

Some *Tritia* spp. were infected rarely by cercariae from the Strigeidae, Pronocephalidae, Diplostomatidae, Schistosomatidae, and Hemiuridae, yet no infections by these families have, as yet, been reported from any other nassariid genera (see Table 2). This could indicate that the host-parasite associations for these parasites are more recent than the divergence of the species, but further examination of other hosts is needed to see if other buccinoid gastropods are common hosts. As well, a cercaria from the Cyathocotylidae was only reported from *Nassarius*. This may also indicate that this host association has occurred after the divergence of the species. Further examination of more nassariid species will indicate if the host-parasite associations described here are consistent within the Nassariidae.

This work presents a glimpse into the complex ecology and biodiversity of the trematode fauna inhabiting Australian intertidal gastropod communities. Unravelling details of all of the hosts involved in the intricate life-cycles of these trematodes present in gastropods in the region, their host specificity and pathological impacts on their hosts driving selection pressures in these communities awaits further exploration.

Acknowledgments: We wish to thank Stephen McKillup, Tom Cribb and Lesley Smales for guidance during the PhD project. We also wish to thank Stephen McKillup, Ruth McKillup, Philip Barton, Mary-anne Jones, Anthony Vize and Haylee Weaver for assistance with field collection.

REFERENCES

1. Galindo L, Puillandre N, Utge J, Lozouet P, Bouchet P. The phylogeny and systematics of the Nassariidae revisited (Gastropoda, Buccinoidea). Mol Phylogenet Evol. 2016;99:337–53.
2. Bouchet P, Rocroi JP, Hausdorf B, Kaim A, Kano Y, Nützel A, et al. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia. 2017;61(1–2):1–526.
3. Beesley PL, Ross GJ, Wells A. Mollusca: The southern synthesis. Fauna of Australia. Part B viii. Melbourne: CSIRO Publishing; 1998. 565–1234 p.
4. Esch GW, Barger MA. J. FK. The transmission of digenetic trematodes: Style, elegance, complexity. Integr Comp Biol. 2002;42(2):304–12.
5. Blakeslee AM, Altman I, Miller AW, Byers JE, Hamer CE, Ruiz GM. Parasites and invasions: A biogeographic examination of parasites and hosts in native and introduced ranges. J Biogeogr. 2012;39:609–22.
6. Russell-Pinto F, Bartoli P. *Cercaria sevillana* n sp, a new

cercaria (Digenea: Microphallidae) from *Nassarius reticulatus* (L) (Mollusca: Prosobranchia) in Portugal. Syst Parasitol. 2002;53(3):175–82.
7. Wilson BR. Australian marine shells. Prosobranch gastropods. Part two (Neogastropods). Kallaroo: Odyssey Publishing; 1994. 78–89 p.
8. Cannon LR. Marine cercariae from the gastropod *Cerithium moniliferum* Kiener at Heron Island, Great Barrier Reef. Proc R Soc Qld. 1978;89:45–57.
9. Schell SC. How to know the trematodes. Dubuque: Wm C. Brown Company Publishers; 1970. 6–43 p.
10. Barnett LJ, Smales LR, Cribb TH. A complex of putative acanthocolpid cercariae (Digenea) from *Nassarius olivaceus* and *N. dorsatus* (Gastropoda: Nassariidae) in Central Queensland, Australia. Zootaxa. 2008;1705:21–39.
11. Curtis LA, Hurd LE. Age, sex, and parasites: spatial heterogeneity in a sand flat population of *Ilyanassa obsoleta*. Ecology. 1983;64(4):819–28.
12. Curtis LA. Growth, trematode parasitism, and longevity of a long-lived marine gastropod (*Ilyanassa obsoleta*). J Mar Biol Assoc U.K. 1995;75(4):913–25.
13. Curtis LA, Kinley JL, Tanner NL. Longevity of oversized individuals: Growth, parasitism, and history in an estuarine population. J Mar Biol Assoc U.K. 2000;80(5):811–20.
14. Tallmark B, Norrgren G. The influence of parasitic trematodes on the ecology of *Nassarius reticulatus* (L.) in Gullmar Fjord (Sweden). Zoon. 1976;4(2):149–56.
15. Barroso CM, Moreira MH, Richardson CA. Age and growth of *Nassarius reticulatus* in the Ria de Aveiro, northwest Portugal. J Mar Biol Assoc U.K. 2005;85(1):151–6.
16. Tallmark B. Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. Mar Ecol Prog Ser. 1980;3:51–62.
17. Curtis LA. *Ilyanassa obsoleta* (Gastropoda) as a host for trematodes in Delaware estuaries. J Parasitol. 1997;83(5):793–803.
18. Vernberg WB, Vernberg FJ, Beckerdite FW. Larval trematodes: double infections in common mud-flat snail. Science. 1969;164(3885):1287–8.
19. McDaniel JS, Coggins JR. Seasonal larval trematode infection dynamics in *Nassarius obsoletus* (Say). J Elisha Mitchell Sci Soc Chapel Hill N C. 1972;88(2):55–7.
20. McKillup SC, McKillup RV. Effect of food supplementation on the growth of an intertidal scavenger. Mar Ecol Prog Ser. 1997;148(1–3):109–14.
21. Puturuhu L. Ecological studies on intertidal dog whelks (Gastropoda: Nassariidae) off northern Minahasa, Sulawesi, Indonesia [PhD]. Kiel: Christian-Albrechts-University; 2004.
22. Poulin R, Mouritsen KN. Large-scale determinants of trematode infections in intertidal gastropods. Mar Ecol Prog Ser. 2003;254:187–98.
23. Torchin ME, Miura O, Hechinger RF. Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. Ecology. 2015;96(11):3033–42.
24. Hechinger RF, Lafferty KD. Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Proc R Soc Lond B Biol Sci. 2005;272(1567):1059–66.
25. Hoff CC. A case of correlation between infection of snail hosts with *Cryptocotyle lingua* and the habits of gulls. J Parasitol. 1941;27:539.
26. Lafferty KD, Hechinger RF, Lorda J, Soler L. Trematodes associated with mangrove habitat in Puerto Rican salt marshes. J Parasitol. 2005;91(3):697–9.
27. Fredensborg BL, Mouritsen KN, Poulin R. Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail: from small to large scale. Mar Biol. 2006;149:275–83.
28. Smith NF. Spatial heterogeneity in recruitment of larval trematodes to snail intermediate hosts. Oecologia. 2001;127(1):115–22.
29. DEH. Information sheet on Ramsar wetlands (Ris): Shoalwater and Corio Bays area (Shoalwater Bay training area, in part - Corio Bay) Canberra: Australian Government, Department of the Environment and Energy; 1999 [cited 2018 May 29]. Available from: https://environment.gov.au/water/topics/wetlands/database/pubs/44-ris.pdf.
30. Lengy J, Shchory M. Studies on larval stages of digenetic trematodes in aquatic molluscs of Israel. 1. On two cercariae encountered in the marine snails *Littorina neritoides* (L.) and *Nassa circumcincta* (Adams, 1851). Isr J Zool. 1970;19(3):135–44.
31. Barnett LJ, Miller TL, Cribb TH. Two new *Stephanostomum*-like cercariae (Digenea: Acanthocolpidae) from *Nassarius dorsatus* and *N. olivaceus* (Gastropoda: Nassariidae) in Central Queensland, Australia. Zootaxa. 2010;2445:35–52.
32. Huston DC, Cutmore SC, Cribb TH. The life-cycle of *Gorgocephalus yaaji* Bray & Cribb, 2005 (Digenea: Gorgocephalidae) with a review of the first intermediate hosts for the superfamily Lepocreadioidea Odhner, 1905. Syst Parasitol. 2016;93(7):653–65.
33. Barnett LJ, Miller TL, Cribb TH. A review of the currently recognised zoogonid cercariae, including the identification and emergence ecology of *Cercaria capricornia* XI (Digenea: Zoogonidae) from *Nassarius olivaceus* (Gastropoda: Nassariidae) in Central Queensland, Australia. Folia Parasit. 2014;64(4):322–30.
34. Nasir P. Marine larval trematodes. I. *Cercariae criollisimae*: five new Venezuelan species and redescription of *Parorchis acanthus* (Nicoll, 1906) Nicoll, 1907. Riv Parassitol. 1976;37(2–3):287–302.
35. Werding B. Morphology, development and ecology of digenous trematode larvae of the littoral snail *Littorina littorea*. Mar Biol. 1969;3(4):306–33.
36. Chubrik GK. Fauna and ecology of trematode larvae from molluscs in the Barents and White Seas. Trudy Murmansk Morsk Biol Inst. 1966;10(14):78–166.
37. Chapman HD, Wilson RA. The distribution and fine structure of the integumentary papillae of the cercaria of *Himasthla secunda* (Nicoll). Parasitology. 1970;61(2):219.
38. Stunkard HW. The morphology and life history of the digenetic trematode, *Himasthla littorinae* sp. n. (Echinostomatidae). J Parasitol. 1966;52(2):367–72.
39. Ishkulov DG. On the taxonomic status of the trematode larvae of the genus *Himasthla* (Trematoda: Echinostomatidae) from the intertidal whelk *Littorina saxatilis* living in the Kandalaksha Bay of White Sea. Parazitologiia.

2001;35(1):81–5.
40. Adams JE, Martin WE. Life cycle of *Himasthla rhigedana* Dietz, 1909 (Trematoda: Echinostomatidae). Trans Am Microsc Soc. 1963;82(1):1–6.
41. Deblock S. Family Microphallidae Ward, 1901. In: Bray RA, Gibson DI, Jones A, editors. Keys to the Trematoda. 3. London: CAB International and Natural History Museum; 2008. pp. 451–92.
42. Kudlai O, Cutmore SC, Cribb TH. Morphological and molecular data for three species of the Microphallidae (Trematoda: Digenea) in Australia, including the first description of the cercariae of *Maritrema brevisacciferum* Shimazu et Pearson, 1991 and *Microphallus minutus* Johnston, 1948. Folia Parasit. 2015;62:053.
43. Barnett LJ, Miller TL, Cribb TH. A review of the currently recognised opecoelid cercariae, including the identification and emergence ecology of *Cercaria capricornia* XII (Digenea: Opecoelidae) from *Nassarius olivaceus* (Gastropoda: Nassariidae) in Central Queensland, Australia. Parasitol Int. 2014;63:670–82.
44. Averbuj A, Cremonte F. Parasitic castration of *Buccinanops cochlidium* (Gastropoda: Nassariidae) caused by a lepocreadiid digenean in San José Gulf, Argentina. J Helminthol. 2010;84(4):381–9.
45. Gilardoni C, Etchegoin J, Diaz JI, Ituarte C, Cremonte F. A survey of larval digeneans in the commonest intertidal snails from Northern Patagonian coast, Argentina. Acta Parasitol. 2011;56(2):163–79.
46. Martorelli SR. Primera cita de una cercaria tricocerca parásita de *Dorsanum moniliferum* (Mollusca, Buccinidae) para el Atlántico sud-occidental aportes al conocimiento de su ciclo de vida. Neotropica. 1991;37(97):57–65.
47. Webb SC. *Cercaria hastata* sp. nov. (Digenea: Trematoda) in *Bullia digitalis*, a sandy beach surfing whelk from the Western Cape coast of South Africa: Epidemiology and sex linked phenomena. J Nat Hist. 1991;25(3):543–58.
48. Brown AC, Webb SC. Organisms associated with burrowing whelks of the genus *Bullia*. S-Afr Tydskr Dierk. 1994;29(2):144–51.
49. Abdul-Salam J, Al-Khedery B. The occurrence of larval Digenea in some snails in Kuwait Bay. Hydrobiologia. 1992;248(2):161–5.
50. Madhavi R, Shameem U. Cercariae and metacercariae of *Stephanostomum cloacum* (Trematoda: Acanthocolpidae). Int J Parasitol. 1993;23(3):341–7.
51. Madhavi R, Shameem U. *Cercaria chilkaensis* II, a new zoogonid cercaria from the snail, *Nassarius orissaensis*, from Chilka Lake, India. J Helminthol Soc Wash. 1991;58(1):31–4.
52. Gnana Mani G. Studies on Indian marine cercariae: A new acanthocolpid cercaria. Indian J Parasitol. 1994;18(1):75–8.
53. Holliman RB. Larval trematodes from the Apalachee Bay area, Florida, with a checklist of known marine cercariae arranged in a key to their superfamilies. Tulane Stud Zool. 1961;9:1–74.
54. Cable RM. Marine cercariae from Curaçao and Jamaica. Z Parasitenkd. 1963;23:429–69.
55. Bartoli P. Redescription de *Cercaria setifera* f. s. Monticelli, 1914 (nec J. Müller) (Trematoda) parasite de *Conus ventricosus* Hwass; comparaison avec quelques cercaires optalmotrichocerques de Méditerranée Occidentale. Ann Parasitol Hum Comp. 1984;59(2):161–76.
56. Palombi A. Il ciclo biologico di *Lepocreadium album* Stossich sperimentalmente realizzato. Osservazioni etologiche e considerazioni sistematiche sulla *Cercaria setifera* (non Joh. Müller) Monticelli. Riv Parassitol. 1937;1(1):1–12.
57. Prévot G, Bartoli P. Demonstration of the existence of a marine cycle in the strigeids: *Cardiocephalus longicollis* Szidat, 1928 (Trematoda: Strigeidae). Ann Parasitol Hum Comp. 1980;55(4):407–25.
58. Yamaguti S. A synoptical review of life histories of digenetic trematodes of vertebrates: With special reference to the morphology of their larval forms. Tokyo: Keigaku Publishing Co; 1975. 590 pp.
59. Bartoli P. Sur le cycle vital de *Lepocreadium pegorchis* (M. Stossich, 1900) M. Stossich, 1903 (Trematoda, Digenea, Lepocreadiidae). C R Acad Sci. 1966;263:1398–400.
60. Stunkard HW. Life history studies and specific determination in the trematode genus *Zoogonus*. J Parasitol. 1940;26 Suppl:33–4.
61. Palombi A. Gli stadi larvali dei Trematodi del Golfo di Napoli. 1. Contributo allo studio della morfologia, biologia e sistematica delle cercarie marine. Pubbl Stn Zool Napoli. 1934;14:51–94.
62. Martin WE. Studies on the trematodes of Woods Hole: II. The life cycle of *Stephanostomum tenue* (Linton). Biol Bull. 1939;77(1):65–73.
63. Stunkard HW. *Cercaria dipterocerca* Miller and Northup, 1926 and *Stephanostomum dentatum* (Linton, 1900) Manter, 1931. Biol Bull. 1961;120(2):221–37.
64. Stunkard HW. *Distomum lasium* leidy, 1891 (syn. *Cercariaeum lintoni* Miller and Northup, 1926), the larval stage of *Zoogonus rubellus* (Olsson, 1868) (syn. Z. *mirus* Looss, 1901). Biol Bull. 1938;75:308–34.
65. Stunkard HW. Observations on the morphology and life-history of the digenetic trematode, *Lepocreadium setiferoides* (Miller and Northup, 1926) Martin, 1938. Biol Bull. 1972;142:326–34.
66. Martin WE. Studies on trematodes of Woods Hole: the life cycle of *Lepocreadium setiferoides* (Miller and Northup), Allocreadiidae, and the description of *Cercaria cumingiae* n. sp. Biol Bull. 1938;75(3):463–74.
67. Curtis LA. Ecology of larval trematodes in three marine gastropods. Parasitology. 2002;124(Suppl):S43–56.
68. Miller HM, Northup FE. The seasonal infestation of *Nassa obsoleta* (Say) with larval trematodes. Biol Bull. 1926;50(6):490–508.
69. Pina S, Tajdari J, Russell-Pinto F, Rodrigues P. Morphological and molecular studies on life cycle stages of *Diphtherostomum brusinae* (Digenea: Zoogonidae) from Northern Portugal. J Helminthol. 2009;83(4):321–31.
70. Bray RA. A revision of the family Zoogonidae Odhner, 1902 (Platyhelminthes: Digenea): Introduction and subfamily Zoogoninae. Syst Parasitol. 1986;9(1):3–28.
71. Køie M. On the morphology and life-history of *Opechona bacillaris* (Molin, 1959) Looss, 1907 (Trematoda, Lepocreadiidae). Ophelia. 1975;13:63–86.
72. Russell-Pinto F, Goncalves JF, Bowers E. Digenean larvae

parasitizing *Cerastoderma edule* (Bivalvia) and *Nassarius reticulatus* (Gastropoda) from Ria de Aveiro, Portugal. J Parasitol. 2006;92(2):319–32.
73. Dolgikh AV. Trematode larvae parasitic in the Black Sea mollusc *Nassa reticulata* var. *pontica* Mont. Benthos. Kiev: Naukova Dumka; 1965. pp. 122–38.
74. Stunkard HW. The marine cercariae of the Woods Hole, Massachusetts region, a review and a revision. Biol Bull. 1983;164(2):143–62.
75. Stunkard HW. The morphology, life-history, and taxonomic relations of *Lepocreadium areolatum* (Linton, 1900) Stunkard, 1969 (Trematoda: digenea). Biol Bull. 1980;158(1):154–63.
76. Jones A, Bray R, Gibson D, editors. Keys to the Trematoda. Volume 2. London: CAB International and Natural History Museum; 2005.
77. Bray R, Gibson D, Jones A, editors. Keys to the Trematoda. Volume 3. London: CAB International and Natural History Museum; 2008.