The life cycle of *Diploproctodaeum arothroni* Bray and Nahhas, 1998 (Digenea: Lepocreadiidae), with a comment on the parasitic castration of its molluscan intermediate host

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Abstract

*Diploproctodaeum arothroni* Bray and Nahhas, 1998 (Digenea: Lepocreadiidae) was found in the intestine of its type-host, *Arothron hispidus*, a tetraodontid fish permanently resident in a lagoon within the mangrove swamps on the Egyptian coast of the Gulf of Aqaba. Larval forms of this trematode (sporocysts, rediae, and cercariae) were found in the gonads and digestive gland of *Crassostrea cuccullata* (Ostreidae), a common oyster in the same lagoon. So, the life cycle of *D. arothroni* is elucidated under natural conditions; eggs are directly ingested by the oyster; mother sporocysts and rediae reach their maturity 3–5 and 9–11 weeks after infection; rediae contain 18–25 developing cercariae; fully mature cercariae are trichocercous, without penetration glands, emerge from the oyster during the night 14–15 weeks after infection, their existence in seawater being very brief and transitory, and rapidly encyst on aquatic vegetation or other surfaces (there is no second intermediate host); encysted metacercaria are not progenetic; 4-day-old metacercariae encysted on filamentous algae fed to *A. hispidus* developed into fully mature worms 8–9 weeks after infection. This cycle is completed in about 24 weeks and has its own characteristics, which differentiate it from the other known lepocreadiid life cycles. All of the developmental stages are figured and described. Parasitic castration in the females of *C. cuccullata* caused by the parasite was studied histologically and is described and discussed.

Keywords: *Diploproctodaeum arothroni*, Gulf of Aqaba, *Lepocreadiidae*, life-cycle, parasitic castration, *Trematoda*

Introduction

The lepocreadiid subfamily Diploproctodaeinae Ozaki, 1928 is a widespread group of intestinal trematodes, mainly found in tetraodontiform teleosts, and unusual in having a scoop-shaped body and intestinal caeca extending to or close to the posterior extremity of the body, and may perforate the body-wall to form ani. Apart from *Diploproctia* Mamaev, 1970, the other genera of this subfamily, i.e. *Bianium* Stunkard, 1930, *Diplocreadium* Park,
1939, *Caecobiporum* Mamaev, 1970, and *Diploproctodaeoides* Reimer, 1981, are closely similar to the type-genus, *Diploproctodaeum* La Rue, 1926. This similarity has led to much confusion: Sogandares-Bernal and Hutton (1958) concluded that *Bianium* is a synonym of *Diploproctodaeum*, stating that there is no single difference between the two genera, but Gupta (1968) resurrected *Bianium* as a valid genus. Overstreet (1969) accepted *Diploproctodaeum* as a monotypic genus and transferred the other species to *Bianium*, but Yamaguti (1971) disagreed and retained these species in *Diploproctodaeum*. Shimazu (1989) doubted the validity of *Diploproctodaeoides*, stating that it is possibly a synonym of *Diploproctodaeum*, and Sey (1996) considered *Diplocreadium* a synonym of *Diploproctodaeum*. In their revision of the Diploproctodaeinae, Bray et al. (1996) recognized *Diploproctodaeum*, *Bianium*, *Diplocreadium*, *Diploproctia*, and *Diploproctodaeoides*, but regarded *Caecobiporum* as a synonym of *Diploproctodaeum*. During the course of these conflicting works and other studies, many species were transferred to or from *Diploproctodaeum* and a large number of synonyms were proposed.

Bray et al. (1996) presented a key for the identification of the 16 species of *Diploproctodaeum* that they recognized. Bray and Nahhas (1998) described *D. arothroni* Bray and Nahhas, 1998 from the tetraodontid fish *Arothron hispidus* Linnaeus off Fiji, and presented a revised key for distinguishing the 17 valid species of *Diploproctodaeum* known at that time. Two more species have since been described: *D. spinosus* Liu, 2002 from the tetraodontid fish *Takifugu oblongus* Bloch, in Taiwan Straits, China and *D. tsubameuo* Bray and Cribb, 2003 from the ephippid fish *Platax bataevianus* Cuvier, off Queensland, Australia. Accordingly, 19 species are now recognized in *Diploproctodaeum*. More recently, in a revision of the Lepocreadiidae, Bray (2005) considered the Diploproctodaeinae a synonym of Lepocreadiinae Odhner, 1905. Thus, the five genera recognized in the former by Bray et al. (1996) were transferred to the latter, but still form a unique group.

So far, the life-cycles of all *Diploproctodaeum* spp. and of all the species of the above-mentioned genera are completely unknown. In the present study, the author takes the opportunity to describe the life-cycle of *D. arothroni* Bray and Nahhas, 1998 under natural conditions and to discuss the parasitic castration which affects its molluscan intermediate host.

**Methods**

Some mangrove thickets of about 20 km in length are found on the Egyptian coast of the Gulf of Aqaba (between 28°7’ N and 28°18’ N). Lagoons scattered within these thickets are permanently water filled, even if sometimes at low tides they are completely separated from the sea. In one of these lagoons (ca 50 m in diameter and 0.8–1.5 m in depth), only five fish species and four molluscs (two gastropods and two bivalves) are permanently resident. Of these fishes, *Arothron hispidus* (Tetraodontidae) was the only one parasitized by *D. arothroni* Bray and Nahhas, 1998. Larval forms of this trematode (sporocysts, rediae, and cercariae) were found only in the gonads and digestive gland of the oyster *Crassostrea cucullata* Born (Ostreidae); other fishes and molluscs were completely free from trematodes.

Fish identifications were based on Randall (1983) and their names follow Froese and Pauly (2004). Mollusc identifications were based on Sharabati (1984). Standard parasitological techniques were used to examine the alimentary canal of the fish and the different organs of the molluscs. Trematodes were removed from their host fishes or molluscs under a stereomicroscope and observed live under a compound microscope.
Some mature worms were fixed in alcohol–formalin–acetic acid (AFA) under a very slight coverslip pressure and preserved in 75% ethyl alcohol. Whole-mounts were stained in alum carmine, cleared in terpineol, and mounted in Canada balsam. The examination of larval trematodes was facilitated by the use of neutral red as a vital stain, and for measurements, 40 specimens of each larval stage were fixed without pressure in hot 5% formalin (to reduce any contraction during fixation). Measurements are quoted as the range, with the mean in parentheses, and are given in micrometres, except where indicated. The specimens are deposited in the Helminthological Collection of the Red Sea Fishes, Marine Science Department, Faculty of Science, Suez Canal University, Ismailia, Egypt.

Numerous specimens of *C. cuccullata* were taken from a large wild bed inhabiting the coast of Sharm El-Sheikh (60 km south to the mangrove thickets), and examined carefully to make sure that they were not naturally infected with any larval trematode. All of these specimens were uninfected. Therefore, 500 specimens of this bed were marked and transferred alive in January 2005 to the lagoon to follow their infection with *D. arothroni* from its beginning; 40 specimens of these oysters were dissected and examined weekly. Similarly and to estimate the approximate time taken by the parasite to reach maturity in its definitive host, some uninfected specimens of *A. hispidus* were transferred to the lagoon and some were kept alive in aquariums during the study.

Numerous eggs were obtained from fully gravid specimens of *D. arothroni*, concentrated in filtered sea-water, placed in embryo cups, and observed for more than 4 weeks at 20–25°C, but no hatching was observed. Attempts to obtain miracidia by coverglass pressure, exposure to light, or by changed osmotic conditions were unsuccessful.

To determine whether the cercariae were released from the oysters or not, some specimens were placed singly in small glass bowls filled with filtered seawater and observed; the addition of a drop of neutral red to the bowls was helpful, since the stain accumulated rapidly in cercariae. Also, the behaviour of cercariae was observed in a petri dish under the microscope.

To estimate the effect of *D. arothroni* larvae on the fecundity of *C. cuccullata*, some uninfected and all infected ovaries were prepared for histological examination. Sections were cut at 6–8 μm, stained with Ehrlich’s haematoxylin and counter-stained in eosin.

**Diploproctodaeum arothroni** Bray and Nahhas, 1998
(Figures 1, 2)

*Final host.* *Arothron hispidus* Linnaeus (Tetraodontidae). Site: intestine.

*Intermediate host.* *Crassostrea cuccullata* Born (Bivalvia: Ostreidae). Site: gonads and digestive gland.

*Locality.* Mangrove swamps on the Egyptian coast of the Gulf of Aqaba.

*Material.* Voucher specimens are deposited in the Helminthological Collection of the Red Sea Fishes, Marine Science Department, Faculty of Science, Suez Canal University, Ismailia, Egypt.

*Material examined.* The holotype specimen in the Natural History Museum, London, reg. no. 1997.8.29.1.
Figure 1. Stages in the life cycle of *Diploproctodaeum arothroni* Bray and Nahhas, 1998. (A) Young mother sporocyst; (B) mature mother sporocyst; (C) young daughter redia; (D) fully mature daughter redia; (E) fully mature cercaria; (F) metacercaria. Scale bars: 500 μm (A–D); 200 μm (E, F).
Egg

Eggs oval, thin-walled, non-operculated, 58–64 × 30–35. As they do not hatch in seawater, infection must be accomplished by the ingestion of eggs and the emergence of miracidia in the digestive tract of C. cucullata. This was confirmed when eggs of the same shape and size were observed in the digestive tracts of many infected individuals of this oyster; also, some egg shells were observed in their faeces. Thus, there is most probably no free-swimming miracidium in the life-cycle of D. arothroni.

Larval forms (from the oyster gonad)

Mother sporocyst (Figure 1A, B). Young mother sporocyst (1–2 weeks after infection) (based on 40 specimens) (Figure 1A): body oval, thin-walled, opaque white, 760–910 × 610–712 (835 × 661). Germinal balls aggregated in round compact mass in one half of body; the other half appeared to be transparent.

Mature mother sporocyst (3–5 weeks after infection) (based on 40 specimens) (Figure 1B): body sausage-shaped, slightly swollen anteriorly, thin-walled, opaque white, 2003–2697 × 397–483 (2350 × 440). Germinal balls aggregated in persistent compact band extending throughout anterior third of body; some balls move posteriorly and give rise to rediae (usually 8–13 per sporocyst), which are usually at different stages of development;
largest 250 × 90, smallest 110 × 61. Lateral birth-pore observed at 624–693 (659) from anterior end. No germinal balls observed in mature sporocysts before and during the gametogenic activity of the oyster, but some were persistent after this period. The walls of the sporocyst are capable of contraction and distension, but no movement was observed.

**Daughter redia (Figure 1C, D).** Young daughter redia (6–8 weeks after infection) (based on 40 specimens) (Figure 1C): body elongate, cylindrical, 2104–2570 (2337) in length, 270–337 (304) in width at its middle and characterized by presence of distinct lateral projection at 250–302 (276) from anterior extremity in place where the birth pore is situated in mature redia. Mouth antero-terminal. Pharynx small, muscular, pyriform, 100–121 × 71–88 (80), connected directly to small saccular caecum extending posteriorly to near lateral projection and filled with granular material which is probably from gonads of oyster. Few spheroidal germinal balls usually present at anterior end of body. Developing cercariae 18–24 in number and usually crowded together in anterior half of body.

**Fully mature daughter redia** (9–11 weeks after infection) (based on 40 specimens) (Figure 1D): body vermiform, usually curved, 2721–3350 (3036) in length, 406–516 (461) in maximum width at level of birth pore. The latter 719–870 (795) from anterior end and easily seen during emergence of cercariae. Mouth antero-terminal. Pharynx pyriform, 105–133 × 73–89 (119 × 81), connected directly to small sub-triangular caecum extending posteriorly to midway between anterior end and birth pore. Germinal balls completely absent. Cercariae 18–25 in number, at different stages of development, usually crowded together in anterior half of body.

**Cercaria (Figure 1E).** After expulsion from redia, cercaria remains for about 2 weeks within the gonad of oyster before their emergence, which occurs at night.

**Fully mature cercaria** (emerges from oyster 14–15 weeks after infection) (based on 40 specimens): trichocercous cercaria. Body oblong, 257–299 × 190–222 (278 × 206). Tegument covered with minute sharp spines. Tail plumose, broad, supported by a medial tubular structure, moderately long, 624–714 (699) in length, bears 22 sharply pointed setae on each side which decrease in size posteriorly; first 10 setae, 88–94 (91); next four, 78–85 (82); next two, 70–73 (72); next two, 55–61 (58); last two, 22–30 (26) in length. Oral sucker sub-terminal, oval, 37–43 × 45–54 (40 × 50). Ventral sucker oval, sessile, situated in middle of body, smaller than oral sucker, 27–31 × 30–38 (29 × 34). Sucker-width ratio 1:0.68–0.75. Prepharynx practically absent. Pharynx moderately large, with wavy anterior border, 22–27 × 30–35 (25 × 33). Oesophagus absent. Intestinal caeca relatively wide, curved, extend backwards to abut posterior body-wall, may give appearance of having ani. Cystogenous glands numerous, relatively large, round, scattered throughout body, negative to neutral red. Penetration glands absent. Testes two, oval, symmetrical, near posterior extremity, sub-equal, 50–58 × 41–47 (54 × 44). Anlagen of ovary median, just pre-testicular. Genital ducts not visible. Excretory vesicle tubulo-saccular, short, lined by granular cells, extends anteriorly as far as rudiments of ovary. Main excretory tubules join antero-lateral margins of excretory vesicle and extend anteriorly to mid-level of ventral sucker. Flame-cell formula $2[(3+3)+(3+3)]=24$. Excretory pore postero-terminal.

**Metacercaria (Figure 1F).** Formation of metacercaria was observed in petri dish filled with seawater. Period of the free-swimming cercaria in seawater is very brief and transitory; emerged cercariae appeared to be at rest for only a few seconds, and then moved rapidly in
clockwise, helical motion near the bottom of the dish. On contact with substratum (e.g. pieces of filamentous algae and other aquatic vegetation placed in dish), the cercaria spreads setae of its tail in different directions, and begins series of writhing movements which result in detachment of tail, causing emission of secretions from the cystogenous glands. This colourless transparent material forms a flexible membranous cyst around the metacercaria; some of the cyst material is anchored to the substratum. This is probably similar to what happens in nature, since the cercaria has no penetration glands to penetrate a second intermediate host. Metacercariae remain alive for about 1 week and no progenesis was observed during this period. Generally, it is closely similar to cercaria in all characteristics but differs in having a widely pyriform body and excretory vesicle filled with relatively large granules. Because the lagoon bottom is very muddy, metacercaria were not seen on the aquatic vegetation, which is usually covered by a layer of mud. Four-day-old metacercariae encysted on filamentous algae fed to uninfected *A. hispidus* developed into fully gravid worms 8–9 weeks after infection. Thus, the complete life cycle of *D. arothroni* extends over about 24 weeks.

**Adult (Figure 2)**

(Based on 20 fully mature specimens.) Body thick, distinctly scoop-shaped, 1968−2952 (2460) long, 1061−1570 (1315) wide at level of ventral sucker. “Scoop” large, mainly glandular, sub-circular, complete posteriorly, 1023−1680 (1352) long, representing 51−57 (54)% of body length. Forebody 708−1140 (924), representing 36−38 (37)% of body length. Tegument contains minute, closely set spines which decrease in size and number posteriorly.

Pre-oral lobe 139−208 (174). Oral sucker well developed, sub-terminal, round, 260−390 × 288−435 (325 × 362). Ventral sucker sub-spherical, just pre-equatorial, 204−282 in diameter. Sucker-width ratio 1:0.64−0.71.

Prepharynx extremely short. Pharynx fairly large, strongly muscular, scallop-shaped due to the presence of five low protuberances on its anterior margin, 204−306 × 232−370 (255 × 301). Intestinal bifurcation about midway between suckers; intestinal caeca wide, extend backwards to abut posterior end open with separate ani.

Testes two, oval, contiguous, obliquely arranged midway between ventral sucker and posterior end, sub-equal, 260−410 × 204−306 (255 × 335). Post-testicular region 288−472 (380) long, representing 14−16% (15%) of body length. External seminal vesicle curved sinistrally, sub-median, in anterior region of second half of body. Cirrus-sac thick-walled, 464−702 × 105−135 (583 × 120), sinistrally sub-median, extends from short distance posterior to ventral sucker to near pharynx, contains funnel-shaped internal seminal vesicle, well-developed prostatic complex and a relatively long ejaculatory duct. Genital pore sinistrally sub-median, just posterior to level of pharynx.

Ovary follicular, median, consisting of 46−57 compact follicles situated between posterior testis and uterus. Seminal receptacle oval, antero-lateral to posterior testis. Uterus pre-ovarian, inter-caecal, moderately long. Distal uterine coil highly muscular, modified to form distinct metraterm. Vitelline follicles numerous, small, extending in lateral fields from posterior end of body to pharyngeal level, confluent in post-testicular region. Eggs oval, thin-shelled, non-operculated, numerous, moderately large, 58−62 × 30−36 (60 × 33).

Excretory vesicle I-shaped, extends anteriorly as far as to ovary; excretory pore terminal.
Oyster fecundity

Observations on the reproduction of *Crassostrea cuccullata* revealed that its gametogenic activity was initiated in early spring (March) with full maturation at the beginning of summer (June). Major spawning was observed in midsummer and continued until the beginning of autumn (September), when spent oysters started to appear.

During the present study, 388 adult female oysters were examined. The gonads of 155 (40%) of them were infected with the above-described larval trematode; in 72 (46%, i.e. 19% of the examined females), the gonads were heavily infected and completely castrated, so that the gonadal follicles had entirely disappeared and were replaced by larval trematodes. Thus, the typical gonadal structure (Figure 3A) was not observed (Figure 3B) due to the breakdown of its normal architecture. These infertile females were observed in the late winter and spring months (i.e. before and during the period of gametogenic activity of the oyster). In the other 83 infected females (54%, i.e. 21% of the examined females), the gonads were slightly infected and partly castrated, in that a few of the gonadal follicles were pathologically affected. These females were observed in summer, i.e. after the gametogenic activity, or during the spawning season of the oyster.

Discussion

Bray (2005) has comprehensively reviewed the family Lepocreadiidae Odhner, 1905, recognizing 74 genera. Studies on the life cycles of these genera are rare and mainly compose those of Palombi (1937), Macfarlane (1951), Stunkard (1969, 1980a, 1980b), Lengy and Shchory (1970), Bartoli and Prevot (1967), Køie (1975), and Watson (1984). In these studies, the life cycles of some species belonging to about six genera were described. Generally, the life cycles of most lepocreadiid genera are still completely unknown, and all known cycles include a first and a second intermediate host, and the first is a gastropod. Unusually, *D. arothroni* uses the oyster *C. cuccullata* as a sole intermediate host.

The development and hatching of lepocreadiid eggs have seldom been reported; eggs of *Stegodexamene anguillae* Macfarlane, 1951 hatch by contractions and extensions of the miracidium as it pushes up the operculum (Macfarlane 1951); eggs of *Neopechona pyriforms* (Linton, 1900) Stunkard, 1969 hatch when kept for 9–10 days at laboratory temperatures (Stunkard 1969); eggs of *Tetracerasta blepta* Watson, 1984 begin to hatch after 7 days at 20–25°C, while eggs of *Stegodexamene callista* Watson, 1984 begin to hatch after 9 days at 15–20°C (Watson 1984). In all of these, the miracidium was obtained and described. In the
present study, all attempts to obtain miracidia from the eggs of *D. arothroni* were unsuccessful. In fact, the eggs do not hatch in seawater, but are ingested by *C. cuccullata*. Thus, unlike the other known lepocreadiid life cycles, there is no free-swimming miracidium in the life-cycle of *D. arothroni*.

Lepocreadiid sporocysts were described in three studies by Stunkard (1969), Lengy and Shchory (1970), and Watson (1984). In other studies, the sporocyst was not observed; for example, Macfarlane (1951) did not find the sporocyst of *S. anguillae*, but assumed that if it did exist it would disappear soon after a single brood of rediae had been liberated. The mother sporocyst of *D. arothroni* is similar to other lepocreadiid sporocysts and is readily found in the gonads of *C. cuccullata*.

All lepocreadiid rediae reported in the literature were only briefly described. Rediae of *D. arothroni* resemble them, but are much longer (2721–3350 μm) versus 143–298 μm in *T. blepta* (see Watson 1984), 165–314 μm in *S. callista* (see Watson 1984), 850 μm in *S. anguillae* (see Macfarlane 1951), 1000 μm in *Lepocreadium pegorchis* (Stossich, 1901) (see Bartoli and Prevot 1967), 1100 μm in *Cercaria levantina* (see Lengy and Shchory 1970), and 1600 μm in *Lepocreadium areolatum* (Linton, 1900) (see Stunkard 1980a).

Lepocreadiid cercariae are mainly characterized by their tails bearing setae. The latter are arranged in different ways: singly as in *T. blepta* (see Watson 1984); partly single and partly paired as in *S. anguillae* (see Macfarlane 1951) and *S. callista* (see Watson 1984); in tufts as in *Lepocreadium album* (Stossich, 1890) Stossich, 1903 (see Palombi 1937), *Neopechona pyriformis* (see Stunkard 1969), *Opechona bacillaris* (Molin, 1859) (see Keie 1975), and *Holorhis pycnoporous* Stossich, 1901 (see Bartoli and Prevot 1967). Single setae, when present, are few, short and thin, and more sensory than locomotory (Watson 1984). Generally, the cercaria of *D. arothroni* is closely similar to other lepocreadiid cercaria, but differs in having no penetration glands, and, as mentioned above, its existence in the seawater is very brief and transitory, so it has no chance to find a second intermediate host.

Lepocreadiid metacercariae have been reported encysted in polychaetes, gastropods, bivalves, echinoids, and fishes, and unencysted in medusae, jellyfish, ctenophores, and molluscs (Martin 1945; Lauckner 1980a, 1980b; Stunkard 1980a; Martorelli 2001). In some species, such as *S. anguillae*, the metacercaria is progenetic and ovigerous (Macfarlane 1951), while in *S. callista*, the metacercaria grows for 2 weeks in the cyst and then stops growing (Watson 1984), whereas in others, such as *Lepocreadium pegorchis* Stossich, 1901, the metacercaria is little advanced from the cercarial stage (Bartoli 1967). The metacercaria of *D. arothroni* is similar to that of the latter species but not encysted in a second intermediate host.

In the light of the above, the life cycle of *D. arothroni* has unique characteristics, which differentiate it from other known lepocreadiid life-cycles.

Parasitic castration (partial or total inhibition of host gamete formation by parasites) commonly occurs in mollusk–trematode associations, where larval trematodes (sporocysts, rediae, and cercariae) infect the gonads of their molluscan hosts and partly or completely castrate them (Malek and Cheng 1974; Lauckner 1980c, 1983). This castration is well known and recorded by several authors from numerous species of snails and bivalves. In oysters, parasitic castration has previously been recorded, for example, in *Ostrea lutaria* (see Millar 1963), in *Grasostrea virginica* (see Cheng and Burton 1965; Feng and Canzonier 1970; Tripp 1973; Turner 1985), in *C. gigas* (see Chun 1974), in *C. madrasensis* (see Mohan 1978), and in *Pinctada radiata* (see Khamdan 1998). Most of these authors agreed that the presence of larval trematodes disturbs gametogenesis in oysters during the annual reproductive cycle. Generally, the castration of oysters by larval trematodes is restricted to
some species belonging to the family Bucephalidae. Unlike other oysters, C. cucullata is parasitized and castrated by the larval forms of the lepocreadiid D. arothroni. The prevalence of this parasite in the females of this oyster examined was high (40%) and significantly affects its reproductive capacity, since in 46% of the infected females (= 19% of the examined females), the gonads were completely castrated, and in the other 54% of the infected females (= 21% of the examined females), the gonads were slightly or partly castrated by the parasite. Several authors (e.g. Kabat 1986; Shelley et al. 1988; Ngo et al. 2004) referred the degree of castration to the intensity of infection with larval trematodes within the molluscan gonad. However, many hypotheses have been proposed to explain the mechanism; Cheng and Cooperman (1964), Wilson and Denison (1980), and Sorensen and Minchella (1998) believed that castration is due to the physical or mechanical actions of the parasite, while Cheng et al. (1973), Pearson and Cheng (1985), Coustau et al. (1991), and Valderrama et al. (2004) believed that castration is due to the physiological actions of the parasite. In the present study, complete castration was observed before and during the gametogenic activity of the oyster. Recently, Valderrama et al. (2004) observed a similar result in Eurhomalea lenticularis, a bivalve castrated by larval trematodes of the family Plagiorchiidae. They suggested that larval trematodes have a primary retarding effect on the host’s neuroendocrine and gametogenic systems that regulate gamete production. In my opinion, complete castration is partly due to the infection intensity and partly due to the asexual reproduction of sporocysts and rediae, which increases the numbers of rediae and cercariae, respectively, and so the gonad appears to be severely or densely infected. The energy required for this reproduction is likely mainly derived from that stored by the mollusc for its own gametogenic activity. This may leave insufficient resources for the mollusc to initiate or to complete its gametogenesis, and finally leads to complete castration. Partial castration observed after the gametogenic activity or during the spawning season of the oyster may be due to the physical effect or mechanical compression accompanying the growth of sporocysts and rediae; the former absorb host nutrients via their tegument, and the latter, using their muscular pharynx and primitive gut actively to consume host tissue while moving through the gonad. However, persistent germinal balls observed in mature sporocysts during partial castration reflect the limited capacity of the sporocysts to produce rediae, since not enough energy was available to fuel this process.

In conclusion, the reduction in reproductive capacity caused by larval trematodes may affect the overall fecundity of the oyster C. cucullata, and may increase the ability of larval trematodes to act as a regulator of its population in the study area.

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