



Infection of the gonads of *Glaucosoma hebraicum* by the nematode *Philometra lateolabracis*: occurrence and host response

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(Received 29 August 2001, Accepted 24 January 2002)

The prevalence of infection of the West Australian dhufish *Glaucosoma hebraicum* off the lower west coast of Australia by *Philometra lateolabracis* was greater among females than males, which contrasts with the situation with *Pagrus auratus* in waters off New Zealand. Live *P. lateolabracis* were represented solely by females and were found only in the gonads of fish of mature size (L_{50} at first maturity = c. 300 mm) caught between December and April and thus during the spawning period of dhufish. Since the gonads were largest during that period, they, and particularly ovaries, would provide an abundant food source in the form of blood. The prevalence of the parasite (live+dead individuals) increased with host body size to reach a maximum of c. 80% in the 700–799 mm length class of females and c. 50% in the largest length class of males. During the spawning period of *G. hebraicum*, *P. lateolabracis* developed from small, non-gravid females to large gravid females, representing an increase in mass of more than 200 times. The maximum length of *P. lateolabracis* (470 mm) in *G. hebraicum* is the greatest yet recorded for this species. Gonadosomatic indices provided no evidence that infection by *P. lateolabracis* leads to a conspicuous atrophy of the ovaries, which contrasts with the situation with the gonads of some of the teleosts infected by *Philometra* species, and presumably reflects, in part, the small volume of the ovary occupied by *P. lateolabracis* (c. 3%) and the low intensity of infection (mean = 2.0, maximum = 7). Although the presence of live *P. lateolabracis* did not stimulate an obvious tissue response by the ovaries during the spawning period of *G. hebraicum*, both the dead and any live parasites that remain after spawning become encapsulated in fibrous tissue.

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Key words: West Australian dhufish; *Glaucosoma hebraicum*; spawning period; encapsulation; prevalence; seasonal occurrence; host response.

INTRODUCTION

The West Australian dhufish *Glaucosoma hebraicum* Richardson is one of the most valuable commercial and most sought after recreational marine species of fish in Western Australia (Kailola *et al.*, 1993). Concerns at its apparent decline due to heavy fishing led the Australian Fisheries Research Development Corporation to fund a detailed study of its biology which would provide the data required for developing plans to conserve this important resource. During this study, the gonads of *G. hebraicum* were found often to be infected by a large nematode parasite of the family Philometridae, which was identified as *Philometra lateolabracis* (Yamaguti) and represents the first record of this species

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from Australian waters. Since philometrids can have profound detrimental effects on fishes (Sinderman, 1986), *P. lateolabracis* could have a deleterious impact on *G. hebraicum* and thus be of considerable economic importance.

Philometra lateolabracis typically occurs in the gonads of various perciform fishes in tropical regions of the Pacific, Indian and Atlantic Oceans (Rasheed, 1965; Crisp & Klein, 1973). Studies in New Zealand have demonstrated that the prevalence of infection of the gonads of the pink snapper *Pagrus auratus* (Bloch & Schneider) by *P. lateolabracis* was far greater in male than female fish and in larger than smaller fish and that infection of the testes resulted in partial or even extensive atrophy of those gonads (Hine & Anderson, 1981; Sharples & Evans, 1995a). Furthermore, when *P. lateolabracis* infects the gonads of both *P. auratus* and *Pagrus major* Temminck & Schlegel, it becomes encapsulated in host tissue (Hine & Anderson, 1981; Sakaguchi *et al.*, 1987).

The first aim of the present study was to determine the levels of infection of *G. hebraicum* by *P. lateolabracis* and whether these were seasonal and varied with the size of fish. The second aim was to trace the growth of this parasite during infection and determine whether infection by *P. lateolabracis* has any detectable impact on the gonadal development of *G. hebraicum*. Finally, attention was focused on ascertaining whether *G. hebraicum* possessed mechanisms, such as an ability to encapsulate *P. lateolabracis*, that would help obviate any potentially deleterious effects of infection.

MATERIALS AND METHODS

SAMPLING AND GONADAL STAGES OF *GLAUCOSOMA HEBRAICUM*

Glaucosoma hebraicum were collected by commercial trawling, line fishing and diving and from commercial fish processing plants and weigh-ins at local recreational fishing club competitions. Sampling between September 1996 and March 2001 was initially carried out monthly, but was later restricted to the spawning period of *G. hebraicum*, when the gonads of this species contain live nematodes. Each fish that could be sexed macroscopically was measured to the nearest 1 mm total length (L_T) and weighed to the nearest 0.01 g. The ovaries or testes were removed and assigned to one of the following maturity stages, based on the staging criteria of Laevastu (1965), i.e. I, virgin; II, immature; III, developing; IV, maturing; V, prespawning; VI, spawning; VII, spent; VIII, resting.

CHARACTERISTICS OF *PHILOMETRA LATEOLABRACIS*

Philometra lateolabracis were extracted from the ovaries of *G. hebraicum* and fixed in 10% formalin or 70% ethanol. The anterior and posterior ends of some worms were excised and cleared in lactophenol. Eleven gravid worms were measured using a calibrated eyepiece graticule. Ten larvae from each female worm were measured using an Optimas 5 (Optimas Corporation) image analysis system. The anterior ends of six parasites were dehydrated in an ethanol series, placed in amyl acetate and critical point dried in CO₂, and subjected to scanning electron microscopy using a Phillips XL20. Voucher specimens have been deposited in the Western Australian Museum (WAM V 4243–WAM V 4246).

CHARACTERISTICS OF INFECTION

The ovaries and testes of *G. hebraicum* were opened and the presence of any *P. lateolabracis* recorded. The prevalence of infection *sensu* Bush *et al.* (1997) in each month

and in different gonadal stages and size classes of *G. hebraicum* were then calculated. The prevalence of infection was calculated separately for fish containing live and exclusively dead parasites.

During the spawning season of *G. hebraicum* in 2000–2001, the intensity of infection *sensu* Bush *et al.* (1997) was recorded for individual female fish. It should be noted that when parasites were entwined, it was still possible to determine the intensity of infection by counting the number of heads and tails of the parasites and dividing the resultant value by two. Since the prevalence of infection of testes by live *P. lateolabracis* was very low, the intensity of infection was not recorded for male fish.

Whenever possible, the length and wet mass of each *P. lateolabracis*, collected from ovaries between November 1999 and March 2001, were recorded to the nearest 1 mm and 0.001 g, respectively.

The ovaries of up to 20 fish caught monthly between June 1996 and May 1997 were fixed in Bouin's for 48 h, dehydrated and embedded in paraffin wax. Sections of 6 μ m were cut from the mid region of the ovary and stained with either Mallory's trichrome or Ehrlich's haematoxylin and eosin.

The gonadosomatic index (I_G) was calculated for each female fish that was caught between December and April and possessed gonads at stages V and VI and was >300 mm L_T , the approximate size at which fish reach sexual maturity (Hesp *et al.*, 2002). The mean $I_G \pm 1$ s.e., was determined for each group of uninfected and infected fish in each month from $I_G = 100 M_1 M_2^{-1}$, where M_1 = wet mass of the gonad and M_2 = wet mass of the fish.

RESULTS

CHARACTERISTICS OF GRAVID FEMALES OF *PHILOMETRA LATEOLABRACIS*

The nematode parasites obtained from the gonads of *G. hebraicum* were all females and their morphology and body measurements were consistent with those given in previous descriptions of *P. lateolabracis*. The largest worm (>470 mm), however, was longer than had previously been reported for *P. lateolabracis*.

PREVALENCE, TIMING AND INFECTION OF *PHILOMETRA LATEOLABRACIS*

Philometra lateolabracis was present in the ovaries and testes of some fish in each month of the year, but live parasites were found only between December and early April, i.e. during the host's spawning period (Fig. 1), and only in ovaries at stages V–VIII and in testes at stages IV–VI (Fig. 2). After removal from the infected gonads of recently killed fish, live *P. lateolabracis* were free and moving, whereas dead *P. lateolabracis* were tightly coiled and rigid. Even when fish had been dead for up to a week, the maximum period that elapsed before the gonads were examined for nematode infection, the parasites that had recently been alive could still be clearly distinguished morphologically from those that had been dead at the time of capture of the host. The prevalence of infection with live and dead *P. lateolabracis*, which was greater in ovaries than testes in each month of the year (Fig. 1), ranged in the different months from 29 to 69% in female fish and from 9 to 34% in male fish. Furthermore, the monthly prevalence of live parasites in December to April ranged from 7 to 54% in females compared with 0 to 3% in males (Fig. 1).

No live or dead *P. lateolabracis* were found in either the ovaries or testes of the six *G. hebraicum* that were caught during their spawning period and were

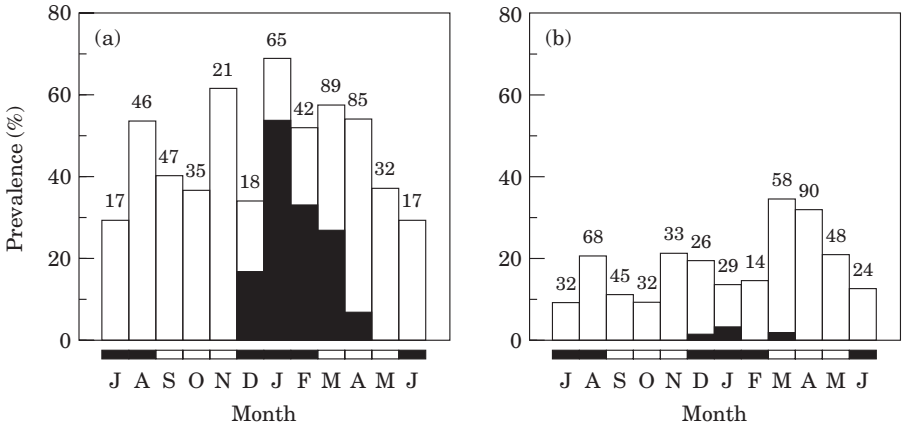


FIG. 1. Prevalence of live (■) and exclusively dead (□) *Philometra lateolabracis* in the ovaries (a) and testes (b) of male *Glaucosoma hebraicum*. Note that some dead parasites are also often found in gonads containing live parasites. Number of fish examined is shown above each month. On the x axis, closed rectangles represent winter and summer months and open rectangles spring and autumn months.

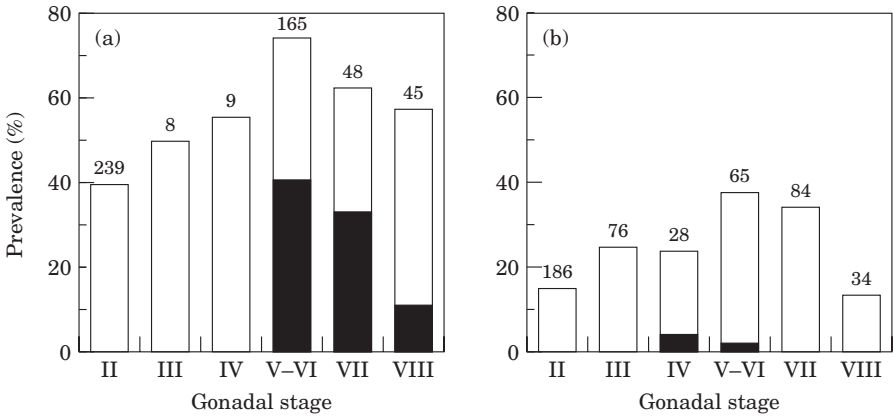


FIG. 2. Prevalence of live (■) and exclusively dead (□) *Philometra lateolabracis* in sequential stages in the development of the ovaries (a) and testes (b) of *Glaucosoma hebraicum*. Number of fish examined is shown above each developmental stage.

<300 mm L_T (Fig. 3). The overall prevalence of infection in females by live and dead parasites rose progressively from 28% in fish of 300–399 mm to a maximum of 81% in those of 700–799 mm, while the prevalence of just live parasites in female fish increased from 16% in the former length class to a maximum of 42% in the latter length class (Fig. 3). During the spawning period of *G. hebraicum*, the overall prevalence of *P. lateolabracis* was far lower in the gonads of males than females, but like females was still greatest in the largest males (Fig. 3).

Intensity of infection in 89 infected female fish examined during the spawning period in 2001, ranged from one to seven with a mean of two.

The mean length and wet mass of individual live *P. lateolabracis* removed from ovaries of *G. hebraicum* increased from *c.* 35 mm and 0.002 g, respectively, in

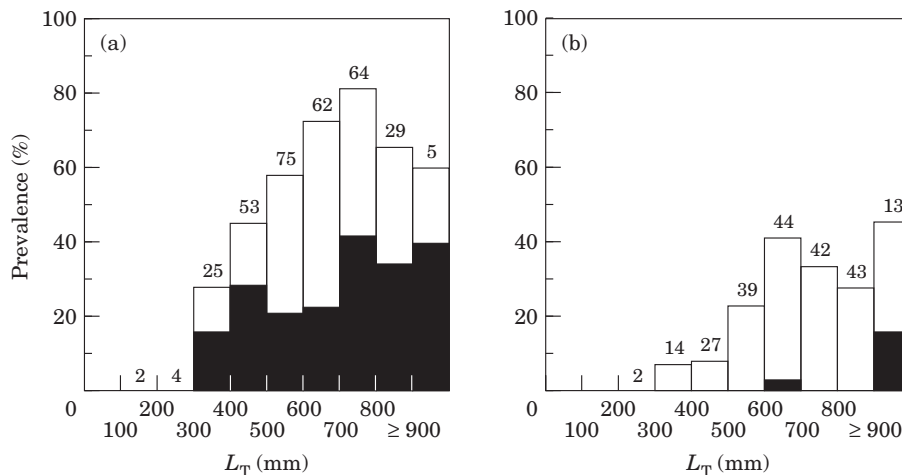


FIG. 3. Prevalence of live (■) and exclusively dead (□) *Philometra lateolabracis* in the ovaries (a) and testes (b) in sequential 100 mm length classes of *Glaucosoma hebraicum* caught during the spawning period, i.e. December–April. Number of fish examined is shown above each length class.

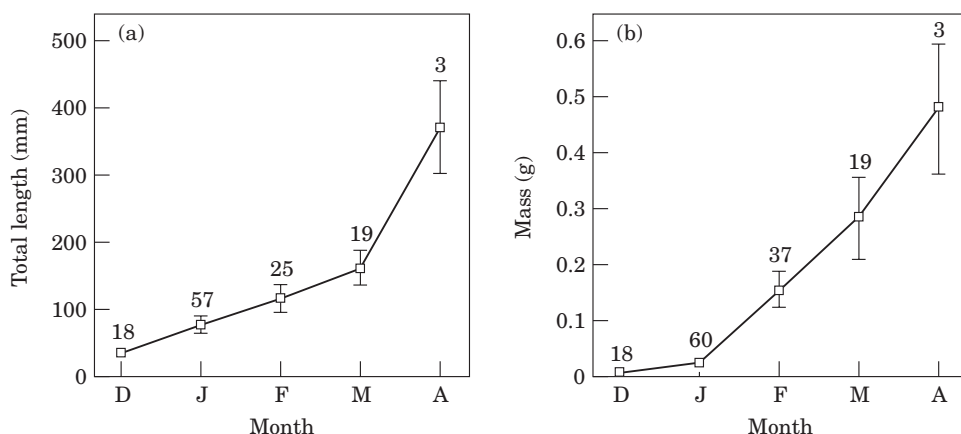


FIG. 4. (a) Mean lengths and (b) mean masses ± 1 S.E. of live or recently dead *Philometra lateolabracis*, removed from the ovaries of female *Glaucosoma hebraicum* caught between December 1999 and April 2001. Samples sizes are given above each mean.

December, just after the commencement of the spawning period, to *c.* 367 mm and 0.48 g, respectively, in April at the end of the spawning period [Fig. 4(a),(b)]. However, it was not always possible to disentangle larger parasites when they were coiled, either individually or in groups, to be able to measure individual lengths and also, even in some cases, to record their individual mass. Thus, the mean values for particularly the parasite lengths towards the end of their host's spawning period, when the parasites were largest, represent an underestimate. The trends exhibited by the above lengths and masses, however, emphasize that *P. lateolabracis* develops and grows rapidly in the ovaries of *G. hebraicum* during the spawning period.

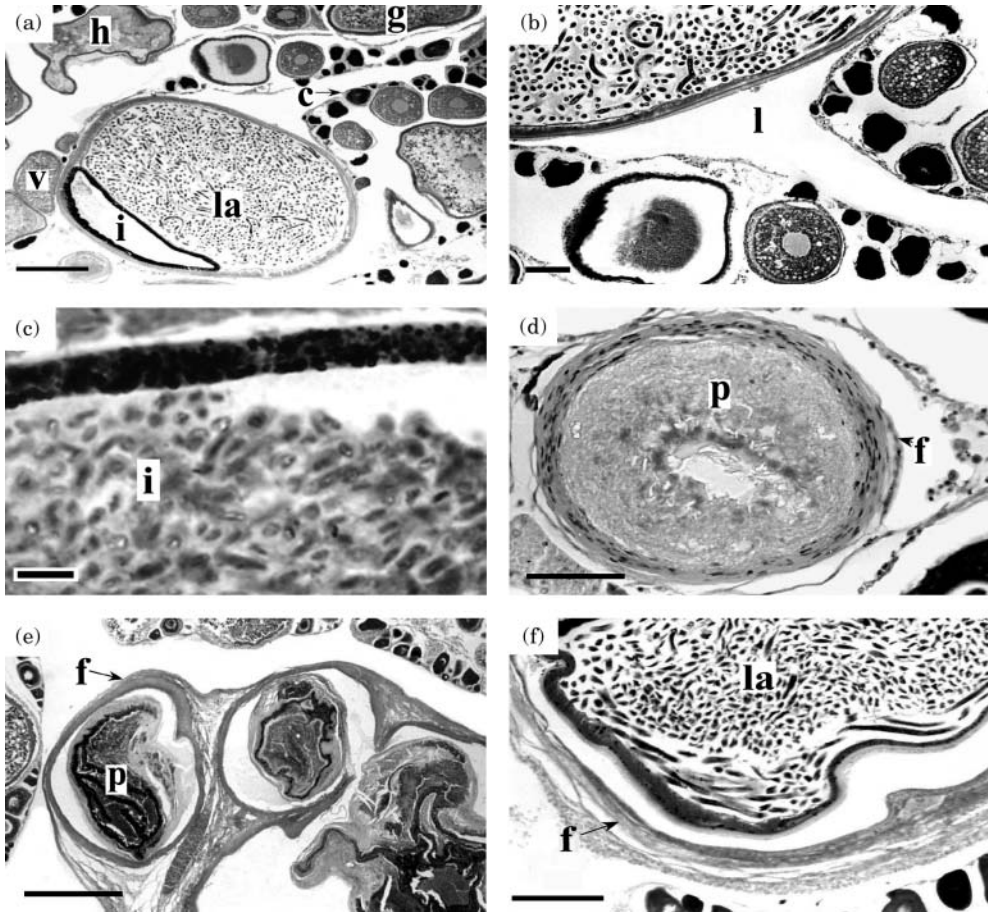


FIG. 5. (a) Section of a stage VI (spawning) ovary of *Glaucosoma hebraicum* with a gravid female of *Philometra lateolabracis* which contains numerous larvae and is surrounded by chromatin nucleolar, yolk vesicle, yolk granule and hydrated oocytes. (b) Part of a gravid female *Philometra lateolabracis* in a lumen of the ovary of *Glaucosoma hebraicum*. (c) Intestine of a *Philometra lateolabracis* containing numerous erythrocytes. (d) Degenerating *Philometra lateolabracis* encapsulated in a fibrous ovarian sheath produced by *Glaucosoma hebraicum* after the completion of its spawning period. (e) Coiled *Philometra lateolabracis* encapsulated in ovarian tissue of *Glaucosoma hebraicum*. (f) A gravid female of *Philometra lateolabracis*, which had not released its larvae prior to the completion of spawning and had become encapsulated in fibrous ovarian tissue of *Glaucosoma hebraicum*. c, Chromatin nucleolar oocyte; f, fibrous sheath encapsulating dead parasite; g, yolk granule oocyte; h, hydrated oocyte; i, intestine of parasite; l, lumen of ovary; la, larvae of *Philometra lateolabracis*; p, parasite (*Philometra lateolabracis*); v, yolk vesicle oocyte. Scale (a) 400 μm , (b) 100 μm , (c) 5 μm , (d) 50 μm , (e) and (f) 300 μm .

The uteri of *P. lateolabracis* in the ovaries of *G. hebraicum*, contain large numbers of larvae [Fig. 5(a)]. These adult nematodes are frequently surrounded by oocytes at all stages of development, i.e. from the chromatin nucleolar to hydrated stages, none of which showed evidence of atresia. During the spawning period, gravid female nematodes typically occupy lumen in the ovaries and are not encapsulated [Fig. 5(b)] and the intestine of these parasites is frequently packed with erythrocytes [Fig. 5(c)].

Dead and degenerating parasites in the ovaries of *G. hebraicum*, are encapsulated by a fibrous sheath [Fig. 5(d)], in the vicinity of which there are often numerous eosinophils. Such parasites are often tightly coiled and enmeshed in a mass of host tissue [Fig. 5(e)]. Sections of ovaries of fish caught soon after the end of the spawning period demonstrate that some *P. lateolabracis* become encapsulated in host tissue before they are able to release their larvae [Fig. 5(f)].

The mean I_G s for uninfected and infected female fish with ovaries at stages V (prespawning) and VI (spawning) were not significantly different ($P > 0.05$) in any month between November and April, i.e. during the spawning period.

DISCUSSION

JUSTIFICATION FOR ASSIGNING PARASITE TO *PHILOMETRA LATEOLABRACIS*

Philometra lateolabracis was originally described from fishes from Japanese waters (Yamaguti, 1935) and has since been redescribed several times (Rasheed, 1963, 1965; Moravec *et al.*, 1988; Sharples & Evans, 1995b). Only one male specimen has ever been recorded (Crisp & Klein, 1973). Two similar species, *Philometra margolisi* Moravec, Videll-Martinez & Auirre-Macedo and *Philometra pellucida* (Jagerskiöld) also occur in the gonads of marine fishes, but both of these are smaller than *P. lateolabracis* and differ in other characteristics including the extent of the oesophageal gland, and the size of the anterior oesophageal bulb lumen. Most gravid specimens from *G. hebraicum* were 200–300 mm long, which is in the range of *P. lateolabracis* redescribed by Sharples & Evans (1995b). The largest female (470 mm), however, was longer than has previously been recorded for this species. It was not possible to find oral papillae on any specimen, even using *en face* mounts and scanning electron microscopy. Although Sharples & Evans (1995b) were also unable to find papillae on their *P. lateolabracis*, Moravec *et al.* (1988) and Rasheed (1963) demonstrated that papillae were present on their specimens of this species. In view of the absence of a male specimen and the close similarity between specimens in the present study and published descriptions of *P. lateolabracis*, it is considered prudent to allocate these individuals to this species.

PREVALENCE AND SITE OF INFECTION

This study provides the first quantitative account of the prevalence and intensity of infection of the gonads of a marine teleost by a philometrid species, which has utilized data collected throughout the year and taken into account the pattern of sexual maturation and duration of the spawning period of the host. The fact that the gonads of *G. hebraicum* do not become infected with *P. lateolabracis* until that species has reached 300 mm L_T and the L_{50} s for female and male *G. hebraicum* at first maturity are *c.* 300 and 320 mm, respectively (Hesp *et al.*, 2002), strongly suggests that some function(s) associated with the attainment of sexual maturity is responsible for the infection of *G. hebraicum* by *P. lateolabracis*. The prevalence of infection of *Glaucosoma hebraicum* > 300 mm L_T by *P. lateolabracis* is relatively high, which parallels the situation recorded for certain *Philometra* species in the gonads of other teleosts, such as those of the

skipjack tuna *Katsuwonus pelamus* (L.) in the eastern and western tropical regions of the Atlantic ocean (Simmons, 1969) and the red sea bream *Chrysophrys major* Temminck & Schlegel in Japan (Nakajima & Egusa, 1979).

The present results also demonstrate that, while *P. lateolabracis* was present in the gonads of 28–81% of the females and 7–42% of the males of the different 100 mm size classes of *G. hebraicum* >300 mm, live individuals were found in ovaries only between December and April and in testes only during December, January and March. The presence of live individuals in gonads was thus restricted to the spawning period of *G. hebraicum*, which extends from November to April (Hesp *et al.*, 2002). Furthermore, the prevalence of live parasites in ovaries was greatest in December to February, when these gonads were largest and thus presumably most capable of supplying nutrition to the developing nematodes. Indeed, *P. lateolabracis* underwent such rapid development and growth between December and April that, during these 5 months, it increased in mass by more than 200 times. Since numerous erythrocytes could be observed in histological sections of the gut of *P. lateolabracis*, this nematode presumably feeds on the blood of *G. hebraicum*, thereby paralleling the situation with other species of *Philometra*, which likewise live in the gonads of fishes (Ramachandran, 1975; Glazebrook *et al.*, 1988).

The far greater prevalence of *P. lateolabracis* in the ovaries than testes of *G. hebraicum* contrasts markedly with the situation recorded for the same species of nematode in the gonads of *P. auratus* in New Zealand in which >50% of the testes were infected by *P. lateolabracis*, compared with $\leq 11\%$ of its ovaries (Hine & Anderson, 1981). The above interspecific differences in the prevalence of gonadal infections in females and males may be partly related to differences in the relationship between the sizes of the ovaries and testes of these two species during their spawning periods. Thus, on the basis of I_G , the mature ovary of *G. hebraicum* is approximately an order of magnitude greater in size than the mature testes of this species, which, even for testes, is relatively small (Hesp *et al.*, 2002). In contrast, in *P. auratus*, the mature ovary is of similar size to the mature testis (Scott & Pankhurst, 1992), which is also relatively far larger than that of *G. hebraicum*. There would thus presumably be a relatively greater source of nutriment for *P. lateolabracis* in the ovaries than the testes of *G. hebraicum* than would be the case with *P. auratus*.

Since the numerous *P. lateolabracis* found in the gonads of *G. hebraicum* were all females, the males presumably occupy another part of the host's body and the females of this nematode had presumably already become fertilized before they were detected in the gonads. Such spatial segregation of the two sexes has been recorded for several other species of philometrid. Thus, for example, in the case of *Philometra cylindracea* Ward & Magath, which parasitises fishes in the Great Lakes of North America, the females occur in the body cavity, while the immature females and males live under the serosa of the swim bladder (Molnár & Fernando, 1975). The search for the males of *P. lateolabracis* in the present study, however, was unsuccessful, as it has been in many other studies of *Philometra* species and in all but one of those on *P. lateolabracis* (Crisp & Klein, 1973) and which is presumably due in part to the very small size of the males of philometrids.

INTENSITY OF INFECTION AND RESPONSE OF GONADS TO INFECTION

The testes of *P. auratus* infected with *P. lateolabracis* undergo extensive atrophy (Hine & Anderson, 1981) and an unidentified species of *Philometra* virtually destroyed the ovaries of *Otolithus argenteus* Cuvier (Annigeri, 1962). Furthermore, a particularly heavy infection of the ovaries of *Mugil cephalus* L. led to most of its oocytes becoming necrotic (Ramachandran, 1975) and some of the oocytes surrounding *P. pellucida* in the ovaries of *Platycephalus bassensis* Cuvier and *Platycephalus longispinis* Macleay that were moderately infected by this parasite were also recorded as necrotic (Hooper, 1983). In addition, an invasion of the gonads of sexually mature *Pomatomus saltatrix* (L.) by *Philometra saltatrix* Ramachandran reduced the reproductive potential of this species (P. J. Cheung, R. F. Higretti & G. D. Ruggieri, pers. comm.). In the case of *G. hebraicum*, however, the I_{GS} of infected female fish were not significantly less than those of uninfected fish and there was no histological evidence that the oocytes in the vicinity of nematodes were undergoing atresia. The absence of obvious deleterious morphological or cytological effects in the ovaries of *G. hebraicum* infected by *P. lateolabracis* may be at least partly attributable to the fact that, although the *P. lateolabracis* found in *G. hebraicum* are large, the intensity of infection is relatively low, i.e. generally less than four and never greater than seven and the total mass of parasites in an ovary corresponded on average to only c. 3% of the mass of the ovary.

The live *P. lateolabracis* found in the ovary of *G. hebraicum* during the spawning period of this teleost did not become encapsulated by a fibrous sheath and would thus have been able to have shed their larvae into the lumen of that organ, from where they could then pass to the oviduct and finally out of the host. Once the spawning period is completed, however, the dead and any remnant live parasites become encapsulated in a fibrous sheath produced by the ovary.

In summary, the gonads and particularly the ovaries of *G. hebraicum* are often infected with the large nematode *P. lateolabracis*. Since live individuals of this parasite are not found in the ovaries until the commencement of the spawning period, infection is presumably stimulated by some function associated with sexual maturation. Live parasites were also only found in well-developed gonads and only during the spawning period, namely at the time when those gonads were largest and could thus provide a plentiful food supply (i.e. blood) to the parasite. Unlike the situation recorded for some other infections of fish gonads by philometrids, *P. lateolabracis* does not appear to have any deleterious effects on the ovary of *G. hebraicum*. While this may reflect in part the low intensity of infection and thus the relatively small volume of ovary that is occupied by *P. lateolabracis*, there was also no histological evidence that the oocytes in the vicinity of this parasite were becoming necrotic.

Gratitude is expressed to many friends and colleagues for help in collecting dhufish, and to the fish processors at Sealanes Food Service, the recreational fishermen at particularly the Marmion Angling and Aquatic Club and commercial fishermen for providing material. Thanks are also due to G. Thomson for preparing the histological sections of ovaries and Fig. 5 and for providing, together with R. Cook, constructive criticisms of this paper. A. Pike made many useful suggestions for making the text more succinct. Financial support was provided by the Australian Fisheries Research and Development Corporation and Murdoch University.

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