The prevalence of *Proctoeces* (Trematoda: Fellodistomidae) metacercarial infections in the brown mussel *Perna perna* (Bivalvia: Mytilidae) around the southern African coast

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Unencysted trematode metacercariae of the genus *Proctoeces* were found embedded in the mantle tissue and visceral mass of the intertidal mussel *Perna perna*. Data on the prevalence and intensity of infection in southern African populations of *Perna* are presented. Results from a geographic survey indicated that *Proctoeces* infections were more prevalent in the region Port Elizabeth to Isilaka. At the majority of sites both prevalence and intensity of infection increased in conjunction with host size. Detailed studies of mussels from Dwesa failed to show seasonal changes in metacercarial infection. A strong relationship, however, was found between sex of host and parasitic infection, with female mussels harbouring the most metacercariae. The most heavily infected mussels examined came, ironically, from two nature reserves situated on a stretch of coastline where otherwise unprotected mussel stocks are subjected to intense exploitation by man. The possible pathogenic effects of *Proctoeces* on such highly stressed mussel populations clearly merits further attention.

Oningekapselde trematode-metaserkarieë van die genus *Proctoeces* is in die mantelweefsel en viscerale massa van die tussengety-mossel *Perna perna* gevind. Gegewens oor die voorkomssyfer en besmettingsintensiteit in *Perna* in suidelike Afrika word gegee. Resultate van 'n geografiese ondersoek het aangetoon dat besmetting met *Proctoeces* meer algemeen in die kusstreek tussen Port Elizabeth en Isilaka was. By die meerderheid van die gebiede wat ondersoek is, het beide die voorkomssyfer en die besmettingsintensiteit saam met die grootte van die voerdier toegeneem. Deeglike ondersoeke van mossels by Dwesa het geen seisonale veranderinge in besmetting met metaserkarieë aangetoon nie, alhoewel daar 'n sterk verwantskap tussen die geslag van die mossel en die intensiteit van parasitisme was. Vroulike mossels het die hoogste besmetting van *Proctoeces* getoon, veral dié wat in natuurreservate gevind is. Buite die reservate is die *Perna*-populasie aan intensiewe benutting deur die mens onderworpe. Die moontlike patologiese effekte van *Proctoeces* op sulke populasies behoort verder ondersoek te word.

Histological studies of the reproductive cycle of the brown mussel *Perna perna* have incidentally revealed evidence of digenean trematode larval infections (Lasiak 1986). These have subsequently been identified as metacercariae belonging to the fellodistomid genus *Proctoeces*, possibly *P. maculatus* (R.A. Bray of Dept. of Zoology, British Museum (Natural History): pers. comm.). Members of the genus are notoriously variable as to body form, size and internal structure and consequently specific identification is difficult (Stunkard & Uzmann 1959; Freeman 1962; Wardle 1980). Many of the previously described species have been synonymized (Bray & Gibson 1980; Bray 1983) with the type species *P. maculatus*. These synonymies have recently been confirmed by Shimazu (1984). As a result of this taxonomic uncertainty, the specimens found in *Perna* will be referred to throughout as *Proctoeces*.

Although the ecology and physiology of South African mytilid bivalves have been extensively studied (Berry 1978; Crawford & Bower 1983; Du Plessis 1977; Griffiths 1977, 1980a & b, 1981a & b; Griffiths & King 1979a & b) there have been no previous references to parasitic infections. The presence of *Proctoeces* is of considerable interest in view of the widespread use of mussels as a protein supplement by some indigenous coastal tribesmen (Bigalke 1973) and as a gourmet delicacy by the more affluent. To evaluate the need for further studies on the possible pathogenic effects of *Proctoeces* on *Perna* it is firstly necessary to establish whether or not the occurrence of these larval trematodes is widespread in natural mussel populations. A survey was therefore undertaken to assess both the prevalence and intensity of infection at various sites along the southern African coast.

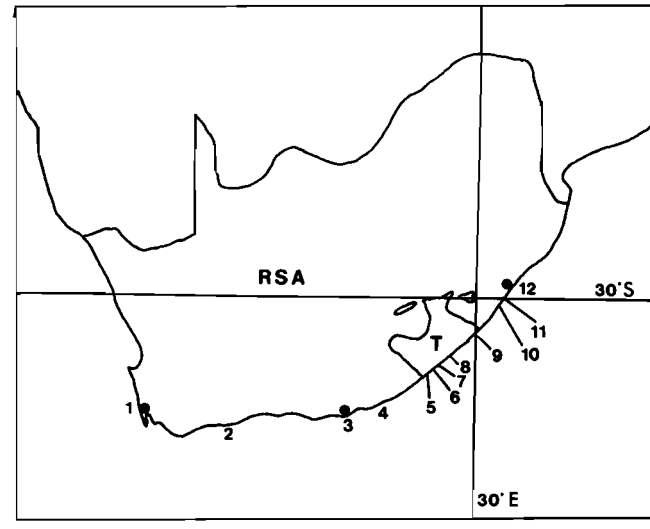

Figure 1 Map showing sites on the southern African coast from which mussels were examined for metacercarial infections (1, Cape Town; 2, Tsitsikamma; 3, Port Elizabeth; 4, Port Alfred; 5, Mazeppa: 6, Dwesa; 7, Hluleka; 8, Isilaka; 9, Mkambati; 10, Pennington; 11, Park Rynie; and 12, Bluff, Durban).

Methods

Samples of intertidal brown mussel populations, encompassing the full size range available, were obtained from twelve locations (Figure 1). To assess the possibility of seasonal changes in the prevalence of infection additional samples were collected at quarterly intervals from the Dwesa Nature Reserve. All mussels were induced to gape by overnight storage in a coldroom, prior to preservation with 10% formalin for a minimum period of one month. The sample size, which varied from 30 to 246, was dependent on the population size composition present at each site. Only mussels of > 30 mm total length were examined as preliminary studies revealed no

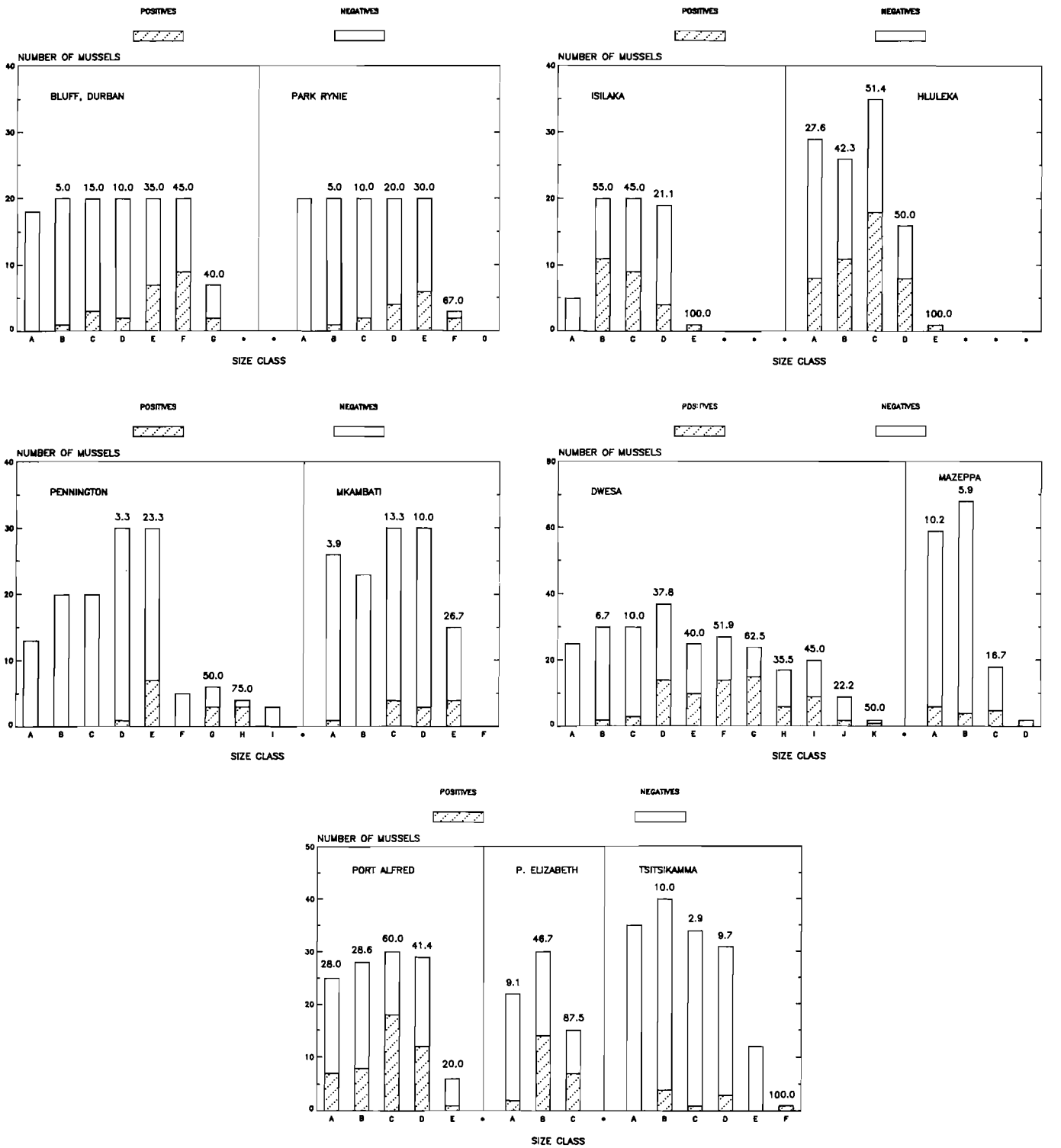

Figure 2 Histograms showing the prevalence of *Proctoeces* metacercarial infections relative to the size class of *Perna* examined at each site. (Positive bars represent the number of infected mussels and negative bars the number of uninfected individuals; the numbers represent percentage prevalence; and A–K represent size classes between 30 and 130 mm separated by 10-mm intervals, so that individuals in Class A are > 30 mm but < 40 mm and so forth).

evidence of metacercarial infection in smaller individuals.

To determine whether or not metacercariae were present the soft tissues were removed from the shell, teased apart where necessary, and examined with the aid of a dissecting microscope. The total length of each individual mussel was recorded along with the number of resident parasites. Chi-squared tests, two- and three-way contingency analysis and Kruskal-Wallis analysis of variance by ranks (Sokal & Rohlf 1981) were used to assess the significance of the various relationships observed between the four factors, namely infection, season, host sex and host size. When necessary data sets were reduced so that statistical comparisons were based only on the size groups common to all sites / seasons.

Results

Geographical survey of metacercarial infections

Unencysted *Proctoeces* metacercariae were found in all of the mussel samples examined with the exception of that obtained from the Western Cape. Most of the larvae were embedded in the mantle tissue, in some cases forming small accumulations at the anterior margin. A few metacercariae were also found in the labial palps and within the visceral mass. Direct site by site comparisons of prevalence (number of infected mussels expressed as a percentage of total number of mussels examined) and intensity of infection (number of metacercariae per individual host) were not possible because of significant differences in the population size structure of mussels at the various sites. To obviate this problem these criteria have been expressed relative to the size of mussel examined and the data expressed on a size class basis. Figure 2 shows the number of mussels examined within each 10 mm size class plus the prevalence of infection for each of these groupings at the eleven affected sites. Mussels from Isilaka, Hluleka, Dwesa, Port Alfred and Port Elizabeth showed the highest prevalences of infection. Chi-squared tests of association revealed significant relationships between prevalence of infection and size of host at eight of these localities (Table 1). This suggests that larger (and probably older) mussels are most likely to be infected. Three-way contingency analysis indicated that the factors prevalence, size and site were not only interactive (G = 231,45; $d.f.$ = 52; $p < 0{,}001$) but also showed that the relationship between size and prevalence varied from site to site (G = 43,61; $d.f.$ = 22; $0{,}001 < p < 0{,}005$).

The majority of mussels, irrespective of their site of origin, showed a low intensity of infection with infected individuals each harbouring between 1 and 20 metacercariae. Considerably higher intensities of infection were, however, observed in some of the mussels obtained from Dwesa and Hluleka nature reserves, where the number of larvae per host ranged from 1 to 337 and 1 to 134, respectively. Figure 3 shows that at both sites the intensity of infection increased with length of mussel. The significance of these differences was confirmed by Kruskal-Wallis tests (Dwesa: H = 12,70; $d.f.$ = 6; $0{,}025 < p < 0{,}005$; Hluleka: H = 11,05; $d.f.$ = 3; $0{,}01 < p < 0{,}05$).

Table 1 Chi-squared tests of association comparing the prevalence of infection with size of host at eleven localities (*d.f.* = degrees of freedom and * indicates significance at the 5% level or more)

Site	χ^2	*d.f.*	Probability level
Park Rynie	21,12	6	0,0019*
Pennington	51,48	8	<0,0001*
Bluff, Durban	21,12	6	0,0019*
Mkambati	9,06	5	0,1077
Isilaka	9,83	4	0,0441*
Hluleka	5,48	4	0,2427
Dwesa	46,83	10	<0,0001*
Mazeppa	8,23	5	0,1449
Port Alfred	14,28	5	0,0144*
Port Elizabeth	27,10	3	<0,0001*
Tsitsikamma	21,50	5	0,0007*

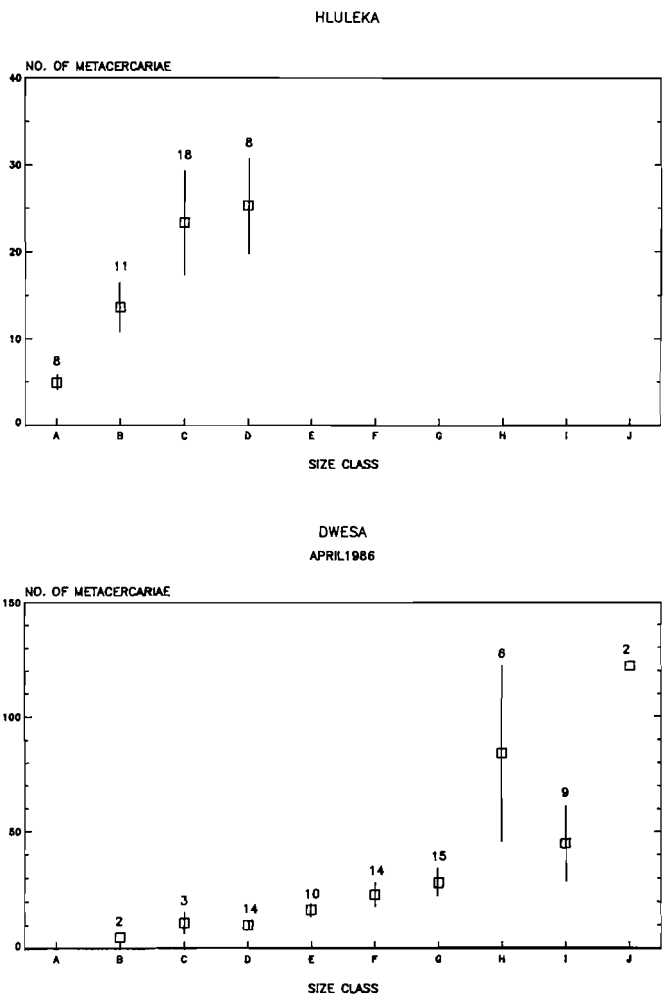

Figure 3 Mean intensity (+ S.E.) of metacercarial infection relative to the size of host mussel at (a) Hluleka and (b) Dwesa. (A–K are size classes as defined in Figure 2; and the numbers represent sample sizes).

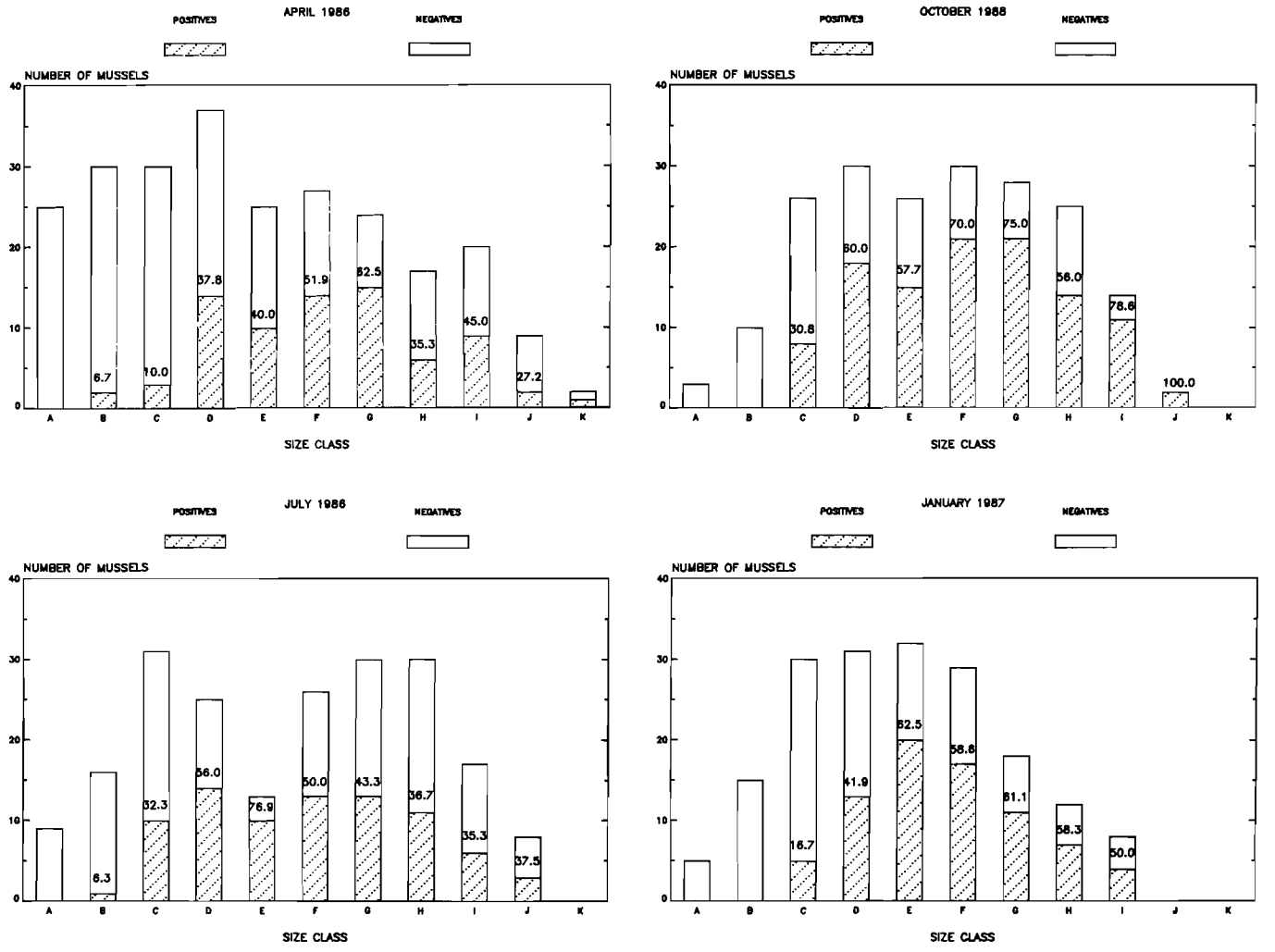

Figure 4 Seasonal fluctuations in the prevalence of *Proctoeces* infections in *Perna* at Dwesa (positive bars represent the number of infected mussels and negative bars represent the number of uninfected individuals; A–K are size classes as defined in Figure 2; and the numbers indicate the percentage prevalence for each size class).

Seasonal survey of metacercarial infections

Two-way contingency analysis indicated that the prevalence of infection did not change from season to season (G = 5,87; $d.f.$ = 3; 0,10 < p < 0,25). However, three-way contingency analysis showed that the three factors prevalence, size and season were interactive (G = 215,02; $d.f.$ = 59; p < 0,001) and that the interaction between prevalence and size varied with season (G = 136,71; $d.f.$ = 32; p < 0,001). The latter observation reflects the fact that the size composition of the mussels examined varied seasonally. Figures 4 & 5 depict respectively the prevalence and intensity of infection for each size class recorded in each of the quarterly samples. Comparisons of seasonal differences in the intensity of infection within each size class based on Kruskal-Wallis tests (Table 2) only revealed significant differences in the 60–70 mm size class. Multiple comparisons showed that the intensity of infection observed within this grouping during July differed from that observed in each of the other quarters. The levels observed in the October and January samples also differed significantly.

Infection relative to sex of host mussel

During the latter part of the survey it became apparent that the observed differences in prevalence and intensity of *Proctoeces* infections were also related to the sex of the host mussel. It was not possible to follow this relationship throughout the study period because *Perna* enters a resting phase at the end of its reproductive cycle at which time sex becomes indeterminate (Lasiak 1986). Figure 6 is a scattergram illustrating the intensity of metacercarial infection relative to sex and size of host based on a collection made at Dwesa during the peak of the reproductive season.

Results presented in Table 3 and Figure 6 indicate that intensity and prevalence of infection were considerably higher in female than male individuals. This was confirmed by two-way contingency analysis which showed that the prevalence of infection was dependent on sex of host (G = 54,32; $d.f.$ = 1; p < 0,001). All of the female mussels of > 65 mm that were examined harboured metacercarial infection. Three-way contingency analysis confirmed that the factors prevalence, sex and size were

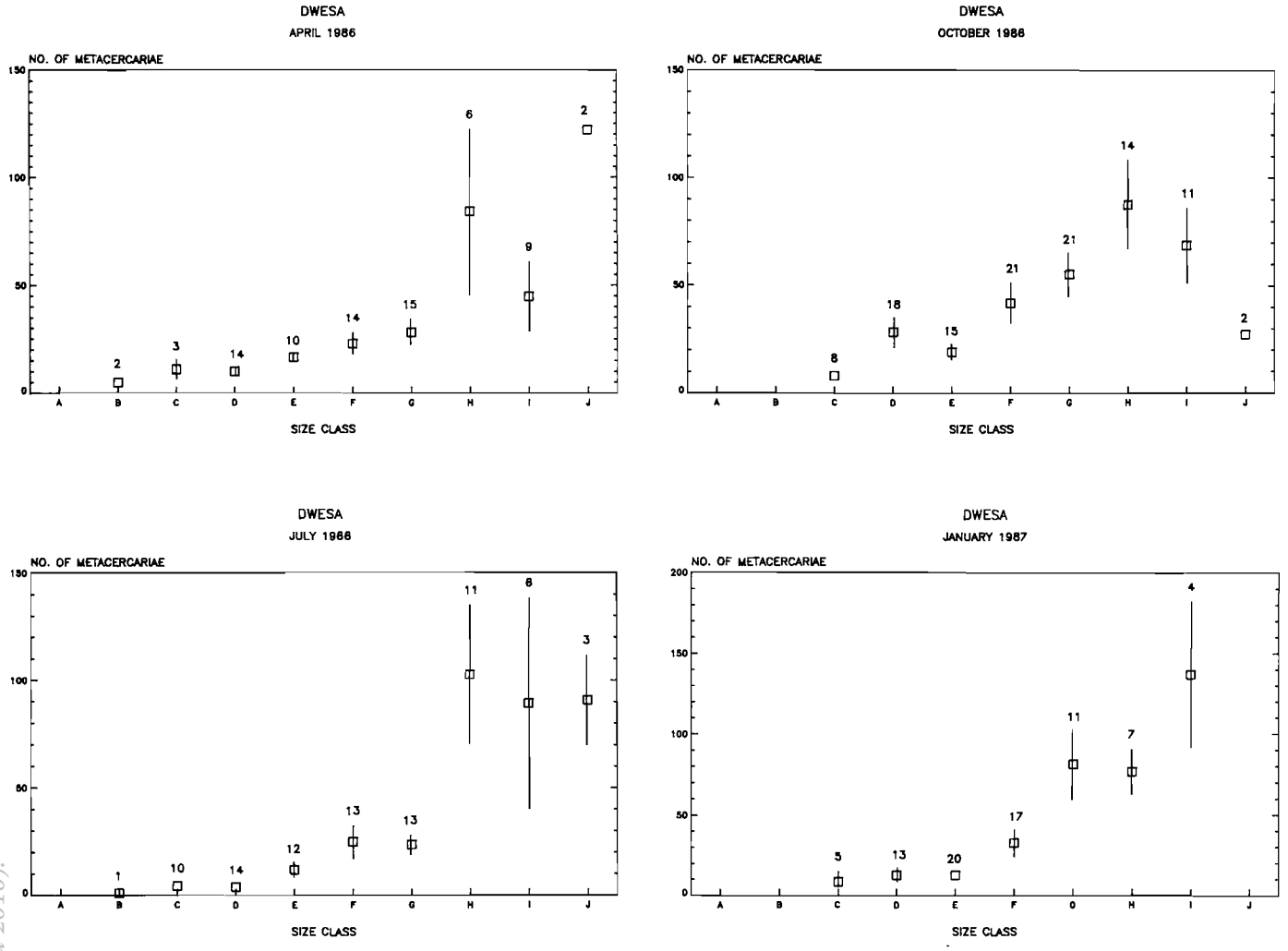

Figure 5 Seasonal fluctuations in the mean intensity (+ S.E.) of *Proctoeces* infections in Dwesa mussel populations expressed relative to size of infected host. (A–K are size classes as defined in Figure 2; and numbers represent sample sizes).

Table 2 Kruskal-Wallis test statistics (*H*) and multiple comparisons of significant (*) data sets derived from quarterly analyses of infection intensities (*d.f.* = degrees of freedom)

Size class (mm)	*H*	*d.f.*	Probability level
50–60	4,47	3	0,2152
60–70	16,18	3	0,0011*
70–80	4,77	3	0,1896
80–90	1,36	3	0,7151
90–100	6,94	3	0,0745
100–110	1,65	3	0,6484
110–120	4,35	3	0,2266

Multiple comparisons for the 60–70 mm size class

Samples compared	Mean difference	Minimum difference
April vs July	14,04	11,41*
April vs October	10,50	10,76
April vs January	1,20	11,63*
July vs October	24,53	10,76*
July vs January	12,84	11,63*
October vs January	11,70	10,99*

Table 3 The numbers of infected and uninfected mussels at Dwesa relative to sex and size of *Perna*. Sample collected in June 1987 at the peak of the reproductive cycle

Size class (mm)	Males		Females	
	infected	uninfected	infected	uninfected
40–50	0	4	0	1
50–60	0	7	3	6
60–70	1	8	7	3
70–80	1	8	11	0
80–90	2	5	12	0
90–100	3	5	11	0
100–110	4	10	5	0
110–120	1	2	8	0

interactive (G = 72,61; *d.f.* = 19; $p < 0{,}001$) and that the relationship between prevalence and sex varied with size (G = 50,45; *d.f.* = 7; $p < 0{,}001$).

Discussion

Previous studies on trematodes of the genus *Proctoeces*

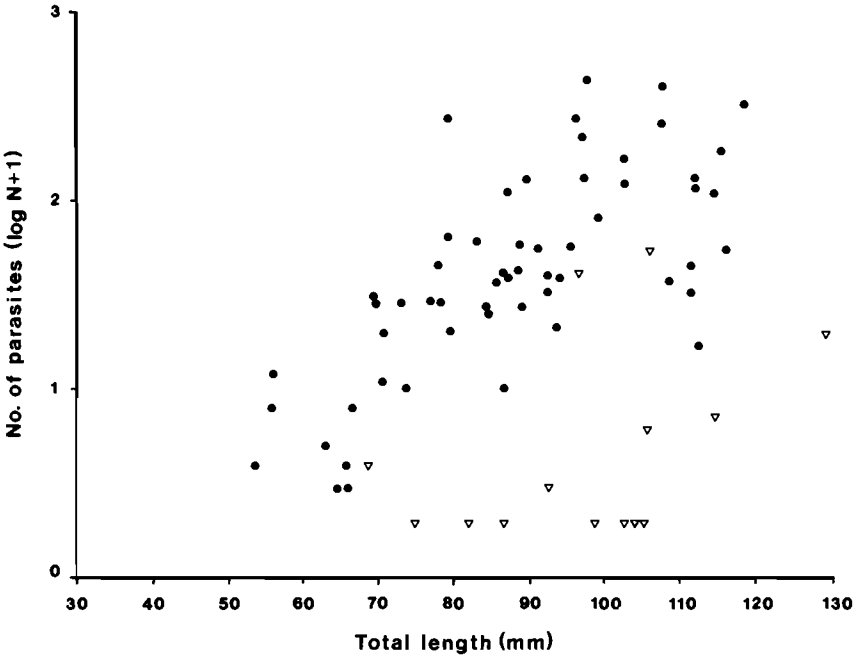

Figure 6 Scattergram showing the intensity of *Proctoeces* infections relative to size and sex of host, based on a sample collected at Dwesa in June 1987. (● represents female and ▽ represents male *Perna*).

indicate considerable plasticity in life-history strategies. The numerous hosts and life-cycle patterns which have been recorded are listed in Bray (1983). In the cold waters of the northern hemisphere the life cycle is often abbreviated, either taking place entirely in one bivalve host, or alternatively, a second molluscan species is utilized as the final host. Thus some workers (Atkins 1931; Cole 1935; Hopkins 1954; Canzonier 1972) have only noted sporocysts in mytilid bivalves whereas others (Prevot 1965; Dupouy & Martinez 1973; Lang & Dennis 1976; Wardle 1980) have also recorded metacercariae and / or adult *Proctoeces* in the same bivalve.

The only previous record of *Proctoeces* in southern Africa comes from the work of Smale & Buchan (1981) who found metacercariae in the stomach and crop of *Octopus vulgaris*. It now seems likely that these cephalopods gained this parasitic infection through ingestion of their preferred prey item *Perna perna* which the current study has shown, at some localities, to be heavily infested with *Proctoeces* metacercariae. The fact that the metacercariae found in *Octopus* were at an advanced stage, with development of the vitelline follicle and deposition of vitelline material in the uterus being evident (Bray 1983), suggests that this animal may act as a final host. Mature specimens of *Proctoeces* have, however, yet to be reported from *Octopus* or any of the other potential final hosts in southern Africa. Elsewhere, adult worms have been recorded from 59 species of teleost fish, one annelid, three bivalve and 14 gastropod species. The intermediate host(s) bearing sporocysts has(have) yet to be identified and it also remains to be established whether or not *Perna* is the sole host of the metacercarial stage in these waters. Recent studies in the Baltic (Machkevskij & Parukhin 1981a & b) suggest that *P. maculatus* has some specificity at this stage in its life cycle, but elsewhere metacercariae have been recorded simultaneously in a variety of echinoderms, polychaete annelids, gastropod and polyplacophoran molluscs (Prevot 1965). Sakaguchi, Hosina & Minami (1970) found that most of the benthic bivalves and gastropods associated with pearl oyster grounds in Japan harboured metacercariae.

The absence of *Proctoeces* from the Western Cape mussel sample suggests that its distribution may be temperature dependent, however, this seems unlikely in view of the known worldwide distribution of this organism (Bray & Gibson 1980). Although direct site by site comparisons of infection were not feasible owing to differences in month of collection and range of mussel sizes examined, the results of the geographical survey indicated that *Proctoeces* infections were most prevalent in the region Port Elizabeth to Isilaka, Transkei. This suggests that transmission of the parasite from definitive to intermediate hosts is more successful in this region than elsewhere along the coast. Such geographical variations in transmission success are undoubtedly indicative of differences in the probability of contact between host and parasite, which is itself dependent on various ecological factors, such as nature of habitat, population density of intermediate hosts and the relative geographic ranges of the various hosts. The exact causative factors cannot be determined until the full life-cycle has been elucidated.

Relatively little information is available on the prevalence of metacercarial infections of *Proctoeces* in bivalves compared with numerous accounts of sporocyst infections (Cole 1935; Uzmann 1953; Hopkins 1954; Stunkard & Uzmann 1959; Prevot 1965; Canzonier 1972; Lang & Dennis 1976). The levels of sporocyst infection reported vary from < 1% (Stunkard & Uzmann 1959) to

> 40% (Lang & Dennis 1976). The significance of these differences is, however, difficult to assess because of the lack of additional information enabling comparisons to be made on the basis of season and/or size of host. Only one of the afore-mentioned studies (Lang & Dennis 1976) fulfils these requirements. Studies on the prevalence of *Proctoeces* metacercarial infections carried out on *Ischadium recurvum, Mytilopsis leucochaeta* and *Mytilus galloprovincialis* (Prevot 1965; Wardle 1980; Turner 1986) revealed similar levels of infection of 20–30%. Prevot (1965) and Turner (1986) also reported seasonal fluctuations in the prevalence of metacercariae, varying from 2 to 35% in *I. recurvum* and from 6–20% in *M. galloprovincialis*. The latter author found that the prevalence of infection in *I. recurvum* dropped sharply from a relatively stable level of 15–20% to 2–3% in mid-summer. This decline, which only persisted for two months, appeared to be linked to the proliferation of sporocysts. Although there was no evidence of sporocyst infection in any of the *Perna* samples examined, the possibility of a similar sudden drop in prevalence of metacercariae being overlooked, as a result of the quarterly sampling interval used in the seasonal study, can not be discounted.

In most instances the numbers of metacercariae harboured by individual *Perna* (usually 1–20) were similar to those reported previously in other bivalve species (Stunkard & Uzmann 1959; Prevot 1965; Sakaguchi, Hosina & Minami 1970). The heavier infections observed in the Dwesa and Hluleka samples may have resulted from the intake of large numbers of cercariae at one time, from repeated infections, or a combination of both. The fact that both prevalence and intensity of infection increased in conjunction with host size is, however, indicative of a cumulative effect. The absence of metacercarial infection in *Perna* of < 30 mm suggests that mussels attain this size before the invasive stage appears. The strong relationship between sex of host and metacercarial infection either reflects the differential immunity of male and female mussels to cercarial infection, or alternatively, the preferential selection of female hosts by cercariae. In that case, the absence of *Proctoeces* in small mussels may even be linked to sexual maturity of the host. It is thus interesting to note that on the Transkei coast *Perna* becomes reproductively active, after approximately one year of growth, at a size of 30–35 mm (Lasiak & Dye 1989). Infections in mussels < 30 mm may also be more difficult to detect because of their disproportionately greater abundance relative to the larger size classes. Age-related differences in the immunity of hosts could also account for these differences. The slower growth rate of *Perna* in Transkei (Lasiak & Dye 1989) and the southern Cape (Crawford & Bower 1983) compared to that of Natal (Berry 1978) is reflected by the appearance of infection in smaller mussels at the former sites. With the exception of recent work by Machkevskij (1985) none of the previously cited workers mention any increase in the prevalence or intensity of *Proctoeces* metacercarial infections with increasing size of host. The present study also appears to be the first to demonstrate a link between infection and sex of host.

The distribution of metacercariae within the soft tissues of *Perna* suggests that the primary route of cercarial invasion is through the external body surface. It is also possible that some cercariae are transported by the ciliary activity of the gill surface, hence the tendency of metacercariae to accumulate at the anterior edge of the mantle. Some may even be ingested with the food, as suggested by Cheng, Shuster & Andersen (1966). The relatively large size of the metacercariae and the fact that they are actually embedded in the mantle suggests they may distort and compress adjacent tissues as well as distend and/or block various sinuses and ducts. Being an active growth phase in the life-cycle it also seems highly probable that these unencysted metacercariae directly ingest material from the host's tissues. This will undoubtedly disturb the host's physiology, particularly growth and reproductive processes.

The extent to which *Proctoeces* is likely to be a problem in *Perna* populations is clearly dependent on the infection level. At sites where the prevalence and intensity of infection is low the presence of this parasite may be of minimal significance. However, at heavily infected sites such as Dwesa and Hluleka the mussel populations may be severely stressed as a result of impaired growth and reproductive potential. Ironically both sites are nature reserve areas intended to provide some degree of protection to communities within their boundaries. The physiological effects of *Proctoeces* on *Perna* is therefore a matter of considerable concern, particularly in Transkei, where natural mussel stocks are subjected to intense exploitation by the indigenous coastal populace (Bigalke 1973; Siegfried, Hockey & Crowe 1985). Further studies may also be of benefit to entrepreneurs involved in the mariculture of *Perna*.

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