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POPULATION BIOLOGY OF A CESTODE, *PROTEOCEPHALUS FILICOLLIS* (RUDOLPHI) FROM *GASTEROSTEUS ACULEATUS* L. IN SCOTLAND

*Zafar Iqbal and Rod Wootten
Institute of Aquaculture, University of Stirling, FK9 4LA, Scotland, UK

ABSTRACT

Seasonal changes in the biology of *Proteocephalus filicollis* were investigated for 27 months in three-spined stickleback, *Gasterosteus aculeatus* from Airthrey Loch Scotland. A total of 1301 fishes were sampled and 1949 *P. filicollis* worms were extracted. *Proteocephalus filicollis* were abundant throughout the year as indicated by high prevalence (38.66%), mean intensity (3.87) and abundance (1.49). Monthly prevalence and abundance showed significant difference in two years. Growth and maturation of *P. filicollis* showed a marked seasonal cycle, as both of these were occurring in spring and summer. The monthly mean length of worm showed positive correlation with water temperature (Year I, r^2=93.1; Year II, r^2=77.9) but negative correlation with mean intensity (Year I, r^2 =30.7; Year II, r^2 =5.6). The recruitment of plerocercoid worms occur throughout the year. Four factors are proposed which influence the maturation of *P. filicollis*; rise in water temperature in summer, low mean intensity; host length and host endocrine system. The natural population of *P. filicollis* is generally high in Airthray Loch and is correlated to abiotic factors and eutrophic nature of the Loch.

Keywords: *Proteocephalus filicollis,* cestode, three-spined stickleback, infection, recruitment, growth maturation.

INTRODUCTION

Seasonal cycle of maturation, growth and recruitment has commonly been observed in species of *Proteocephalus* (Kennedy, 1977). *Proteocephalus filicollis* is a cestode parasite of *Gasterosteus aculeatus* (Willemese, 1969). Hopkins (1959), Chappall (1969) and Iqbal (1998) studied some aspects of biology and seasonal cycle of this parasite from *G. aculeatus. Proteocephalus filicollis* has two host life cycles, the intermediate host is a cyclope copepod, *Acanthocephalus robustus* and the final host is *G. aculeatus* (Iqbal and Wootten, 2001). *Proteocephalus filicollis* worms are recruited in summer and autumn grow throughout the year and shed eggs in spring and summer (Iqbal and Wootten, 2008a, b). Some of the studies on biology of genus *Proteocephalus* are by; Fischer and Freeman (1969), Kennedy and Hine (1969), Willemse (1969), Wootten (1974), Eure (1976), Hanzelova *et al*. (1990), Pertierra and Nunez (1990), Nie and Kennedy (1991), Ieshko and Anikieva (1992), Iqbal, (1998), Wilson and Camp Jr (2003), Gilliland and Muzzall (2004) and Maillo *et al*. (2005). The studies by Willemse (1969), Chappall (1969), Dartnall (1972) and Rodland (1979) have given a much diversified picture of infection and biology of *P. filicollis* in *G. aculeatus* from different localities in Britain and Europe. Although, there is some conflict concerning the seasonality of other members of genus *Proteocephalus*, but most authors observed that in temperate water, worms mature and shed eggs in spring and early summer and recruitment starts in summer and autumn. The aim of this study was to further look into the population biology of *P. filicollis* from a wild population of *G. aculeatus* and compare it with previous studies from Britain.

MATERIALS AND METHODS

The fish, *G. aculeatus* were collected with help of hand net on monthly basis (April 1993 to June 1995) from Airthrey Loch (situated within the grounds of University of Stirling, Scotland; Grid Reference 806965). Iqbal and Wootten (2004) have described the physicochemical and biological features of the Loch. The procedures of sampling, examination of fish and processing of parasites are given by Iqbal and Wootten (2005). *Proteocephalus filicollis* worms were identified according to Hopkins (1959). The worm samples are divided in to two populations as; Year I (July 1993- June 1994) and Year II (July 1994 to June 1995). The measurement of worms (total length) was taken from Mayer's paracarmine stained and mounted specimens. Each worm was assigned to one of the five groups according to their maturity state. Plerocerciforms: newly recruited worms, Immature: worms which started segmentation, Maturing: worm with developing genital structure, Mature: worms with developed genital structure, Gravid: worms containing eggs. Prevalence, abundance and mean intensity was followed after Margolis *et al*. (1982). Pearson correlation was applied to see the relationship in prevalence, mean intensity and abundance; monthly mean length, water

*Corresponding author present address: Department of Zoology, University of the Punjab, Quaid-E-Azam Campus, Lahore, Pakistan
Email: dr.zafariqbal.pu@gmail.com

temperature and mean intensity of *Protoecephalus filicollis*.

RESULTS

A total of 1301 *G. aculeatus* were examined, of which 503 fishes were infected with *P. filicollis.* Altogether, 1976 worms were recovered from rectum and various sections of the intestine of the fish. The prevalence of *P. filicollis* was 38.66%, mean intensity 3.87 and abundance 1.49. The monthly prevalence fluctuated over study period, which rose from July (Year 1) to October then falling and rising through November to January and declining gradually from February to June. In the Year II, the same pattern of prevalence was observed i.e. rising from July to October then falling and rising through November to February and declining in March and rising from April to May and falling in June (Fig.1A). Mean intensity increased from July (Year 1) to November and dropped from December until June. In the Year II, mean intensity rose from July to December and dropped from February until June (Fig.1B). The mean intensity observed in Year I, followed the same pattern in the Year II. The rise and fall of mean intensity almost followed the same pattern as exhibited by prevalence in both years. There was a significant difference in the monthly prevalence and abundance of *P. filicollis* in Year I and Year II (T =-7.04, df. 545 P= 0.000; Mean intensity T = -7.04, df. 565, P=0.000).

The seasonal prevalence and abundance of *P. filicollis* showed a clear pattern rising from summer (Year I) 23.4% through autumn (28.0%) to winter (36.4%) and then dropping from spring (31.0%) to summer (30.70%). The same pattern is observed in the Year II, prevalence and rising from autumn (56.6%) through winter (72.2%) and falling considerably from spring (62.2%) to summer (32.3%). Similarly, mean intensity showed the same pattern rising from summer (2.50) through autumn (3.76) to winter (3.17) and falling in spring (2.11). In Year II, mean intensity rose from summer (4.2) through autumn (4.41) to winter (5.36) and then falling in spring (4.58). The prevalence and mean intensity of *P. filicollis* was high in Year II generation (52.38%; 2.43) than in Year I generation (29.68%; 0.87).

Plerocerciform worms (total length 0.32 to < 1.0mm) were found throughout the year. In April and May 1993 these worms comprised < 18%, and were 100% in July and August (Year I) but dropped to 88.75% in September. However, from October to April (Year I) the population of these worms was <14% and these worms were not present in May and June. In Year II, *P. filicollis* exhibited a different cycle of recruitment. The recruitment started in July and continued in September. Small plerocerciform worms (<16%) were present from October to June. Thus, in Year I recruitment of new generation of *P. filicollis* occurred within two months of the loss of previous generation but in Year II there was some overlap of the two generations.

The growth of *P. filicollis* starts just after the recruitment in summer and continue over autumn. In winter growth slows down or stops. However, from spring the growth starts again and is accelerated from April to June (Year I). A similar pattern occurred in Year II, although the increase in length was slow over winter and subsequent increase in length was rapid. Monthly mean length of *P. filicollis* was more in Year I than in Year II population (Fig. 2). The monthly mean length (ML) of *P. filicollis* (January to June 1994 and 1995 (Year I and II) showed positive regression with water temperature. The regression equation for Mean length vs. Temperature for year I was: ML= 1.51+ 0.69Temp; (P= 0.002); (r^2=93.1) and for year II was: ML=0.96+0.58Temp; (P=0.020); (r^2=77.9). However, monthly mean length of *P. filicollis* (January to June 1994 and 1995 (Year I and II) showed negative regression with mean intensity (MI). The regression equations for mean length vs. Mean intensity for year I was: ML = 14.25 - 2.86 MI; (r^2 =30.7); (P= 0.254) and for year II; ML = 10.25 – 0.95 MI; (r^2 =5.6); (P=0.651).

Maturation of *P. filicollis* showed a marked seasonal pattern with bulk of population maturing in spring and early summer (Table 1). Occurrence of individual maturity stages of worm showed that immature (un-segmented) worms are present from July to May-June next year. Maturing (segmented) worms and mature worms (without eggs) were found from October to June. The maturing (segmented) worms comprise large population from April to June as compared to mature worms in the same period. Gravid worms were present from September to June in both years with some fluctuation in Year II. But these worms were always present from April to June.

DISCUSSION

This is another detailed investigation of population biology of *P. filicollis* in *G. aculeatus.* Prevalence of *P. filicollis* was high compared to earlier reports on this parasite. Low prevalence of *P. filicollis* i.e. 5% from *G. aculeatus* in Norway (Rodland, 1979) and high prevalence 40.2% in *G. aculeatus* in Netherlands (Willemse, 1969); 41% and 50% in *G. aculeatus* in Britain (Dartnall, 1972; Kenndy *et al*. (1992) has been observed. Mean intensity of *P. filicollis* was also high and it showed seasonal pattern of change. The high mean intensity in Year II generation may reflect high rate of recruitment. Population size of *P. filicollis* therefore, was high in this locality in *G. aculeatus.* The eutrophic nature of Airthray Loch and diversity of zooplankton in the loch (Iqbal and Wootten, 2004) may be suggested to increase

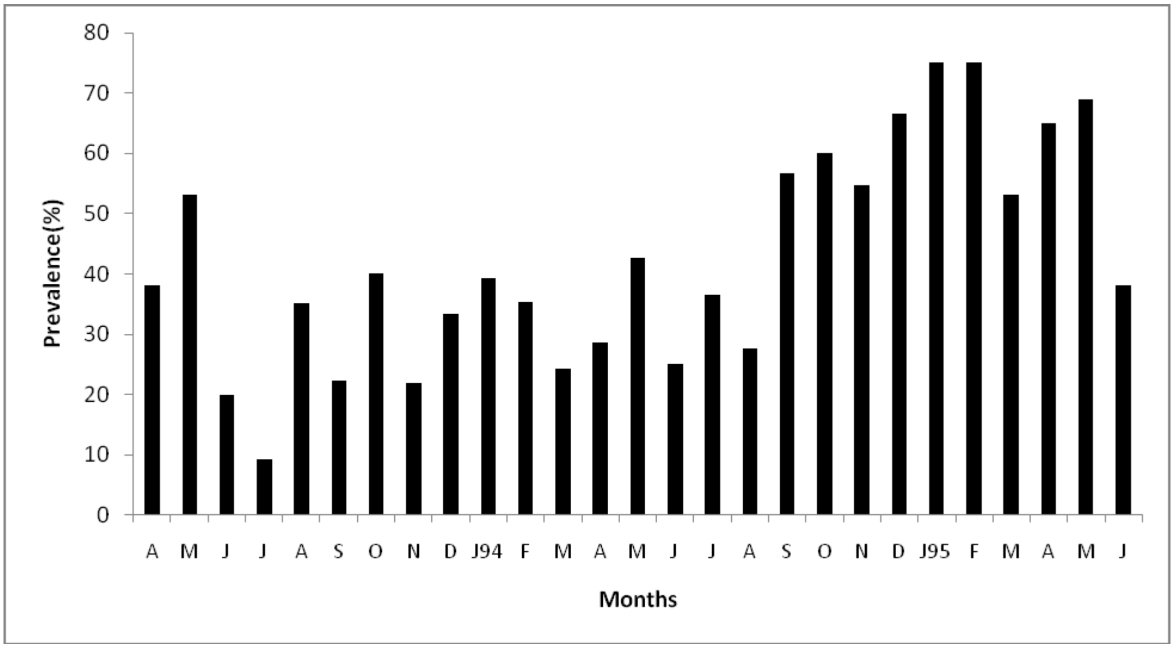

Fig.1A

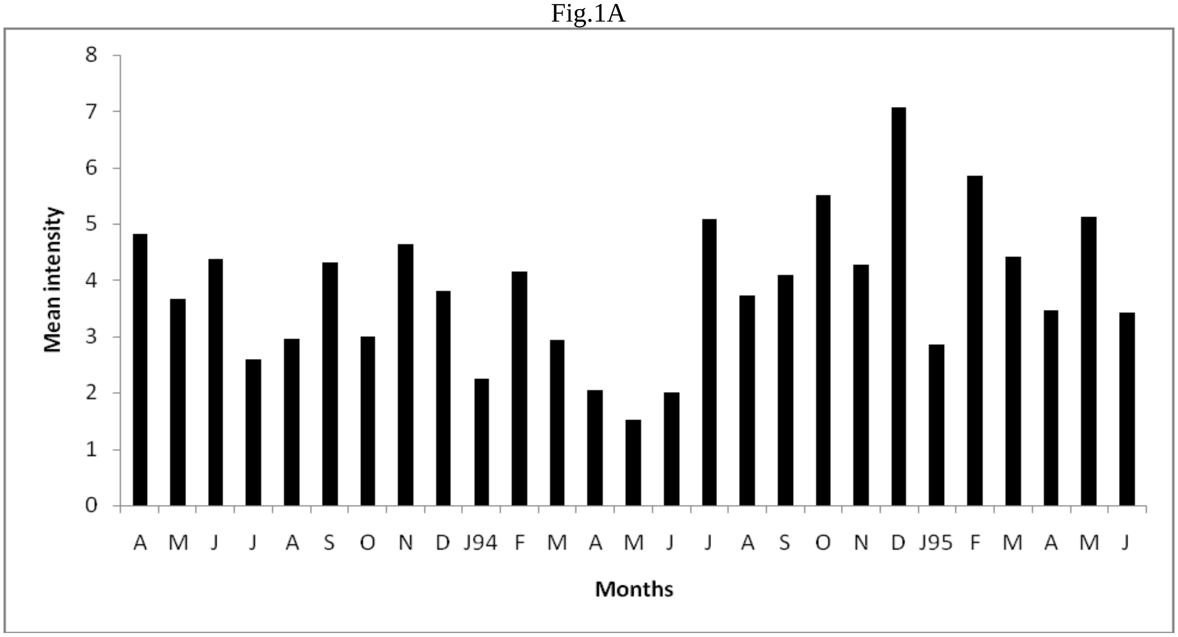

Fig. 1B

Fig.1. Monthly prevalence (1A) and mean intensity (1B) of *Proteocephalus filicollis* in *Gasterosteus aculeatus* from Airthrey Loch, Scotland.

the mean intensity. Moreover, the large population of infected copepod may have influenced the high transmission of *P. filicollis* in the final host. The high prevalence may be associated with warm late summer and autumn of Year I and Year II (Iqbal and Wootten, 2004). The high water temperature in Year I in Airthrey Loch may have operated by; 1) enhancing the feeding rate of *G. aculeatus*; 2) by favoring the establishment of worms in the fish; 3) providing higher biomass of zooplankton resulting in higher population of larval worms. The parasite populations fluctuate on year to year basis as reported by Kennedy (1996) and the transmission rate of a parasite may be determined by the size of parasite population (Nie and Kennedy, 1991). The composition and abundance of suitable intermediate host in a locality may contribute to the distribution and infection level of a parasite. This view is supported by studies on *Proteocephalus* sp. indicating that more than one species of Cyclops may act as intermediate host in these cestodes (Wootten, 1974; Iqbal and Wootten, 2001).

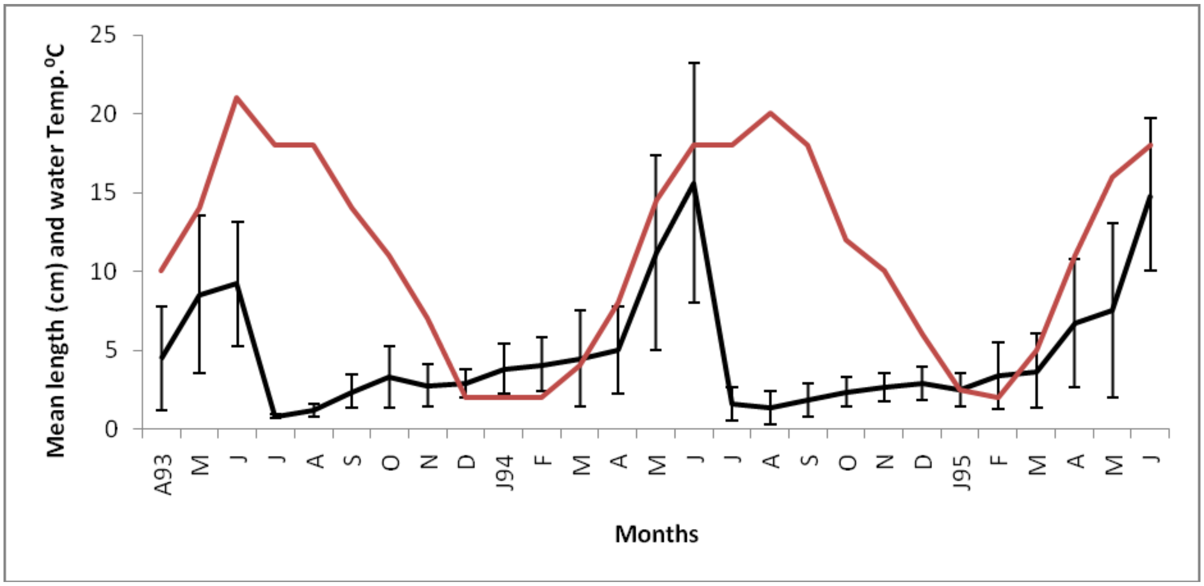

Fig. 2 Monthly mean length (with standard deviation) of *Proteocephalus filicollis* from *Gasterosteus aculeatus* and maximum water temperature of Airthrey Loch, Scotland.

Proteocephalus filicollis showed continuous growth throughout the year. Increase in monthly mean length was greater in spring and summer but not in winter. Hopkins (1959) suggested that growth and development of *P. filicollis* is checked at low temperature from autumn to spring. The time of occurrence of gravid worms, reported in present study and is rather intermediate between two extremes reported by Hopkins (1959) and Chappall (1969). The majority of worm population became gravid in spring and summer. The reason for the discrepancy between results of present study and two earlier studies may be associated with difference in environmental conditions and habitat from where the fish was collected. It is clear that *P. filicollis* has definite period of maximum reproduction in spring and summer which coincide with rise in water temperature. The reproduction of *P. filicollis* exhibits seasonal pattern, with egg production taking place mainly in spring and summer. This type of reproductive cycle has adaptive significance for parasites requiring an intermediate host, as it ensures that most eggs are produced and released at the time of maximum copepod population, (when large number of susceptible copepod are available for infection). The *P. filicollis* eggs are larger in winter and spring and smaller in summer. Moreover, the number of eggs is positively correlated to length of gravid worm (Iqbal and Wootten, 2008a, b). Hence, *P. filicollis* was similar to other species in this genus (Kennedy and Hine, 1969; Fischer and Freeman, 1969; Wootten, 1974) as it showed basic seasonal pattern in egg production.

The increase in water temperature in spring appears to be a major factor influencing growth and maturation of *P. filicollis*. Water temperature has been proposed as an explanation for seasonal maturation of *Proteocephalus* sp. in their host (Kennedy, 1977). Variations in mean length of *P. filicollis* indicated that the parasite grow throughout the year. However, growth is accelerated in spring and summer. There is also fall in mean intensity of infection during this period. The low mean intensity of infection may also reduce competition within the parasite infrapopulation at a time when metabolic requirement of individual cestode associated with growth and eggs production is presumably increasing. *Proteocephalus filicollis* is expelled from *G. aculeatus* after egg production. Temperature related rejection appears to be a possible cause of parasite mortality. When water temperature rises most of the parasites are lost from the host.

It is suggested that there may be four main factors, which influence the maturation of *P. filicollis* in *G. aculeatus* from Airthrey Loch; rise in water in spring and early summer, low mean intensity; host length and host endocrine system. The length range of various maturity stages of worms observed is comparable to previous studies (Hopkins, 1959; Chappell, 1969; Willemse, 1969). Recruitment of new generation of worms was at peak in summer. Recruitment has been reported to occur for various length of time during the year in different *Proteocephalus* species (Wootten, 1974; Eure, 1976; Nie and Kennedy, 1991; Ieshiko and Anikeva, 1992). The occurrence of gravid worms over autumn and winter months and the fact that these eggs are infective (Iqbal and Wootten, 2001) may indicate that some limited recruitment occur over this period. It is concluded that the population of *P. filicollis* was generally high in Airthrey Loch compared to earlier reports. The high prevalence of

Table 1. Maturity stages and mean length (mm) of *Proteocephalus filicollis* in *Gasterosteus aculeatus.*

Months	Immature worm			Maturing worms			Mature worms			Gravid worms		
	%	M.L	S.D	%	M.L	S.D	%	M.L	S.D	%	M.L	S.D
Apr. 93	36.3	2.6	±1,85	18.9	3.2	±0.52	25.9	5.0	±0.95	18.9	11.6	±2.39
May	18.2	2.1	±0.77	-	-	-	31.8	9.2	±1.72	5.0	10.6	±4.66
Jun.	05.7	3.4	±1.49	-	-	-	48.6	6.8	±1.23	45.7	12.4	±4.29
Jul.	100	0.6	±0.10	-	-	-	-	-	-	-	-	-
Aug	100	1.1	±0.47	-	-	-	-	-	-	-	-	-
Sept.	97.6	2.4	±1.10	-	-	-	-	-	-	2.4	4.0	-
Oct.	90.0	2.7	±0.89	1.3	2.4	-	2.6	5.0	-	5.1	8.2	±4.79
Nov.	96.1	2.4	±0.91	-	-	-	-	-	-	3.9	6.2	±0.06
Dec.	95.1	2.4	±0.86	3.3	3.2	±0.12	-	-	-	1.6	4.8	-
Jan.94	81.5	3.3	±1.28	1.9	3.7	-	9.2	4.0	±0.17	7.4	6.0	±1.12
Feb.	90	4.4	±0.25	2.0	5.7	-	4.0	8.1	-	4.0	8.0	-
Mar.	83.0	3.3	±1.28	7.5	8.5	±4.71	1.9	5.2	-	7.6	10.9	±4.7
Apr.	70.3	3.6	±1.60	18.9	5.4	±1.33	2.7	7.8	±460	8.1	9.3	±2.7
May	17.1	3.9	±1.70	14.3	6.2	±0.76	5.7	11.4	±4.60	62.9	13.8	±5.38
Jun.	-	-	-	20.0	6.2	±0.76	5.0	13.8	-	75.0	15.5	±8.06
Jul.	94.6	0.9	±0.37	5.4	3.3	-	-	-	-	-	-	-
Aug.	100	1.0	±0.55	-	-	-	-	-	-	-	-	-
Sept.	92.7	1.4	±0.69	1.6	2.4	-	-	-	-	5.7	5.0	±1.59
Oct.	95.5	2.30	±0.82	3.0	2.8	±0.49	-	-	-	1.5	3.6	-
Nov.	99.0	2.51	±1.04	-	-	-	-	-	-	1.0	4.0	-
Dec.	96.5	2.60	±0.90	3.5	3.9	±1.25	-	-	-	-	-	-
Jan.95	95.4	2.59	±1.28	2.3	3.2	-	2.3	9.8	-	-	-	-
Feb.	89.4	2.79	±1.12	4.9	5.6	±1.36	1.6	10.0	±8.32	4.1	9.1	±2.32
Mar.	77.3	2.69	±1.12	10.7	4.3	±1.34	2.7	7.9	±0.93	9.3	8.6	±0.85
Apr.	21.7	2.76	±1.40	44.4	6.7	±2.13	6.7	6.7	±3.99	26.7	9.9	±4.05
May	25.0	2.44	±1.46	32.9	6.1	±2.66	11.0	12.0	±5.39	31.1	11.3	±6.17
Jun.	15.3	1.91	±1.05	2.8	8.0	±2.92	16.7	12.7	±1.70	65.2	15.0	±4.56

P. filicollis is correlated to abiotic factors and eutrophic nature of the Loch.

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