Incidence and intensity of *Cyathocephalus truncatus* and *Schistocephalus solidus* infection in *Gasterosteus aculeatus*

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Cyathocephalus truncatus, a cestode usually found in salmonids, and plerocercoids of *Schistocephalus solidus* are reported from a population of *Gasterosteus aculeatus* on the Queen Charlotte Islands, British Columbia. Adult *C. truncatus* attached at the anterior of the intestine adjacent to the pyloric sphincter, whereas in salmonids the pyloric caeca is the usual attachment site. Mean intensities of infection for *C. truncatus* and *S. solidus* were 2.7 (maximum 26) and 3.4 (maximum 87), respectively, with intensities increasing in larger fish. The highest incidence of *C. truncatus* infection was from February to May (80%) and for *S. solidus*, from April to September (50%). Infection rates for *C. truncatus* during different seasons and among different length classes of fish were directly correlated with the relative abundance of amphipods (the intermediate hosts of *C. truncatus*) in the fish stomachs. Possible modification of host feeding behaviour is indicated by a relative increase in the consumption of amphipods by infected fish.

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Un cestode *Cyathocephalus truncatus*, ordinairement parasite des salmonidés, et des plerocercoïdes de *Schistocephalus solidus* ont été trouvés chez une population de *Gasterosteus aculeatus* des Iles de la Reine Charlotte, Colombie Britannique. Les adultes de *C. truncatus* se fixent à la partie antérieure de l'intestin, au voisinage du sphincter pylorique, alors que, chez les salmonidés, le cestode se fixe ordinairement sur les caecums pyloriques. Le nombre moyen de parasites par poisson est de 2,7 (maximum 26) dans le cas de *C. truncatus* et de 3,4 (maximum 87) dans le cas de *S. solidus*; les infections sont plus graves chez les gros poissons. Les infections par *C. truncatus* atteignent leur fréquence maximale de février à mai (80% des poissons) et celle de *S. solidus*, d'avril à septembre (50%). Les taux d'infection par *C. truncatus* sont reliés directement à l'abondance relative des amphipodes (hôtes intermédiaires de *C. truncatus*) dans l'estomac des poissons, en toutes saisons et chez toutes les classes de longueur des poissons. Il semble se produire une modification du comportement alimentaire de l'hôte, car les poissons infectés augmentent leur consommation relative d'amphipodes.

[Traduit par le journal]

Introduction

During a study of a morphologically divergent population of *Gasterosteus aculeatus* (three-spined stickleback) from the Queen Charlotte Islands, British Columbia (Reimchen 1980), fish were found to be infected with the cestodes *Cyathocephalus truncatus* and *Schistocephalus solidus*. Whereas *S. solidus* is a common parasite of *G. aculeatus* and has been widely studied (see Wootten 1976 for review), *C. truncatus* has been reported from gasterosteids only in one locality in Europe (Vik 1954) and one in western North America (Lester 1974). Usual hosts are much larger fish such as those of Salmonidae, Esocidae, Gadidae, and Percidae (Vik 1954; Ginetsinskaya 1958).

This paper, dealing principally with *C. truncatus*, describes seasonal and age differences in the incidence and intensity of infection in fish and considers the feeding habits of the fish with respect to infection rates. A subsequent paper will cover differential infection of the sexes and spine phenotypes.

Study area and methods

Descriptions of Boulton Lake and its biota and the collecting techniques used are described in Reimchen (1980). The lake (18 ha, maximum depth 4.5 m, pH 4.8) occurs in a low-lying area of *Sphagnum* bog and has an intermittent stream draining to marine waters. *Gasterosteus aculeatus* is the only fish species resident in the lake, and it is preyed on by odonate nymphs (*Aeshna*) and birds (including *Gavia immer*, *Podiceps* spp., *Lophodytes cucullatus*, and *Megaceryle alcyon*). Salmonids (*Salvelinus malma*) have been observed in the drainage creek and may gain access to the lake during high water in winter.

Fish used for parasite analysis were collected in 1970 (N = 792), 1976 (N = 1803), 1977 (N = 2326), 1978 (N = 1737), 1979 (N = 2257), and 1980 (N = 341). Those from 1970 and 1975 were examined only for the presence of *S. solidus*, whereas in the remaining samples, all *C. truncatus* and *S. solidus* were removed and counted. Some 150 *C. truncatus* were measured for total length and scored for numbers of reproductive sets. All *S. solidus* were measured for length.

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Since fish had been initially preserved in 50% formaldehyde, these lengths represent cestodes in a contracted condition.

Infection estimates were influenced by collecting techniques; significantly higher percentages of fish infected with *S. solidus* occurred in collections made with the fine-mesh beach seine than with minnow traps during the same period ($\bar{x}$ = 43% and 17% for seine and traps, respectively; $P = 0.04$, paired t-test). *Cyathocephalus truncatus* was underrepresented in the seine captures but the differences were not significant ($\bar{x}$ = 25 and 40 for seine and traps, respectively; $P = 0.14$, NS).

Stomach contents were examined in fish collected between 1976 and 1980. Relative abundance (absent, rare (< 20%), common (20–80%), and abundant (> 80%)) was visually estimated for Cladocera, Copepoda, Amphipoda (*Crangonyx* sp.), Odonata, Trichoptera, and Diptera, which are the major food taxa. In this article I deal principally with Amphipoda and Copepoda, as these are intermediate hosts of the parasites (Clarke 1954; Vik 1958).

During the examination of stomach contents, I observed that fish parasitized with *C. truncatus* appeared to contain a greater abundance of amphipods than did those of uninfected fish. Accordingly, the data were reanalyzed to allow a comparison between nonparasitized fish and those with light infection (one to three *C. truncatus*) and those with heavy infection (more than three *C. truncatus*); all fish with *S. solidus* were excluded. Next, I excluded *C. truncatus* infections and compared nonparasitized fish with those containing *S. solidus*. Since significant differences in the fish diet were detected for both species of parasites, general feeding habits were reexamined using only nonparasitized fish.

Results

Among adult fish (40–65 mm standard length), maximum incidence of infection ranged between years from 50 to 80% in *C. truncatus* and from 12 to 50% in *S. solidus*. Mean number of parasites per infected fish was 2.7 (maximum 26) and 3.4 (maximum 87), respectively, for the two species.

Cyathocephalus truncatus was firmly attached to the intestinal wall immediately behind the pyloric sphincter and was not observed in the coelom nor was it encysted. In heavy infections (> 10 worms) the parasites were occasionally observed throughout the intestinal tract, although attachment sites were anterior to the midintestinal region. Total length ranged from 3 to 16 mm ($\bar{x}$ = 8.7) and numbers of reproductive sets from 11 to 26 ($\bar{x}$ = 16.6).

Infection by *C. truncatus* was restricted to fish greater than 35 mm in length with the incidence increasing in larger fish, whereas *S. solidus* occurred in all except the smallest length group (< 15 mm) and reached a maximum in the 30- to 40-mm and 60- to 70-mm classes (Fig. 1). For each species, numbers of cestodes per infected fish increased in successive length classes (Fig. 2).

Seasonal abundance of the two cestodes was inversely related when assessed from minnow trap captures (Fig. 3). *Cyathocephalus truncatus*, absent during the summer months, was present from October to May, reaching

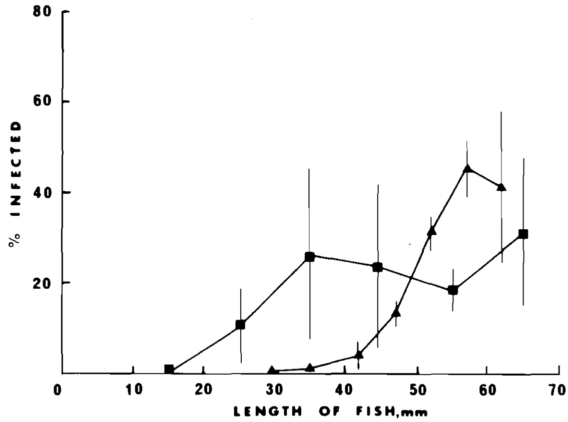

FIG. 1. Incidence of infection with *Cyathocephalus truncatus* and *Schistocephalus solidus* for length class of fish. Standard deviation (vertical line) represents variability in percent infected between years (1976–1980) for each length class. Sample sizes: 10–30 mm, N = 1351; 30–40 mm, N = 792; 40–50 mm, N = 2539; 50–60 mm, N = 2588; 60–70 mm, N = 88. ▲, *C. truncatus*; ■, *S. solidus*.

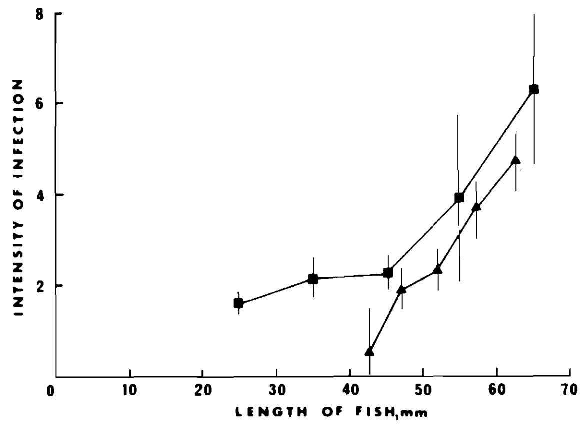

FIG. 2. Intensity of infection (number of worms per infected fish) with *Cyathocephalus truncatus* and *Schistocephalus solidus* for length class of fish. Sample sizes include all parasitized fish shown in Fig. 1. Vertical line, one standard deviation; ▲, *C. truncatus*; ■, *S. solidus*.

a maximum in February; *S. solidus* occurred throughout the year but was most abundant from July to October. Inclusion of the data from seine captures shows *S. solidus* also prevalent from March to May when it was uncommon in minnow traps. Numbers of cestodes per infected fish (data not shown) were highest during the maximum incidence of infection.

The diet of *G. aculeatus* included dipterans and trichopterans (71.5% of the stomachs), cladocerans (40.2%), amphipods (3.8%), and copepods (1.4%). Amphipods (intermediate hosts of *C. truncatus*) were absent in fish less than 30 mm but became more

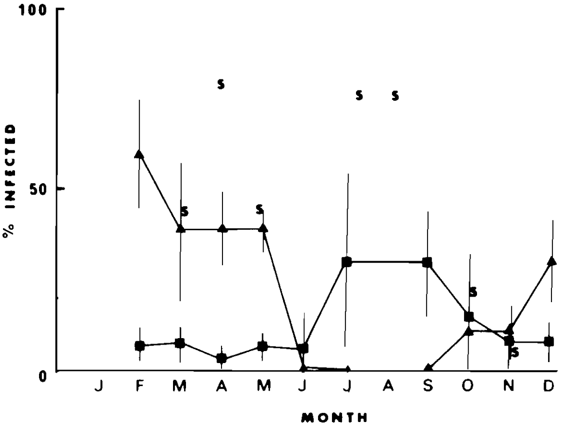

FIG. 3. Incidence of infection with cestodes at monthly intervals. Sample sizes for *Cyathocephalus truncatus* (▲): J, $N = 0$; F, $N = 87$; M, $N = 420$; A, $N = 519$; M, $N = 433$; J, $N = 16$; J, $N = 284$; A, $N = 844$; S, $N = 183$; O, $N = 733$; N, $N = 731$; D, $N = 146$. Sample sizes for *Schistocephalus solidus* (■): J, $N = 0$; F, $N = 97$; M, $N = 592$; A, $N = 695$; M, $N = 671$; J, $N = 74$; J, $N = 893$; A, $N = 2025$; S, $N = 752$; O, $N = 903$; N, $N = 934$; D, $N = 147$. Continuous lines show data for minnow traps only while *S* shows incidence of *S. solidus* in fish captured by seine from similar regions of the lake. Sample sizes for *S* range from 100 to 200 fish. For *C. truncatus*, fish less than 40 mm were excluded and for *S. solidus*, all length classes were included.

abundant in progressively larger fish, whereas copepods (first intermediate hosts of *S. solidus*) were uncommon in all length classes (Fig. 4). Seasonal effects were also evident; amphipods were infrequent (<5% of the stomachs) during summer months, thereafter increasing through winter, reaching a maximum (20%) in April (Fig. 5). Although copepods showed no major seasonal variation, other zooplankton such as cladocerans were

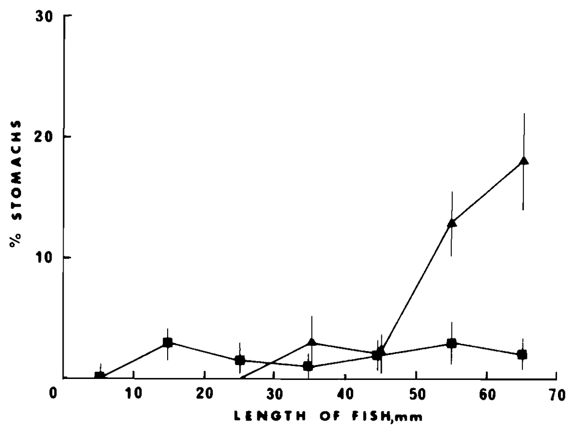

FIG. 4. Occurrence of amphipods and copepods in relation to length of fish. For sample sizes, see Fig. 1 (data restricted to nonparasitized fish). Vertical line, 1 SD; ▲, amphipods; ■, copepods.

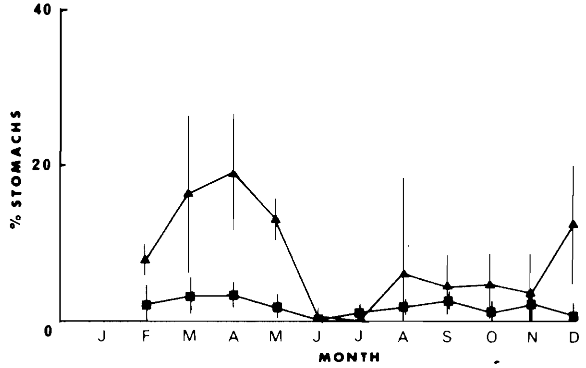

FIG. 5. Occurence of amphipods and copepods in fish at monthly intervals. For sample sizes, see Fig. 3 (data restricted to nonparasitized fish). Vertical line, 1 SD; ▲, amphipods; ■, copepods.

approximately twice as frequent in the diet during summer than during winter months (unpresented data).

Comparison of the stomach contents of parasitized and nonparasitized fish shows differences in the proportion of prey. For fish collected in winter, amphipods occurred in 6.6% of the stomachs of nonparasitized fish, in 24.9% of the fish containing one to three *C. truncatus*, and in 36.2% of the fish with more than three *C. truncatus*. This difference was significant ($P < 0.001$, χ^2) and occurred during each of the 4 years examined (Table 1). There was no increase in amphipod consumption among fish infected with *S. solidus*, and during 1 year a significant deficiency occurred.

Discussion

Cyathocephalus truncatus is circumboreal in distribution and has been reported from Siberia (Shulman 1958), northern Europe (Vik 1954; Halvorsen and MacDonald 1972), the northern slopes of Canada and Alaska (Mudry and McCart 1976), and as far south as Michigan (Amin 1977) and Washington (Mamer 1978). In British Columbia, the species appears to be uncommon. It was undetected in an early survey of cestodes from the region (Wardle 1932), but was recently found in two localities in the southern part of the province (Bangham and Adams 1954; Lester 1974). The species could have been overlooked in some of these areas since collections were made primarily in summer, a season when the cestode may be absent from the fish, as shown in this study. It is not restricted to the population in the present study but has been found in 13 of 34 *G. aculeatus* populations on the Queen Charlotte Islands (unpublished data).

Definitive hosts for *C. truncatus* are normally Salmonidae, Thymallidae, Esocidae, and Percidae (Ginetsinskaya 1958), and less frequently Gadidae (Vik 1954) and Cottidae (Bangham and Adams 1954). In North America, the cestode has been reported from *Coregonus*

TABLE 1. Occurrence of Amphipoda in stomachs of nonparasitized and parasitized fish

Year	Amphipods in stomachs	Numbers of *C. truncatus* 0	1–3	>3		*S. solidus* Absent	Present	
1976–77	Absent	622	159	21	***	622	24	NS
	Present	23	19	13		23	2	
1977–78	Absent	627	86	30	***	627	102	NS
	Present	48	29	10		48	4	
1978–79	Absent	380	150	37	***	380	142	***
	Present	54	52	8		54	1	
1979–80	Absent	586	102	6	***	586	31	NS
	Present	21	24	3		21	0	

NOTE: Data excludes summer samples, multiple-species infections and fish less than 40 mm. Chi-squared tests give probabilities of $P < 0.001$ (***) and $P > 0.1$ (NS). When expected values were less than 5, Fisher's exact probability was calculated.

clupeaformis by Cooper (1918), from *Salvelinus malma* by Wardle (1932), from *S. alpinus* by Mudry and McCart (1976), from *Salmo clarkii* by Mamer (1978), from *Cottus asper* by Bangham and Adams (1954), and from *C. cognatus* by Amin (1977). The two records of the parasite in *Gasterosteus* include Vik (1954) in Norway and Lester (1974) in southern British Columbia. Vik (1954), in an examination of the pseudophyllidean cestodes of northern Europe, concluded that *G. aculeatus* did not act as a host for *C. truncatus*. In the populations he examined, amphipods were not a food item of the stickleback and, during experimental observations, the fish would not consume these relatively large prey.

The presence of attached adult *C. truncatus*, the high infection incidence (80%) and intensity (maximum 25), its regularity in seasonal abundance and annual occurrence indicate that *G. aculeatus* can act as a normal host for this species. Although the sticklebacks are small, they contain an intensity of infection similar to that of larger hosts such as *Salmo trutta* (Vik 1958). However, maximum intensities are much lower in the smaller fish (26 vs. 200). Presumably, this is, in part, attributable to the absence of pyloric caeca in *G. aculeatus* which in salmonids are numerous and represent the major attachment sites for *C. truncatus*. Average length of *C. truncatus* and numbers of reproductive sets in this population are lower than those reported for European populations, but comparable to those from eastern North American hosts (Wardle 1932; Amin 1977).

Although fish size and seasonal differences in the diet were correlated with the rate of infection, the frequency with which infected amphipods are consumed may be influenced also by induced modifications of host behaviour. For example, *Gammarus lacustris* infected with *Polymorphous paradoxus* are positively phototactic, which increases the probability of predation by surface-feeding ducks, the definitive host (Bethel and Holmes 1977). In *G. aculeatus*, there were differences in the stomach contents between parasitized and nonparasitized fish, suggesting a difference in the feeding preferences or habitat. The number of stomachs containing amphipods was significantly greater in fish with *C. truncatus*, and this was most expressed in heavily infected fish. The excess of amphipods cannot be satisfactorily explained as a consequence of increased energy demands, since fish infected with *S. solidus*, which exerts major energetic loads on the host (Arme and Owen 1967; Lester 1971), showed no increase in the food item. If the behaviour of the host has been modified by the parasite, it is unlikely that the behaviour would involve a preference for additional amphipods, as this would lead to multiple infections, which are injurious to the host as well as the parasite (Vik 1954, 1958). Feeding differences could be explained if infected fish preferred sheltered regions such as benthic or vegetated areas. Indirect evidence for this occurs in *Salmo trutta*, with infected fish being more frequent in benthic than in surface habitats (Vik 1958). In principle, such a behaviour would be an adaptive host response for the parasite, since predation by piscivorous birds would be reduced and, as well, greater spatial overlap would occur between the eggs of *C. truncatus* and the intermediate hosts, which are prevalent in benthic and vegetated areas. Conversely, fish infected with *S. solidus* are known to prefer surface water, which facilitates transmission of the cestode to piscivorous birds (Lester 1971).

Cyathocephalus truncatus has attracted attention because of its pathogenicity in salmonid hosts; cyathocephalosis is characterized by body lesions and emaciation which can result in host mortality (Vik 1954; Petrushevski and Shulman 1958; Amin 1977). In exceptional cases, a single infection can cause death in small salmonids (Vik 1954). Numerous species of fish are used in transplantation or stocking programs and, accordingly, there have been attempts to restrict the spread of the cestode by utilizing source populations that are free of the parasite (Vik 1958; Amin 1978). Since *G. aculeatus* has not been previously recognized as a normal host for *C. truncatus*, and yet in both Europe and North America is widely introduced into lakes and ponds, the possibility exists for inadvertent spread of the cestode and for confusion in biogeographical interpretations.

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