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TRIAENOPHORUS NODULOSUS AND T. CRASSUS IN FISH FROM NORTHERN FINLAND

VALTONEN E. T., RINTAMÄKI P.[1] and LAPPALAINEN M.[1]

Department of Biology, University of Jyväskylä, Jyväskylä and [1]Department of Zoology and Oulanka Biological Station, University of Oulu, Oulu, Finland

Abstract. 10,288 fish specimens of 34 species from three water bodies in northern Finland were studied mainly in 1978–1982 *Triaenophorus nodulosus* and *T. crassus* parasites. Six of the 31 species from the Bothnian Bay were found to harbour *T. nodulosus* plerocercoids, four of the 11 from the cold, oligotrophic Lake Yli-Kitka in northeastern Finland and only one of the 6 from the small, eutrophic Lake Kuivasjärvi. The ruff (*Gymnocephalus cernuus*) was most essential intermediate host in the lakes, as supported by stomach analysis of predator fish. Although the highest prevalences were found in adult burbot (*Lota lota*) in two of the areas, these fish are more likely a blind end in the life cycle of *T. nodulosus* in the present case. *T. crassus* larvae were found only in three coregonid species and once in the intestine of a lamprey (*Lampetra fluviatilis*) from the sea. Neither the prevalence nor the intensity of infection in most of the intermediate fish hosts of *T. nodulosus* was seen to increase with the length of the fish. The only exception was the ruff in Lake Yli-Kitka, where a sharp increase was encountered. No prominent seasonal variation in *Triaenophorus* larvae infections was found in any of the cases. The prevalence of *T. nodulosus* infection in its final host, the pike (*Esox lucius*), was highest in the sea (93 %) and lowest in the eutrophic lake (47 %). Seasonally, the lowest *T. nodulosus* infections were found in June–July in the two lakes. A clear maturation cycle was also found, with the youngest worms in the summer months in all cases. *T. crassus* was found in every third pike in the sea and its proportion in relation to *T. nodulosus* is higher in the smallest and largest fish. In only 12 % of the pikes did the number of *T. crassus* exceed that of *T. nodulosus*, however, the mean ratio being 1 : 13 to favour of *T. nodulosus*. The results give an indication that the composition of the fish fauna in each water body has a considerable influence on the *T. nodulosus* burden and its distribution among its potential intermediate fish hosts. With the most stable environmental conditions and the greatest variety of fish species, the parasite burden in the Bothnian Bay is most evenly distributed among the 6 intermediate hosts. The fewer fish species occur in the water body, as in the present eutrophic lake, the more the significance of a few or even one intermediate host will increase.

Triaenophorus nodulosus (Pallas, 1781) and *T. crasus* Forel, 1868 are widely distributed in fish in the northern hemisphere. According to reviews by Lawler and Scott (1954), Michajlow (1962) and Kuperman (1973a), about 85 fish species may act as a second intermediate host for *T. nodulosus* and about 35 species for *T. crassus*. The pike is the definite host (Miller 1943, Copland 1956, Vik 1959, Chubb 1963, Lawler (1969). Many separate description of the occurrence and seasonality of *Triaenophorus* spp. larvae and adults have been published (Miller 1943, 1945a and b, Copland 1956, Vik 1959, Chubb 1963 and 1964, Borgström 1970, Pronin 1975). It has been suggested by Ieshko (pers. comm.) that the composition of the fish fauna in each ecosystem and also the age (size) structures of the fish populations may have an influence on the prevalences and intensities of *Triaenophorus* infections. An attempt is made here to explain this aspect in addition to supplying basic data on the occurrence of *Triaenophorus* species in the fish of three water bodies differing in size, limnological nature and fish species composition in northern Finland.

STUDY AREAS, MATERIALS AND METHODS

A total of 10,288 fish of 34 fish species from three water bodies in northern Finland (Table 1) were studied for *Triaenophorus* species, mainly between 1978 and 1982 (Fig. 1). The most northerly

Table 1. Fish fauna studied in three water-bodies in northern Finland. The occurrence of *Triaenophorus nodulosus* (○, ●) and *T. crassus* (△, ▲) is shown in the columns A—D. Open symbols indicate larvae and black symbols adult worms

		Bothnian Bay no. of fish	A	B	C	D	Lake Yli-Kitka no. of fish	A	B	C	D	Lake Kuivasjärvi no. of fish	A	B	C	D
1. FRESHWATER SPECIES																
Esox lucius L.	pike	84				●	61				●	114				●
Coregonus albula L.	vendace	342			△		380									
C. widegreni Malmgren	sea-spawnig whitefish	*1,164			△											
C. acronius Rapp							445									
C. pallasi Valenciennes							28									
Osmerus eperlanus (L.)	smelt	772		○												
Alburnus alburnus (L.)	bleak	42														
Carassius carassius (L.)	Crucian carp	7										33				
Leuciscus idus (L.)	ide	28														
L. leuciscus L.	dace	67														
Phoxinus phoxinus (L.)	minnow	172					104									
Rutilus rutilus (L.)	roach	263					237					218				
Lota lota (L.)	burbot	106		○			39		○							
Gasterosteus aculeatus L.	three-spined stickleback	1,092		○												
Pungitius pungitius (L.)	ten-spined stickleback	328		○			90		○							
Myoxocephalus quadricornis (L.)	fourhorn sculpin	293														
Gymnocephalus cernuus (L.)	ruff	713		○			307		○			92		○		
Perca fluviatilis (L.)	perch	311		○			212		○			292				
2. MARINE SPECIES																
Clupea harengus L.	Baltic herring	1,212														
Zoarces viviparus L.	eelpout	65														
Myoxocephalus scorpius (L.)	bull-rout	30														
Ammodytes tobianus L.	sandeel	172														
Pomatoschistus minutus (Pallas)	sand goby	28														
4. IMMIGRATING SPECIES																
Gadus morhua L.	cod	15														
4. MIGRATING SPECIES																
Lampetra fluviatilis (L.)	lamprey	50			△											
C. lavaretus (L.)	river-spawnig whitefish	**146			△											
Salmo salar L.	Atlantic salmon	21														
S. trutta L.***	sea trout	55					41									
ACCIDENTAL SPECIES																
Abramis brama (L.)	bream	2														
Liparis liparis (L.)	common sea snail	2														
Platichthys flesus (L.)	European flounder	3														
Acipenser sturio L.	sturgeon	2														
Anguilla anguilla (L.)	European eel.	2														
C. peled (Gmelin)												6				

* Muscles were studied from 126 fish.
** Muscles were studied from 9 fish.
*** *S. trutta* m. lacustris in lake.

study area, Lake Yli-Kitka, forms part of the large Lake Kitkajärvi complex which is the tenth largest lake in Finland (295 km²). It is oligotrophic and still in a natural state, with at least 15 freshwater fish species occurring in appreciable numbers (Hyytinen 1985). The vendace (*Coregonus albula* L.) is the most abundant and most important fish species, and is known for its very small size in this lake (Table 2). Among the cyprinids, only the bream (*Abramis brama* (L.)), ide (*Leuciscus idus* (L.)), minnow (*Phoxinus phoxinus* (L.)) and roach (*Rutilus rutilus* (L.)) are found in the area. The water is cold and may be covered by ice for as much as 7—8 months a year. The water of Lake Yli-Kitka flows eastwards to the White Sea.

Lake Kuivasjärvi is located within the city of Oulu, beside the Bothnian Bay. It is a small (0.81 km²), shallow (max. depth 3.0 m), eutrophic or almost hypereutrophic lake (Myllymaa 1982). In late winter or spring when the lake is still covered by ice, fish mortality can be high due to oxygen deficiency. This has resulted in a limited number of fish species in the lake, the more abundant ones being the pike (*Esox lucius* L.), perch (*Perca fluviatilis* (L.)), roach, ruff (*Gymnocephalus cernuus* (L.)) and Crucian carp (*Carassius carassius* (L.)). Recruitment of fish from the sea is known to occur during spawning in spring.

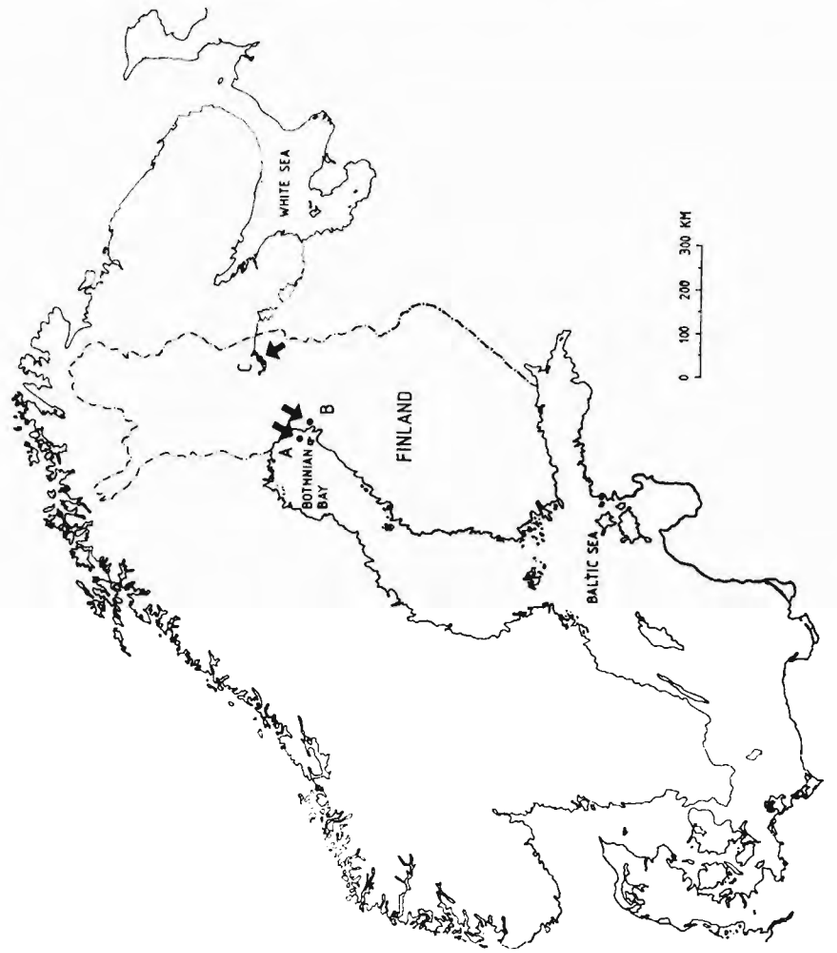


Fig. 1. Map of the areas studied in northern Finland. A) Bothnian Bay, B) Lake Kuivasjärvi, C) Lake Yli-Kitka.

The Bothnian Bay is the northernmost part of the Baltic Sea, with a salinity of about 0.2—0.3 ‰ in the area studied here, which is covered by ice for half of the year, on average from 15th November to 15th May. The Baltic Sea has a complex history (see Voipio 1981), and this together with the decrease in salinity from the Baltic proper towards the heads of its gulfs has influenced the fish fauna of the area studied here. Although Andreasson and Petersson (1982) list 69 fish species found in the Gulf of Bothnia, only 32 species occur fairly commonly in the northeastern Bothnian Bay, excluding accidental visitors. 17 of these are freshwater species, 8 marine and 7 migrating (Andreasson and Petersson 1982, Valtonen 1983).

Table 2. Average sizes ($\bar{x}$, mm) of pike and fish species which serve as second intermediate hosts for the two *Triaenophorus* species in three areas of northern Finland

	Bothnian Bay no. of		Lake Yli-Kitka no. of		Lake Kuivasjärvi no. of	
	fish	$\bar{x}$ (mm)	fish	$\bar{x}$ (mm)	fish	$\bar{x}$ (mm)
Esox lucius	84	482	61	315	114	398
C. albula	342	169	380	97	—	
Coregonus lavaretus	206	328	—		—	
C. widegreni	1,164	208	—		—	
C. acronius	—		445	176	—	
Osmerus eperlanus	772	154	—		—	
Lota lota	106	487	39	413	—	
Gasterosteus aculeatus	1,092	67	—		—	
Pungitius pungitius	328	48	90	35	—	
Gymnocephalus cernuus	713	131	307	93	92	114
Perca fluviatilis	311	188	212	111	292	166

The present material from the Bothnian Bay and Lake Yli-Kitka reflects roughly the proportions of each fish species in the catches of the local fishermen, monthly or bimonthly samples of about 20—30 specimens of the most common fish species having been collected throughout the year using seine nets in Lake Yli-Kitka and in the Bothnian Bay during the period of ice cover. The sea samples for the open water period were caught using trawl of fyke nets. The samples from Lake Kuivasjärvi were caught with gill-nets. The body cavities, including inner organs as liver and intestine of 7,589 fish and muscles of 6,414 fish from the Bothnian Bay representing 31 species were studied for *Triaenophorus* species (for catching methods and dates, see also Valtonen 1983), 755 fish of 6 species from Lake Kuivasjärvi and 1,944 fish of 11 species from Lake Yli-Kitka (Table 1).

In order to assess the proportion of *Triaenophorus* spp. fish intermediate hosts in the diet of the pike, burbot (*Lota lota* (L.)), ruff and perch, the fullness of the stomachs of fish from the three areas was studied and the fish species in their diet were identified whenever possible.

RESULTS

Both *T. nodulosus* and *T. crassus* were found in the Bothnian Bay area but only *T. nodulosus* in Lake Yli-Kitka. In the eutrophic Lake Kuivasjärvi *T. nodulosus* was the main species and *T. crassus* occurred only accidentally. Six fish species among the 31 studied in the Bothnian Bay area were found to be infected with *T. nodulosus* larvae, with the highest prevalence of infection in burbot (50 %), where the intensity of infection was also highest. Among the non-predatory fish of the sea, the ruff and three-spined stickleback (*Gasterosteus aculeatus* L.) were the most heavily parasitized (Table 3). In Lake Yli-Kitka every burbot was infected with *T. nodulosus* larvae, this species again having the highest intensity of infection (11.9 worms per fish). In this lake, as also in Lake Kuivasjärvi, the ruff was an important second intermediate host for *T. nodulosus*, with 36 % and 55 % prevalences of infection, respectively. The intensity of infection was much lower than that found in the Lake Yli-Kitka burbot. The definitive host, the pike, was found to be infected most often in the Bothnian Bay, with a 93 % prevalence and an intensity of infection of 15 worms per fish, while both values were lower in the two lakes (Table 3).

A *T. crassus* larva was found once in the intestine of a sea lamprey (*Lampetra fluviatilis* (L.)) and once among the 9 river-spawning whitefish (*C. lavaretus* (L.)) of the Bothnian Bay. The prevalence of infection in the sea spawning whitefish (*C. widegreni*, Malmgren, 1863; syn. *C. nasus* (Pallas) sensu Svärdson) was 11 % (Table 3). *T. crassus* was not found in the few whitefish specimens (*C. peled* (Gmelin)) studied from Lake Kuivasjärvi evidently because there is no real whitefish or vendace population in the lake. Some *C. peled* had been accidentally introduced into the lake in the year concerned. *T. crassus* was less common than *T. nodulosus* in the pikes of the Bothnian Bay, only every third pike being infected. The proportion of specimens was 1 : 13. 4 in favour of *T. nodulosus* and in only 12 % of pikes were there *T. crassus* specimens in the majority.

TRIAENOPHORUS INFECTION BY LENGTH OF FISH

Intermediate fish host

In most cases neither the prevalences nor the intensity of *T. nodulosus* infection varied according to the length of the intermediate fish hosts in the Bothnian Bay. As far as the ten-spined stickleback (*Pungitius pungitius* (L.)), smelt (*Osmerus eperlanus* (L.)), vendace and three-spined sticleback were concerned, it was only in the last case that there was a slight increase with increasing length of fish, the prevalence in the largest fish ($\geqq$ 80 mm) being 14 %. In all the other cases it varied randomly below or around 10 % in all the size classes. The prevalence of *T. nodulosus* larvae infection in the perch of the Bothnian Bay was only accidental, and no infected perch were found in Lake Kuivasjärvi. No variation in *T. nodulosus* infection with the length of the perch was found in Lake Yli-Kitka, nor was any variation found in the prevalence of infection in the burbot in either the Bothnian Bay or Lake Yli-Kitka, although some increase in the intensity of infection in fish longer than 360 mm occurred in the lake (Fig. 2).

The only peculiar difference was seen between the Bothnian Bay and Lake Yli-Kitka in the infection of the ruff by *T. nodulosus*. In the Bothnian Bay neither the prevalence nor the intensity of infection varied significantly according to the length of the fish, the prevalence values being around 10 % in most cases, whereas in Lake Yli-Kitka there was a clear increase in the prevalence with increasing length of fish except in fish larger than 110 mm, when the figure remained quite even (Fig. 3). The ruff of Lake Kuivasjärvi had quite an even prevalence of infection which varied between 50 and 70 %.

Definitive host

The prevalences of *T. nodulosus* infection were lowest in the smallest size classes of pike in each study area (Fig. 4). 23 % of the pikes smaller than 260 mm (n = 13) were infected in Lake Yli-Kitka, although later on the prevalence of infection had similar patterns as in the Bothnian Bay, the prevalence increasing to 100 % in the Bothnian Bay and to more than 90 % in Lake Yli-Kitka in subsequent size classes. In contrast, prevalence values in the older pikes in Lake Kuivasjärvi varied between 33 and 48 % (Fig. 4). The prevalence of *T. crassus* in different size-classes of pike from the Bothnian Bay may also be seen in Fig. 4. It is interesting to note that the prevalence of the two *Triaenophorus* species is equal in the smallest fish, but that of *T. crassus* increases only in the largest size-class.

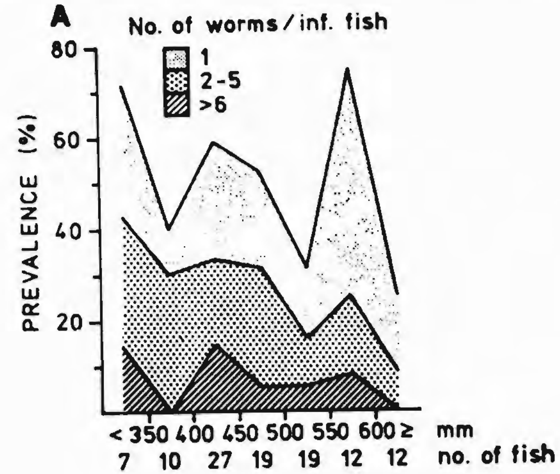
Table 3. Occurrence of *Triaenophorus nodulosus* (a) and *T. crassus* (b) in fish from three areas of northern Finland

	Bothnian Bay					Lake Yli-Kitka					Lake Kuivasjärvi				
	no. of fish	%	$\bar{x}$/fish	S. D.	max	no. of fish	%	$\bar{x}$/fish	S. D.	max	no. of fish	%	$\bar{x}$/fish	S. D.	max
a) *Osmerus eperlanus*	772	1.7	0.02	0.14	2	—					—				
Lota lota	106	50.0	1.5	2.6	16	39	100.0	11.9	6.9	33	—				
Gasterosteus aculeatus	1,092	7.2	0.11	0.64	12	—					—				
Pungitius pungitius	328	2.1	0.02	0.15	1	90	1.1	0.01	0.11	1	—				
Gymnocephalus cernuus	713	10.8	0.12	0.38	3	307	36.2	1.1	2.3	22	92	55.4	0.9	1.3	8
Perca fluviatilis	311	1.0	0.01	0.10	1	212	7.1	0.1	9.22	2	292	—			
**Esox lucius*	84	92.9	14.5	17.2	86	61	63.3	7.6	8.4	44	114	47.4	2.1	4.8	35
b) *Coregonus lavaretus*	9	22.2	0.22	—	1**	—					—				
C. widegreni	126	11.1	0.14	0.41	2***	—					—				
C. albula	342	8.2	0.09	0.33	2	380	—				—				
Lampetra fluviatilis	50	2.0	0.02	—	1										
**Esox lucius*	84	29.8	1.1	2.2	12	61	—				114	0.9	0.01	0.09	1

* adult stage of *Triaenophorus* spp.
** see also Fagerholm and Valtonen 1980
*** see also Valtonen and Valtonen 1980

Intermediate fish host

No seasonal variation was found in the prevalences of *T. nodulosus* larvae infection in ruff from the Bothnian Bay during the two years studied. Among the 23 monthly or bimonthly samples (18 samples in 1977—1978, two in 1979 and three in 1980) the prevalences variated between 5 and 23 % in 17 cases. The highest value, 28 %, was found in July 1978. In the case of Lake Kuivasjärvi the highest prevalence values



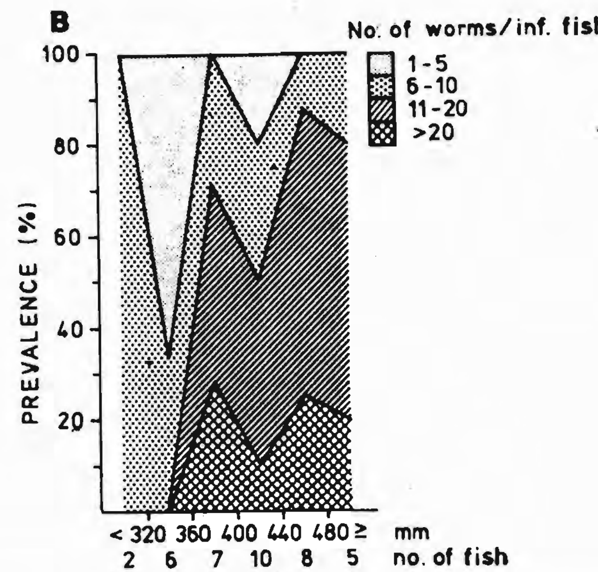


Fig. 2. Prevalence (%) and mean intensity of *Triaenophorus nodulosus* plerocrecoid infection in the burbot (*Lota lota*) in the Bothnian Bay (A) and Lake Yli-Kitka (B) according to size-classes of fish.

were found in July—September in 1979 and 1980, when 92 % and 63 % of the ruff studied were infected, and the lowest, 38 and 30 %, in March and October 1980, respectively. Lake Yli-Kitka was the only area where some seasonal variation in *T. nodulosus* infection was found in the ruff, with the highest values occurring in April and May 1980 (Fig. 5).

As far as the other more relatively heavily infected fish species were concerned, no seasonal variation was found in either the smelt or the three-spined stickleback from the Bothnian Bay. The prevalence of *T. nodulosus* larvae infection in the smelt was under 7 % in the 25 samples obtained from July 1977 to December 1979. In the case of three-spined stickleback some increase in the prevalence values was found towards the end of the year in 1977 and 1978 (Fig. 6).

The prevalence of *T. nodulosus* infection in the burbot of the Bothnian Bay during the period December 1977—December 1978, when 86 specimens out of the total 106 fish were studied, varied from 36 % in December 1977—February 1978 to the highest recorded, 92 %, in September—October 1978, followed by a decline to 44 % in November—December 1978. The highest mean intensity of 4.5 worms per infected fish was also found during September—October 1978. There were also three occasions when one *T. nodulosus* larva was found in the intestine of a burbot, twice in January and once in December 1978.

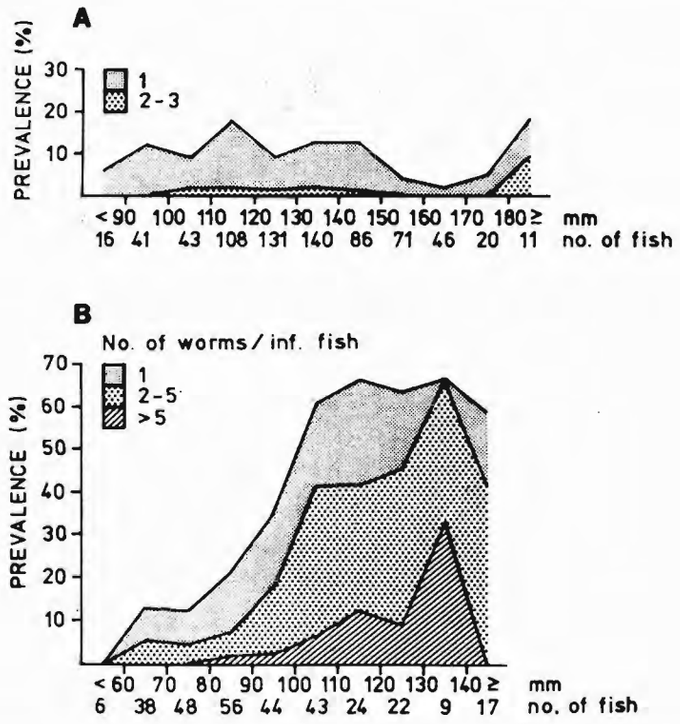


Fig. 3. Prevalence (%) and mean intensity of *Triaenophorus nodulosus* plerocercoid infection in the ruff (*Gymnocephalus cernuus*) in the Bothnian Bay (A) and Lake Yli-Kitka (B) according to size-classes of fish.

T. crassus was found consistently only in the Bothnian Bay, where its occurrence in the two sympatric whitefish species has been documented earlier by Valtonen and Valtonen (1980) and Fagerholm and Valtonen (1980). No seasonal or size-bound variation was found in the sea-spawning whitefish (*C. widegreni*). *T. crassus* was found quite evenly in the muscles of the vendace of the Bothnian Bay without any seasonal variation. The prevalence of infection was between 5 and 16 % in 8 out of the 12 samples collected in 1977 and 1978, and only in December 1978 was a higher prevalence value found (25 %). The *T. crassus* plerocercoid was found in the intestine of a sea lamprey caught in September 1978.

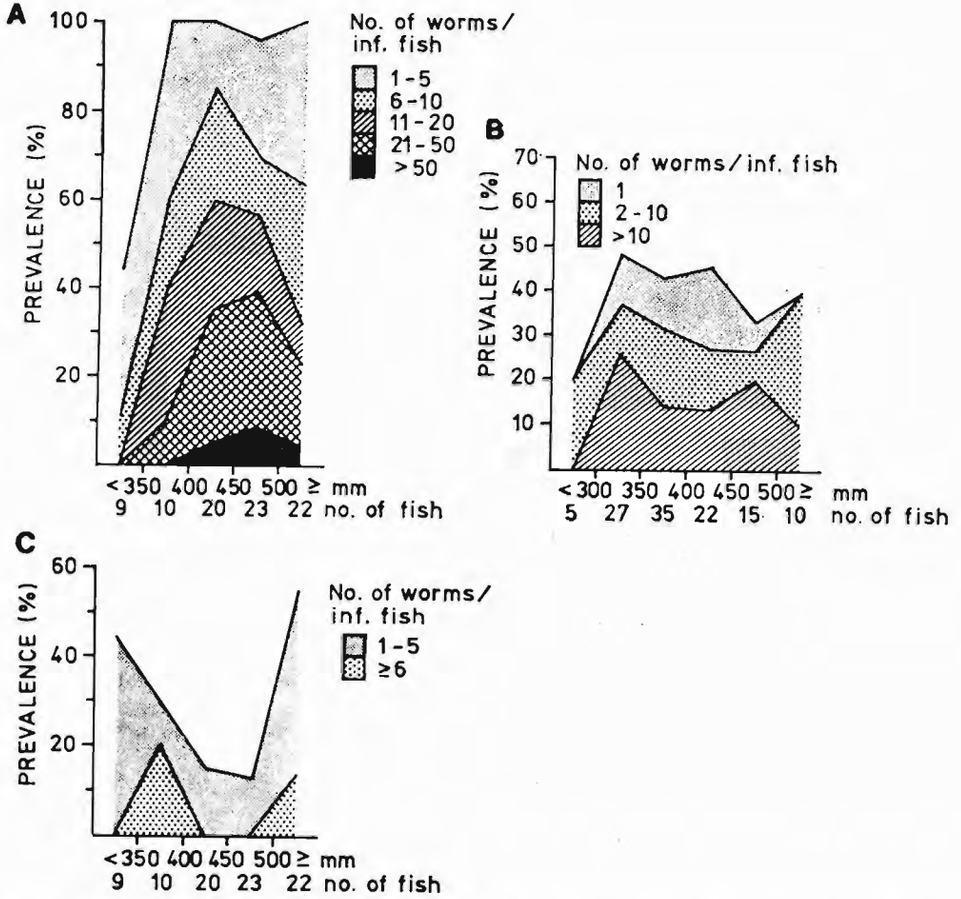


Fig. 4. Prevalence (%) and mean intensity of *Triaenophorus nodulosus* infection in the pike (*Esox lucius*) in the Bothnian Bay (A) and Lake Kuivasjärvi (B) and of *T. crassus* infection in the pike of the Bothnian Bay (C) according to size-classes of fish.

Definitive host

The high prevalence of *T. nodulosus* infection in the pike of the Bothnian Bay is also reflected in the seasonal data. The lowest infection value, 64 %, was found in

October—December 1978, but unfortunately no specimens from the Bothnian Bay were available for examination in June—July, when the lowest values were found in the lake material. A prevalence of 27 % was found in both lakes in June—July, although no infected pikes were caught from Lake Kuivasjärvi at the same time in 1980 (Table 4). The pikes caught from the sea in June 1982 were landlocked in a small bay following the spring high-water season and may not represent the normal pike population of the Bothnian Bay. Although a high prevalence of infection was recorded in this sample, the majority of the worms were plerocercoids. The prevalence of *T. crassus* infection in the pike of the Bothnian Bay varied between 31 and 56 % most of the year, except in June 1982, when only 6 % of the landlocked pikes were infected (Table 4).

Almost all the *Triaenophorus* worms in the three areas were gravid in May, although also some immature (unstrobilated) worms were found in the Bothnian Bay and in

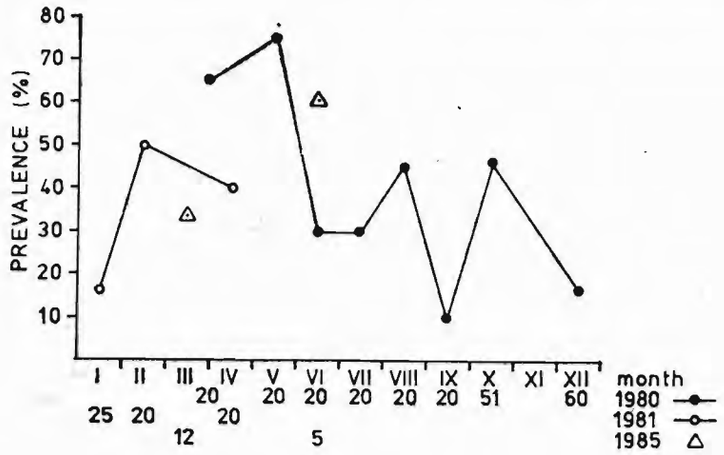


Fig. 5. Seasonal variation in the prevalence (%) of *Triaenophorus nodulosus* infection in the ruff (*Gymnocephalus cernuus*) of Lake Yli-Kitka. Numbers of fish studied are depicted under the figure.

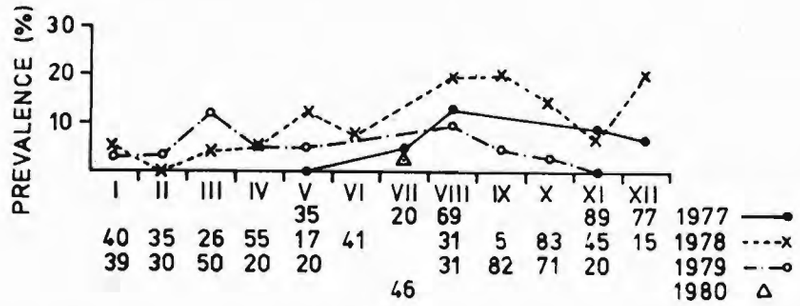


Fig. 6. Seasonal variation in the prevalence (%) of *Triaenophorus nodulosus* infection in the three-spined stickleback (*Gasterosteus aculeatus*) of the Bothnian Bay. Numbers of fish studied are depicted under the figure.

Lake Yli-Kitka, while all the worms found in June—August were young plerocercoids. Mature worms without eggs were seen in the Bothnian Bay and in Lake Yli-Kitka for first time in October, and the first ripe eggs in January in Lake Yli-Kitka.

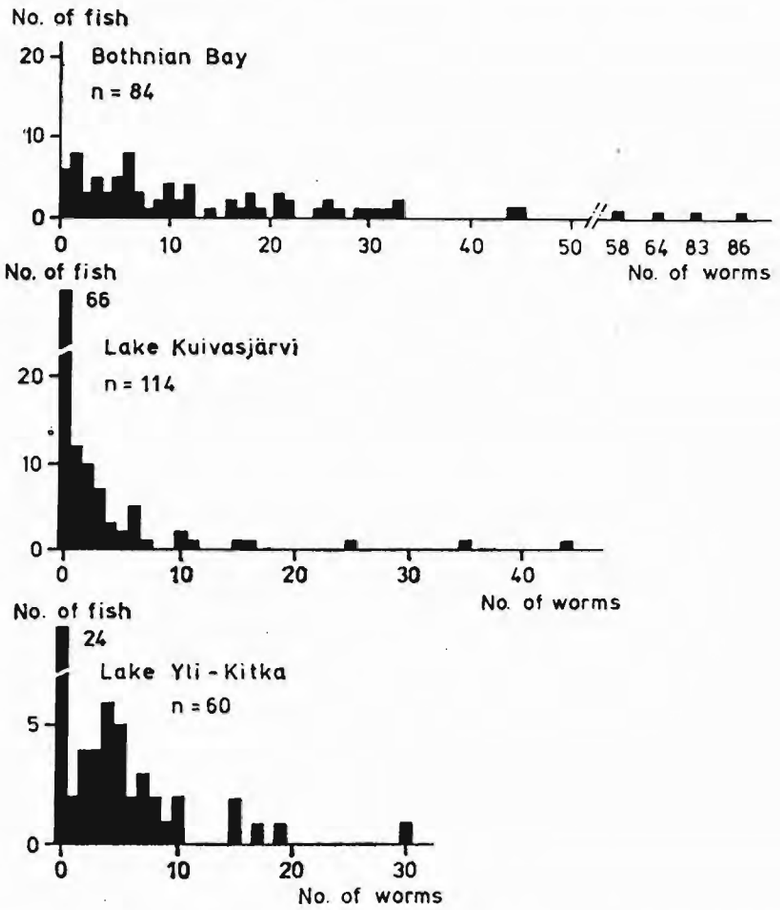


Fig. 7. Frequency distributions of *Triaenophorus nodulosus* in the pike (*Esox lucius*) in the three areas studied in northern Finland.

Frequency distributions for *T. nodulosus* in the pikes of the three areas studied are depicted in Fig. 7. The occurrence of the highest prevalence in the pike of the Bothnian Bay is also reflected in the frequency distribution of worms in the area, the proportion of fish with more than 20 parasites each being greatest there and the tail of the frequency distribution longest.

Table 4. Seasonal occurrence of *Triaenophorus nodulosus* in *Esox lucius* from three areas of northern Finland and *T. crassus* in *E. lucius* from the Bothnian Bay

	date	no. of fish	%	$\bar{x}$/inf. fish	S. D.	max
T. nodulosus						
Bothnian Bay						
XII	1977	13	100.0	17.2	17.7	45
I—II, V	1978	16	100.0	21.4	23.6	86
VIII—IX		9	88.9	3.0	2.2	7
X—XII		11	63.6	27.7	31.4	83
VI	1982	35	97.1	12.9	7.6	27
Lake Yli-Kitka						
IV	1980	2	50.0	5.0	—	5
VI—VII		11	27.3	2.3	1.2	3
VIII		11	54.5	8.2	6.5	19
IX—XI		8	62.5	6.2	6.1	17
I—II, IV	1981	3	100.0	16.7	23.7	44
III—IV	1982	10	100.0	5.2	2.1	8
V—VI		16	68.8	9.4	8.3	30
Lake Kuivasjärvi						
V	1979	6	83.3	8.6	9.3	25
VI—VII		15	26.7	10.0	16.7	35
VIII—X		23	17.4	6.3	6.2	15
XI—XII		22	59.1	4.9	3.6	11
V	1980	27	66.7	3.2	3.5	16
VII—VIII		11	—			
X		10	40.0	2.0	0.8	3
T. crassus						
Bothnian Bay						
XII	1977	13	30.8	3.0	1.4	5
I—II, V	1978	16	56.3	3.4	2.4	7
VIII—IX		9	55.6	5.4	4.2	12
X—XI		11	45.5	2.6	2.0	6
VI	1982	35	5.7	3.0	2.8	5

PROPORTIONS OF FISH IN THE DIET OF PIKE, BURBOT, RUFF AND PERCH

76—100 % of the pike and burbot in all the areas studied and of the Bothnian Bay perch which had food in their stomach had fish among their diet, of which a great proportion were potential second intermediate hosts of *T. nodulosus* (Table 5). The most common food items in the stomachs of the pike were three-spined sticklebacks in the Bothnian Bay, ruff and perch in Lake Kuivasjärvi and vendace and ruff in Lake Yli-Kitka (Table 6). Other food items found in the stomachs of the present specimens were copepods, cladocerans, chironomid larvae, amphipods, ostracods and mysids, mainly in ruff and perch, and isopods in burbot. The proportions of copepods, potential first intermediate hosts of *Triaenophorus* species, are also given in Table 5.

Table 5. Percentages of pike, burbot, ruff and perch in three areas of northern Finland with potential *Triaenophorus nodulosus* intermediate fish hosts and copepods in their stomachs

	no. of fish studied	fish with food in stomach %	fish with potential *T. nod.* int. fish hosts in stomach %	fish with copepods in stomach %
Esox lucius				
Bothnian Bay	84	100.0	47.8	—
Lake Kuivasjärvi	114	95.0	65.0	—
Lake Yli-Kitka	60	76.2	31.0	—
Lota lota				
Bothnian Bay	106	84.4	37.5	—
Lake Yli-Kitka	39	100.0	20.0	—
Gymnocephalus cernuus				
Bothnian Bay	713	5.4	—	5.7
Lake Kuivasjärvi	92	—	—	38.2
Lake Yli-Kitka	307	0.7	—	12.3
Perca fluviatilis				
Bothian Bay	311	79.6	31.8	1.7
Lake Kuivasjärvi	292	20.2	10.6	14.4
Lake Yli-Kitka	212	10.1	4.1	22.3

DISCUSSION

The most important second intermediate hosts in the life cycle of *T. nodulosus* are reported to be small burbot (Miller 1945a, Lawler 1968), perch (Chubb 1963, Lawler 1969, Lien 1970, Kuperman 1973b) and smelt (Barysheva and Bauer 1957, Lawler 1969). Chubb (1964) states that in most lakes only on fish species will serve as the principal second intermediate host with scattered occurrence in other fish. This fish species has been shown to be the burbot, when small in size, in the Lesser Slave Lake in Canada (Miller 1945a) and the perch in Llyn Tegid in Wales (Chubb 1964).

In the present case the smallest size classes of the fish were not studied, but in any case none of the earlier reported main second intermediate hosts seems to be of principal importance in this material, for the prevalence of *T. nodulosus* in the smelt is low, its proportion among the food items of the pike is small and the mean size of the burbot studied is too large for them to be consumed by pikes. Ecologically, an important fish host for *T. nodulosus* could be the ruff in all of the present water areas, especially in the lakes, as is supported by the stomach analyses from pikes. Such high *T. nodulosus* infections in the ruff have rarely been reported earlier. When studying fish parasites in five Karelian lakes in the USSR, Shulman (1961) found *T. nodulosus* larvae in the ruff only in one lake, with a prevalence of 13 %. Higher infection rates are also possible in the ruff of the Soviet Karelian lakes, however, as reported by Rumjantsev and Maslov (1985), who found that 93 % of those studied in Lake Janis'jarvi were infected with *T. nodulosus* larvae.

Although the present ruff were also seen to feed on other fish, no fish species serving as an intermediate host could be identified in their diet in either of the lakes or in the Bothnian Bay, and hence the ruff could have acquired its worms directly from the first intermediate hosts, the high proportion of copepods in their stomach serving to support this notion.

Table 6. Pike, burbot and perch with fish in their stomachs and percentages of potential second intermediate hosts of *Triaenophorus* spp. among the prey fished

	no. with fish in stomach	vendace	whitefish	smelt	burbot	three-spined stickleback	ten-spined stickleback	ruff	perch
Esox lucius									
Bothnian Bay	23	—	—	8.7	—	34.8	—	4.4	—
Lake Kuivasjärvi	19	—	—	—	—	—	—	36.8	31.6
Lake Yli-Kitka	32	34.4	—	—	—	—	3.1	25.0	12.5
Lota lota									
Bothnian Bay	81	7.4	7.4	14.8	2.2	13.6	2.2	23.5	1.2
Lake Yli-Kitka	30	80.0	—	—	—	—	3.3	20.0	—
Perca fluviatilis									
Bothnian Bay	144	0.7	—	2.8	—	14.6	1.4	0.7	—
Lake Kuivasjärvi	21	—	—	—	—	—	—	47.6	4.8
Lake Yli-Kitka	15	6.7	—	—	—	—	26.7	13.3	—

As in the present burbot from Lake Yli-Kitka, high rates of *T. nodulosus* infection have been found in Lake Sjamozero in the USSR (Shulman 1961) and in Lake Janis'jarvi (Rumjantsev and Maslov 1985). High prevalences of *T. nodulosus* in young burbot (80—90 %) have also been reported by Miller (1945a) and Lawler (1968).

Burbot of the size captured here (see Table 1) are predators which apparently received their parasites by post-cyclic transmission from their prey fish; i.e. ruff, smelt, three-spined stickleback, small burbot and ten-spined stickleback were in the majority among the food items analysed from the stomach contents of the burbot of the Bothnian Bay, their mean proportion in all stomachs being 38 %. Transmission of cestode larvae from a fish to its predator has been also demonstrated experimentally by Halvorsen and Wissler (1973). On the other hand, the burbot studied are of a size that they may not easily be caught by pike, as seen from the stomach analyses on pikes. Thus the burbot could be a blind end rather than a real intermediate host in the life-cycle of *T. nodulosus*, as Vik (1959) and Hoffmann (1984) have also observed.

The perch is one of the most often reported second intermediate host of *T. nodulosus*. Chubb (1963), Lawler (1969) and Kuperman (1973b) all found that over half of the perch in their material were infected (58 %, 69 % and 52 %, respectively), most often with 1—5 *T. nodulosus* plerocercoids in one fish. Lower prevalences of *T. nodulosus* infection in perch have been reported by Vik (1959) and Tedla and Fernando (1969), however.

The minor importance of perch in the life-cycle of *T. nodulosus* both in the Bothnian Bay and in Lake Kuviasjärvi is interesting in relation to the results of Chubb (1963) and Lawler (1969). The small perch population in the Bothnian Bay as compared with the size of this water body may explain the low rate of infection there. The repeated deaths of fish from oxygen deficiency in spring in Lake Kuivasjärvi may have caused recruitment of new perch from the sea each year, whereas the ruff is a more resistant species and could be more obviously responsible for the completion of the life cycle of *T. nodulosus* in this lake. Stomach content analyses on pikes from Lake Kuivasjärvi also support this interpretation, the proportion of ruff among the food items being higher than in the other two water-bodies.

Concerning other intermediate fish hosts of *T. nodulosus* in the Bothnian Bay, the three-spined stickleback, for instance, is apparently of essential importance for the *T. nodulosus* population in spite of the low prevalence figure because it is common food item for predatory fish in that area.

The prevalences of *T. crassus* infection in the intermediate fish hosts of the Bothnian Bay were much lower than those found in Canadian lakes (Miller 1952, Lawler 1970) on in lakes in Norway (Vik 1959) or Sweden (Lawler 1969), where the figures were 40—90 %. The reason may be the less abundant coregonid stocks in the Bothnian Bay as compared with the Canadian lakes (see Miller 1952). Petterson (1969) found that the two whitefish species, *C. lavaretus* and *C. widegreni*, which live sympatrically in the Baltic had markedly different levels of *T. crassus* infection, the latter having a much higher incidence of infection than the former. This cannot be seen in the present material because of the small number of *C. lavaretus* studied. The role of the vendace may be of great importance for the life-cycle of *T. crassus* the Bothnian Bay because of the small average size of the fish. It has not been found in stomach analyses from pike, but this may be due to the fact that partly or totally digested vendace are not easy to identify.

Both potential first and second intermediate hosts of *T. crassus* occur in Lake Yli-Kitka (Hyytinen 1985, Vasama 1986), and hence the lack of this parasite

from the lake may be due to chance introductions, a factor of importance in the zoogeographical distribution of parasites (Kennedy 1981). The interval of 8400 years for which this waterbody has been isolated from the Bothnian Bay (see Heikkinen and Kurimo 1977) will have ensured that no parasites have been able to migrate to it from the western side of the Maanselkä watershed, while migration from the east is prevented by a 13 m high waterfall on the river Kitkajoki. The accidental occurrence of *T. crassus* in the pike of Lake Kuivasjärvi is a sign of some migration of pikes from the Bothnian Bay during the spawning time in May. *T. crassus* cannot survive in the lake because of the lack of permanent coregonid fish stocks.

A significant increase in the prevalence and intensity of *T. nodulosus* infection with length of the fish was found only in the case of ruff of Lake Yli-Kitka and an increase in the intensity of infection in the burbot of the same lake. Neither Chubb (1964) nor Lien (1970) found any differences in *T. nodulosus* infection in relation to the size of the perch in Llyn Tegid (Bala Lake) in Wales or Lake Bogstad in Norway, respectively. Lien (1970) found only younger fish to have newly recruited worms. On the other hand, Stromberg and Crites (1974) found an increase of *T. nodulosus* infection in the white bass (*Morone chrysops* (R.)) of Lake Erie in the USA with increasing size and age, as in the case of the Lake Yli-Kitka ruff, and Hoffmann (1984) found an increasing number of *T. nodulosus* plerocercoids with age in the arctic char (*Salvelinus alpinus* (L.)) in Lake Königssee, Western Germany. The even infection throughout the size-classes of ruff in the Bothnian Bay may reflect the greater variability in the diet of the sea ruff: i.e. amphipods which do not transmit *Triaenophorus* are very common in their diet.

Keleher (1952) did not find any differences in *T. crassus* infection according to size in three cisco species in Lake Winnipeg, Canada, as is the case in the present vendace and the sea-spawning whitefish of the Bothnian Bay. Some increase in *T. crassus* infection in larger whitefish (*C. lavaretus*) in Lake Schuchsee, Western Germany, was nevertheless found by Jürgensen and Braum (1985).

No clear seasonal variation was found in most intermediate fish hosts in the present material, any more than has been found earlier in perch from Llyn Tegid in Wales (Chubb 1964), Lake Bogstad in Norway (Lien 1970) or Lake Dargin in Poland (Wierzbicki 1970). This lack of variation has been attributed to the life span of *T. nodulosus* plerocercoids of 1—2 years (Chubb 1964) or 2—3 years (Lien 1970). This may also be the main reason in the present case, as living plerocercoids were often found concurrently with degenerated and dead worms in the same hosts. Pronin (1975), however, found that the prevalence of *T. nodulosus* infection in young perch regularly decreased from July to October, and attributed this to high mortaility among infected perch. On the other hand, Ieshko et al. (1988) found *T. nodulosus* infection in different size-classes of perch to differ according to the time of year. In the present case the prolonged low temperatures during the long winter season, when the water is covered by ice also favour a prolonged life-span for parasites, as has been suggested earlier by Gibson and Valtonen (1984) for *Bunoderae luciopercae* (Müller) trematode.

The highest prevalences of *T. nodulosus* infection in the ruff were found in February—May in the large, oligotrophic Lake Yli-Kitka, at a time when lower values were being recorded in the small, eutrophic Lake Kuivasjärvi. In the latter case it may be postulated that parasitized ruff would be killed by the low oxygen values in this lake in spring more often than unparasitized fish, just as the influence of stress factors may have caused high losses of young trout at a fish farm due to *T. nodulosus* (Sheuring 1919). It may also be suggested that more stable environmental conditions

in the Bothnian Bay may be reflected as quite even prevalences, of *T. nodulosus* larvae throughout the year.

Apart from the ruff from Lake Yli-Kitka, no great variation in the prevalence and intensity of *T. nodulosus* infection in relation to lenght or seasonal occurence in any other intermediate fish host were found. Chubb (1964) found a dynamic balance between the establishment of procercoids from copepod hosts and the loss of plerocercoids by degeneration and encapsulation within the perch. He also reports quite a low intensity of *T. nodulosus* plerocercoids in the perch, suggesting that this may be the low level of occurrence of infected in copepods or by an immunity effect towards the parasite, or both.

Copland (1956) found plerocercoids of *T. nodulosus* in the liver of young pikes (9—29 cm) in Loch Lomond, Scotland. In the present case no young pikes were studied, and no *T. nodulosus* larvae were found in the inner organs of older ones, even though larvae have been found in the liver and other visceral organs of the pike in central Finland in some lakes where the pike population is very prominent in relation to other fish species (Valtonen unpubl., Copland 1956).

Scheuring (1929), Miller (1943) and Lawler (1969) have reported mixed infections of *T. crassus* and *T. nodulosus* in pike, and all of them have found that in most cases *T. crassus* is smaller in number in the intestine of the pike than *T. nodulosus*, as in the present case. Both Miller (1943) and Lawler (1969) have shown larger pike to have more *T. crassus* than *T. nodulosus* in the Lesser Slave Lake in Canada and in Lake Mälaren in Sweden, respectively. The proportion of *T. crassus* in relation to *T. nodulosus* in the present Bothnian Bay material increases as the pikes become larger, although *T. nodulosus* was in the majority even in the largest individuals. In two lakes in the valley of Pasvik in Norway the relationship between the two *Triaenophorus* species was the opposite, 100 % and 73 % of the pikes having *T. crassus* infection and 33 % and 0 % *T. nodulosus* (Vik 1959), Scheuring (1929) has stated that major invasion by *T. crassus* can take place only in the absence of *T. nodulosus*.

It seems that the main food chains in each water body affect the *Triaenophorus* fauna in the definitive host, and the minor importance of coregonids in the diet of the pike of the Bothnian Bay must be reflected in a minor *T. crassus* population as compared with *T. nodulosus*.

The rapid increase in *T. nodulosus* infection with increasing length of pike in the present material is in accordance with the early change in the behaviour of the pike in the direction of predation (Scott and Crossman 1973). The same has been reported by Moravec (1979). All the pikes in the present material are of a size to be predators.

Both Chubb (1963) and Borgström (1970) have reported 8 fish species found in the diet of pike. Although perch did not constitute the most important food item in the stomach of the pike in Llyn Tegid in Wales (Chubb 1963) or in Lake Bogstad in Norway (Borgström 1970), it was the only intermediate fish species in which *T. nodulosus* was found in both areas. The stomach contents of the pikes from the Bothnian Bay point to the significance of the three-spined stickleback among the potential intermediate hosts as a use of the passage of *T. nodulosus* to its final host, although the smelt and ruff are also identifiable as food items.

As reported earlier by Miller (1943), Copland (1956), Chubb (1963) and Borgström (1970), the maturation of *Triaenophorus* species follows a regular seasonal pattern, and the same is true in the present case. Eggs were released during the spawning time of the pike in May. A decrease in the prevalence of *Triaenophorus* infection in the pike after its spawning time is seen in both lakes in the present material, but no gap in infection as reported by Miller (1943) and Copland (1956). The high prevalence of *T. nodulosus* juveniles in the Bothnian Bay in June 1982 is in accordance

with the results of Chubb (1963) and Borgström (1970) who did not find any decrease in the prevalence after the loss of mature cestodes in spring.

It seems that the variation in the intermediate fish hosts of *T. nodulosus* is greatly dependent on the species composition of each water body and the abundances of the different species. The Bothnian Bay, which is most stable water body of the three studied here and which has the greatest number of fish species, also has the greatest number of intermediate fish hosts, so that burden of *T. nodulosus* parasites is most evenly distributed among them and the seasonal prevalences of infection are most even. The smaller the water body is and the fewer the fish species it has, the more the role of the most favoured intermediate fish host increases, as in the present case of the ruff in the small, eutrophic Lake Kuivasjärvi. As a whole the role of the ruff as a preferred intermediate host in both lakes is interesting, especially because the role of the perch is at the same time such a minor one, even though it is such a common food item for the pike. It may also be stated that adult burbot are not of great importance for transmission of *T. nodulosus* to the pike, even though the burbot is the most heavily parasitized intermediate host in both places where it was studied. This also is supported by the stomach analysis from pikes.

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TRIAENOPHORUS NODULOSUS И *T. CRASSUS* В РЫБАХ СЕВЕРНОЙ ФИНЛЯНДИИ

Э. Т. Валтонен, П. Ринтамеки и М. Лаппалайнен

Резюме. В 1978–1982 гг. изучалась встречаемость паразитов *Triaenophorus nodulosus* и *T. crassus* в 10 228 экземплярах рыб 34-х видов из трех водоемов в северной Финляндии. В заливе Bothnian Bay плероцеркоиды *T. nodulosus* обнаружены в шести видах из 31 изученных, в холодном олиготрофном озере Yli-Kitka в северо-восточной Финляндии в четырех видах из 11 изученных и в малом эвтрофном озере Kuivasjarvi лишь в одном из 6 изученных. Изучение желудочного содержимого хищных рыб показало, что основным промежуточным хозяином в озерах является ерш (*Gymnocephalus cernuus*). Самая высокая встречаемость в двух из трех областей обнаружена во взрослых экземплярах обыкновенного налима (*Lota lota*) но в данном случае этот вид рыб является скорее всего тупиком в жизненном цикле *T. nodulosus*. Личиночные стадии *T. crassus* обнаружены только в экземплярах трех видов лососей и один раз в кишечнике речной миноги (*Lampetra fluviatilis*) из залива. Встречаемость и интенсивность заражения в большинстве промежуточных хозяинов *T. nodulosus* зависела от размеров рыб. Исключение составили ерши из озера Yli-Kitka, у которых отмечено резкое увеличение встречаемости и интенсивности заражения с ростом размеров рыб. Ни в одном случае не обнаружены выраженные сезонные изменения в заражении личиночными стадиями рода *Triaenophorus*. Встречаемость *T. nodulosus* в его дефинитивном хозяине — щуке (*Esox lucius*), максимальная в море (93 %) и минимальная в эвтрофном озере (47 %). Минимальная встречаемость *T. nodulosus* отмечена в обоих озерах в июне — июле. Обнаружен цикл созревания, самые незрелые формы во всех случаях встречаются в летние месяцы. *T. crassus* найден в каждой третьей щуке в море и его доля по сравнению с *T. nodulosus* выше в самых малых и самых больших экземплярах рыб. Лишь в 12 % щук количество экземпляров *T. crassus* было выше количества экземпляров *T. nodulosus*, но несмотря на это, в среднем отношение составило 1 : 13 в пользу *T. nodulosus*. Эти результаты приводят к заключению, что состав фауны в каждом водоеме оказывает заметное влияние на встречаемость *T. nodulosus* и его распространение среди возможных промежуточных хозяев. В случае самых стабильных окружающих условий и самой большой разновидности видов рыб, паразиты в заливе Bothnian Bay распространены в 6 видых промежуточных хозяев. Чем меньше количество видов рыб в водоеме (как например в случае эвтрофного озера), тем больше возрастает значение некоторых или даже одного промежуточного хозяина.

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E. T. V., Dept. of Biology,
University of Jyväskylä,
SF-40100 Jyväskylä, Finland