64A
37443

OPHELIA, 23(2): 195-222 (December 1984)

Vlaams Instituut voor de Zee
Flanders Marine Institute

DIGENETIC TREMATODES FROM *GADUS MORHUA* L. (OSTEICHTHYES, GADIDAE) FROM DANISH AND ADJACENT WATERS, WITH SPECIAL REFERENCE TO THEIR LIFE-HISTORIES

MARIANNE KØIE
Marine Biological Laboratory, DK-3000 Helsingør, Denmark

ABSTRACT

A total of 890 specimens of the Atlantic cod *Gadus morhua* L. (Osteichthyes, Gadidae) have been examined for infestations with digenetic trematodes. The cods were caught at 15 sampling stations in Danish and adjacent waters with salinities ranging from 8 ‰ (the Baltic off Bornholm) to 35 ‰ (the North Sea and the Atlantic Ocean off the Faroes), and from shallow water down to a depth of 230 m. 18 species (metacercariae and adults) were found.

The following species were found in the alimentary tract: *Prosorhynchus squamatus* Odhner, 1905 (Bucephalidae), *Podocotyle atomon* (Rudolphi, 1802), *P. reflexa* (Creplin, 1825) (Opecoelidae), *Lepidapedon elongatum* (Lebour, 1908), *L. rachion* (Cobbold, 1858), *Opechona bacillaris* (Molin, 1859) (Lepocreadiidae), *Stephanostomum pristis* (Deslongchamps, 1824) (Acanthocolpidae), *Derogenes varicus* (Müller, 1784), *Lecithaster gibbosus* (Rudolphi, 1802), *Brachyphallus crenatus* (Rudolphi, 1802), *Hemiurus communis* Odhner, 1905, *H. luehei* Odhner, 1905, *H. levinseni* Odhner, 1905, immature encapsulated *Lecithochirium* sp. (Hemiuridae), and the metacercaria of *Otodistomum* sp. (Azygiidae). The metacercaria of *Bucephaloides gracilescens* (Rudolphi, 1819) (Bucephalidae) was found in the brain cavity, the metacercaria of *Diplostomum spathaceum* (Rudolphi, 1819) (Diplostomatidae) was found in the eye lens, and the metacercaria of *Cryptocotyle lingua* (Creplin, 1825) (Heterophyidae) occurred in the skin throughout the fish body. *O. bacillaris*, *H. luehei* and *Lecithochirium* sp. have not previously been reported from the cod.

The infestation in relation to host size of the most common cod digeneans was examined. The incidence of infestation at all stations is compared with the geographical distribution of the first intermediate host (when known) to examine whether the digeneans may be used as natural tags.

The number of digenean species increased from the Baltic to the northern Øresund and the western Kattegat, where it reached a maximum value, then decreased again in the North Sea and Faroese waters, reflecting the different diversity of the benthic fauna in the different areas.

IZWO
Instituut voor Zeewetenschappelijk Onderzoek (V.Z.W.)
Institute for Marine Scientific Research
VICTORIALAAN 3 - B-8400 OOSTENDE BELGIUM
Tel. +32-(0)59-321045 — Fax: +32-(0)59-32117

Contr. No. 203
Marine Biological Laboratory
Helsingør Denmark

INTRODUCTION

The commercially important Atlantic cod, *Gadus morhua* L., has been the subject of many parasitological studies, and it is apparently the marine fish from which most helminth species have been recorded. Dollfus (1953) reviewed most of the literature on cod parasites up to about 1950, and since then many papers have appeared, e.g. by Shulman & Shulman-Albova (1953), Polyanski (1955), and Appy & Burt (1982).

Nobody has examined the digenetic trematodes of the cod from Danish waters, but Thulin (1971) and Möller (1975) have examined cods from the western coast of Sweden and the Kiel Fjord (the western Baltic), respectively.

In the present study, 890 cods were examined from 15 sampling stations ranging from the Faroes to the Baltic off Bornholm, but mostly from the North Sea and the Øresund. The cods from the northern Øresund were examined throughout a two-year period. Among gadoid fishes in Danish and adjacent waters the cod harbours most digenean species. 18 species of Digenea (metacercariae and adults) were found.

Appreciation is expressed to Drs H. Gislason and E. Nielsen, the Danish Institute for Fisheries and Marine Research, Charlottenlund, for research space aboard the research vessel *Dana*, and to the staff of Fiskirannsóknarstovan, Tórshavn, for fishes, to Dr D. Block, Museum of Natural History, Tórshavn, the Faroes, for excellent working facilities during my stay there, and to Mr A. Barnes, Faculty of Science, University of Queensland, Brisbane, Australia, who did the principal coordinate analysis.

MATERIALS AND METHODS

The cods were caught at 15 sampling stations (Fig. 1, Table 1). The cods from stations 1 & 4 were caught in nets; those from station 6 in an eel trap, and those from station 14 on long lines. The remaining cods were caught by trawl. The cods from each of the stations 2-4, 7-13 and 15 were caught within a few hours, whereas the cods from the remaining stations were caught over a longer period.

All the cods from stations 1, 6 and 14, and most of those from station 5 were kept dry at about 4°C and examined within 24 hours after capture. The remaining cods from station 5 were kept alive in tanks for up to one week before being examined. The whole alimentary tract of the cods from station 2 was fixed in 4% formaldehyde shortly after capture. The cods from stations 7-13 were trawled by the research vessel *Dana* and deep-frozen almost immediately, except for a few specimens from each station, which were examined on board within a few hours after capture, whereas all the cods from stations 3 & 15 were deep-frozen shortly after capture.

The total length of each cod was measured to the nearest cm. With a few exceptions the external surface and the brain cavity were examined for meta-

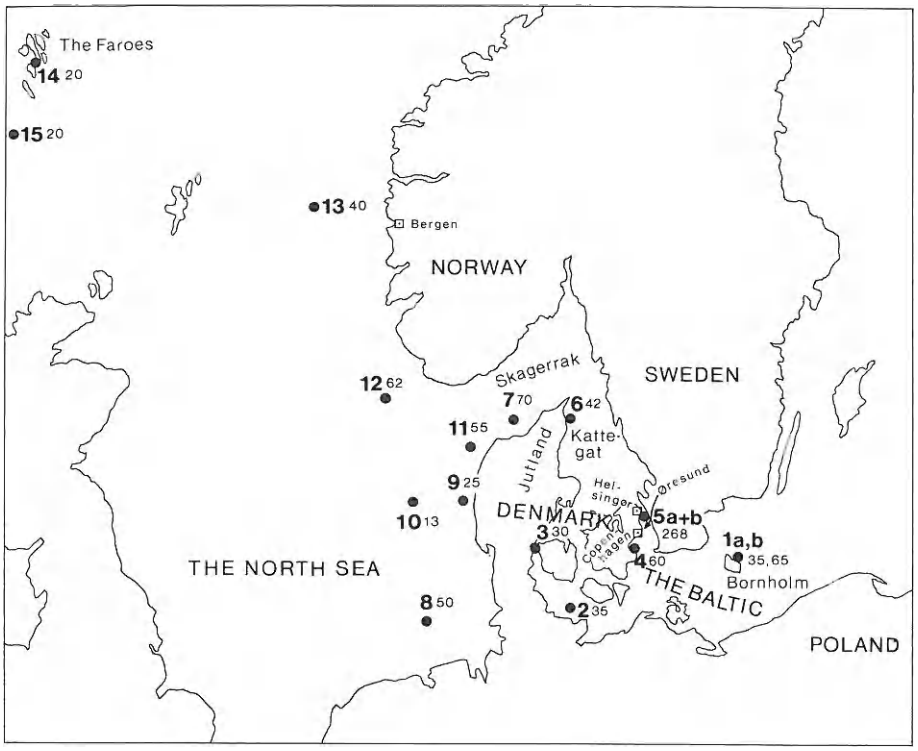


FIG. 1. Location of sampling stations 1-15. Number of examined cods from each station shown in smaller numerals beside the bold station numbers.

cercariae. The eye lenses of all the cods from stations 1 & 4 were examined (before freezing) using a stereomicroscope. The whole alimentary tract was removed and divided into sections. Each section was placed in a petri dish with diluted sea water (about 10‰ salinity), opened and scraped thoroughly, after which the contents were examined using a stereomicroscope. All the digeneans were removed, identified, counted, and divided into three groups according to degree of development. For specimens occurring in large numbers, round figures are given. The numbers of metacercariae are minima as only fully developed specimens were counted, but the magnitude of error was considered to be the same for all samples.

Incidence (= prevalence) refers to the percentage of fish infested and intensity refers to number of parasites per infested fish.

The geographical distribution of the molluscan and fish hosts are based on: Davis (1925), Spärck & Thorson (1933), Jensen & Spärck (1934), Ankel (1936), Jaeckel (1952), Muus & Dahlstrøm (1964), Tebble (1966), Joensen & Tåning (1970), Petersen (1968, 1977), Jägerskiöld (1971), and Dr J. Knudsen, Zool. Mus., Copenhagen (pers. comm.).

TABLE 1. Digenetic trematodes in *Gadus morhua* from Danish and adjacent waters. For explanation of figures in the trematode entries see footnotes to the *Podocotyle atomon*/station 1a entry.

Station number	Locality and depth	Time of year	Number examined	Host size, cm mean and range	*Bacciphaloides gracilescens* (metac.)	*Prosorhynchus squamatus*	*Podocotyle atomon*	*Podocotyle reflexa*	*Opechona bacillaris*
1a	The Baltic, off the north of Bornholm. 10-50 m	Oct. 1980	35	41.3 (21-69)	—	2.9% 6(6)	65.7%* 50** (3-250)***	—	—
1b	do.	May 1981	65	39.9 (24-58)	—	—	20.0% 35 (1-200)	—	—
2	Western Baltic, Kiel Bay, 15 m	Dec. 1980	35	32.3 (20-55)	—	—	37.1% 10 (1-60)	—	—
3	Lillebælt, off Fredericia, 20 m	July 1984	30	42.8 (25-59)	—	—	10.0% 3.7 (1-9)	10.0% 6 (2-11)	—
4	Øresund, south of Copenhagen (Køge Bay) 5-10 m	Sep. 1983	60****	41.7 (27-55)	—	—	8.3% 6.4 (1-10)	—	—
5 a+b	Øresund, north of Copenhagen (north of Veen), 25-28 m	Jan. 1980-Nov. 1981	268	33.9 (17-58)	[5%]	0.4% 1 (1)	4.1% 1.8 (1-10)	42.2% 3.2 (1-40)	2.2% 5.0 (1-10)
5a	do.	Jan. 1980-Dec. 1980	(136)		[5%]	—	1.5%	36.8%	3.7%
5b	do.	Jan. 1981-Nov. 1981	(132)		[5%]	0.8%	6.8%	47.7%	0.8%
6	Western Kattegat, off Frederikshavn, 10 m	July-Aug. 1980, 1982	42	27.9 (18-47)	[20%]	—	—	23.8% 1.3 (1-3)	14.3% 7.0 (2-12)
7	Skagerrak, Jammer Bay, 20 m	May 1983	70	25.5 (15-47)	78.6% 7.3 (1-100)	—	—	1.4% 1 (1)	2.9% 1 (1)
8	The North Sea, west of Helgoland, 37 m	May 1983	50	32.2 (18-49)	[25%]	—	—	2.0% 1 (1)	—
9	The North Sea, off the west coast of Jutland, 17 m	May 1983	25	23.6 (16-44)	12.0% 1.7 (1-2)	—	—	4.0% 1 (1)	—
10	The North Sea, off the west coast of Jutland, 40 m	May 1983	13	21.8 (15-32)	38.5% 1.2 (1-2)	—	—	7.7% 1 (1)	—
11	The North Sea, off northern Jutland, 27 m	May 1983	55	27.8 (17-45)	30.9% 3.3 (1-10)	—	—	—	1.8% 1 (1)
12	The North Sea, off Egersund, 82 m	Apr. 1983	62	34.0 (18-49)	100.0% 50 (10-200)	—	—	—	—
13	The North Sea, Viking Bank, 144 m	Apr. 1983	40	36.5 (15-49)	100.0% ?	—	—	—	—
14	The Faroes, coastal waters, 40 m	Oct. 1981	20	39.8 (32-57)	100.0% ?	40.0% 5.0 (1-13)	—	35.0% 2.7 (1-6)	—
15	The Faroes, southwest of Munkagrunnur (Munken rock), 230 m	Oct. 1981	20	51.6 (34-67)	100.0% ?	30.0% 4.8 (1-11)	—	—	—
			890						

*incidence; **intensity, mean; ***intensity, range; ****data of Chr. Jacobsen (pers. comm.); [ ] approx. incidence as not all the cods were examined.

Lepidapedon elongatum	*Lepidapedon rachion*	*Stephanostomum pristis*	*Otodistomum* sp. (metac.)	*Derogenes varicus*	*Lecithaster gibbosus*	*Brachyphallus crenatus*	*Hemiurus communis*	*Hemiurus luehei*	*Hemiurus levinseni*	*Lecithochirium* sp. (immature)	*Cryptocotyle lingua* (metac.)	*Diplostomum spathaceum* (metac.)
51.4% 20 (1-125)	—	—	—	—	—	2.9% 3 (3)	—	—	—	—	5.7% 125 (50-200)	17.1% 8.3 (2-19)
73.8% 60 (1-500)	—	—	—	—	—	10.8% 4.1 (1-10)	—	7.7% 4.2 (2-10)	—	—	3.1% 150 (100-200)	13.8% 6.9 (1-14)
94.3% 150 (1-1000)	—	—	—	—	—	5.7% 1.5 (1-2)	42.9% 3.6 (1-10)	2.9% 30 (30)	—	—	17.1% 100 (30-1000)	—
60.0% 125 (7-800)	3.3% 3 (3)	—	—	6.7% 1 (1)	—	30.0% 5.7 (1-11)	80.0% 15.3 (3-57)	—	—	—	96.7% 250 (10-1000)	
66.7% 50 (1-200)	—	—	—	1.7% 1 (1)	—	50.0% 8.7 (1-60)	66.7% 5.5 (1-26)	16.7% 2.6 (1-5)	—	—	96.7% 65 (1-300)	1.7% 11 (11)
71.3% 60 (1-1000)	6.7% 4.2 (1-21)	16.4% 1.3 (1-3)	—	49.3% 2.6 (1-11)	1.1% 1.3 (1-2)	1.1% 8.7 (1-24)	25.4% 2.2 (1-10)	4.9% 4.8 (1-12)	—	—	[90%]	—
64.0%	8.8%	17.6%	—	41.9%	—	—	31.6%	3.8%	—	—	[90%]	—
78.8%	4.5%	15.1%	—	56.8%	1.5%	2.3%	18.9%	6.1%	—	—	[90%]	—
57.1% 150 (1-1000)	4.8% 10.5 (7-14)	45.2% 10.3 (1-100)	—	50.0% 3.6 (1-18)	4.8% 1 (1)	2.4% 40 (40)	47.6% 2.5 (1-12)	4.8% 21.5 (3-40)	—	14.3% 1 (1)	[80%]	—
14.3% 100 (10-300)	—	91.4% 13.8 (1-60)	—	84.3% 3.9 (1-23)	—	11.4% 1.5 (1-3)	10.0% 1.1 (1-2)	—	—	—	1.4% 30 (30)	—
2.0% 30 (30)	—	80.0% 10.3 (1-50)	—	84.0% 7.8 (1-36)	12.0% 1.2 1-2)	30.0% 6.7 (1-17)	—	—	—	—	—	—
—	—	88.0% 12.4 (1-40)	—	64.0% 2.3 (1-5)	—	12.0% 1 (1)	8.0% 2 (2)	—	—	—	—	—
7.7% 70 (70)	—	76.9% 29.0 (10-60)	—	100.0% 5.8 (1-14)	—	7.7% 1 (1)						
—	—	85.5% 20.6 (1-70)	—	70.9% 4.4 (1-18)	21.8% 1.7 (1-4)	16.4% 1.1 (1-2)	14.5% 1.3 (1-3)	—	—	—	7.3% 100 (2-200)	—
—	—	1.6% 1 (1)	—	46.8% 2.7 (1-12)	—	—	1.6% 1 (1)	—	40.3% 3.2 (1-11)	—	—	—
—	—	27.5% 4.3 (1-12)	15.0% 1 (1)	32.5% 1.7 (1-3)	—	—	2.5% 1 (1)	—	97.5% 30 (4-80)	—	—	—
45.0% 40 (1-100)	20.0% 6.8 (1-14)	—	—	100.0% 22.3 (6-50)	—	—	—	—	5.0% 1 (1)	15.0% 1 (1)	—	—
5.0% 30 (30)	—	—	—	100.0% 9.1 (1-20)	—	—	—	—	100.0% 7.4 (3-20)	—	—	—

RESULTS

BUCEPHALIDAE Poche, 1907

Bucephaloides gracilescens (Rudolphi, 1819) Hopkins, 1954

Metacercariae of *B. gracilescens* were found in the intra-cranial fluid surrounding the brain. They were found at all sampling stations except stations 1-4 (Table 1, Fig. 2A).

Only the brain cavity was examined. As the metacercariae in other gadoids have been found in other parts of the nervous system, e.g. in the spinal cord (Matthews 1974, Johnston & Halton 1981), the intensity – and probably also the incidence – is probably higher than listed. From the northern Øresund and the western Kattegat only about half of the cods were examined. Metacercariae were only found in the largest cods from the northern Øresund, whereas they also occurred in smaller size groups from the western Kattegat. However, in all localities the largest size groups showed the highest incidence and intensity (Fig. 3A).

The bivalve *Abra alba* is described as the only first intermediate host (Matthews 1974) (Table 2). The cercariae penetrate gadoid fishes in which they encyst, mainly in the nervous system. The cercaria of *B. gracilescens* has apparently only been found in British waters (see Matthews 1974). It was not found in Danish waters, although hundreds of *A. alba* from the northern Øresund and the western Kattegat were examined.

It is apparent that neither the vertical nor the horizontal distributions of *A. alba* and infested cods coincide (Fig. 2A). *A. alba* is a shallow-water bivalve. Matthews (1974) found infested *A. alba* at a depth of 70 m, which according to Tebble (1966) is the greatest depth for *A. alba* in British waters.

Metacercariae of *B. gracilescens* were found in all the cods caught at a depth of 230 m in Faroese waters, as well as in the other gadoids caught at the same depth, including the blue ling *Molva dypterygia* (Pennant), Norway pout *Trisopterus esmarkii* (Nielsson) (new host records), and blue whiting *Micromesistius poutassou* (Risso). Metacercariae were also found in the silvery pout *Gadiculus thori* Schmidt (new host record) from the northern North Sea (between stations 12 & 13) at a depth of 150-200 m. None of these gadoids, except *T. esmarkii*, enter shallow water where *A. alba* lives. This indicates that another bivalve must function as first intermediate host for *B. gracilescens* in areas where *A. alba* does not exist. One or more of the three species belonging to the genus *Abra* (*A. nitida* (Müller), *A. longicallus* (Scacchi), *A. prismatica* (Montagu)) which occur in the northeast Atlantic Ocean are most likely to act as intermediate host and they all live at greater depths than *A. alba*.

The only final host is the angler *Lophius piscatorius* L., which lives in the Skagerrak and in the western Kattegat, but it is not common in these areas. It

TABLE 2. The life-cycle of digeneans in *Gadus morhua* from Danish and adjacent waters.

Species	Main or only 1. intermediate host(s)	Main 2. interm. host and/or transport host(s) (3. interm. host)	Main or only final host(s)	References
Bucephalidae				
Bucephaloides gracilescens (metac.)	*Abra alba* (Wood)	Gadidae	*Lophius piscatorius* L.	Matthews 1974
Prosorhynchus squamatus	*Mytilus edulis* L. *Musculus discors* (L.)	*Liparis* spp. Cottidae	Cottidae, Pleuronectidae	Odhner 1905 Chubrik 1952
Opecoelidae				
Podocotyle atomon	*Littorina saxatilis* (Olivi)	Amphipods, isopods, mysids	Various fish families.	Hunninen & Cable 1943
Podocotyle reflexa	*Buccinum undatum* L. *Neptunea antiqua* (L.)	Shrimps	Gadidae	Køie 1981
Lepocreadiidae				
Opechona bacillaris	*Nassarius pygmaeus* (Lamarck)	Medusae, ctenophores, chaetognaths	Scombridae, Gadidae	Køie 1975
Lepidapedon elongatum	*Onoba aculeus* (Gould)	Polychaetes	Gadidae	Køie 1985
Lepidapedon rachion	?	?	Gadidae	
Acanthocolpidae				
Stephanostomum pristis	*Natica alderi* Forbes	Gobiidae	Gadidae	Køie 1978
Azygiidae				
Otodistomum sp. (metacercaria)	?	Pleuronectidae	Elasmobranchs	
Hemiuridae				
Derogenes varicus	*Natica* spp.	Copepods, chaetognaths, ctenophores, a.o.	Various fish families	Køie 1979
Lecithaster gibbosus	(?) *Odostomia* spp.	Copepods	Various fish families	(see Køie 1983)
Brachyphallus crenatus	(?) *Rissoa* spp.	Copepods, chaetognaths, ctenophores	Various fish families	(see Køie 1983)
Hemiurus communis	?	Copepods, chaetognaths, ctenophores	Various fish families	
Hemiurus luehei	?	(?) Copepods	Various fish families	
Hemiurus levinseni	?	(?) Copepods, chaetognaths	Various fish families	
Lecithochirium sp. (immature)	?	(?) Copepods; (*Ctenolabrus rupestris* (L.))	*Anguilla anguilla* (L.), *Conger conger* (L.)	
Heterophyidae				
Cryptocotyles lingua (metacercaria)	*Littorina littorea* (L.)	Various fish families	Laridae, a.o.	Stunkard 1930
Diplostomatidae				
Diplostomum spathaceum (metacercaria)	*Lymnaea* spp.	Various fish families	Laridae, a.o.	Szidat 1924

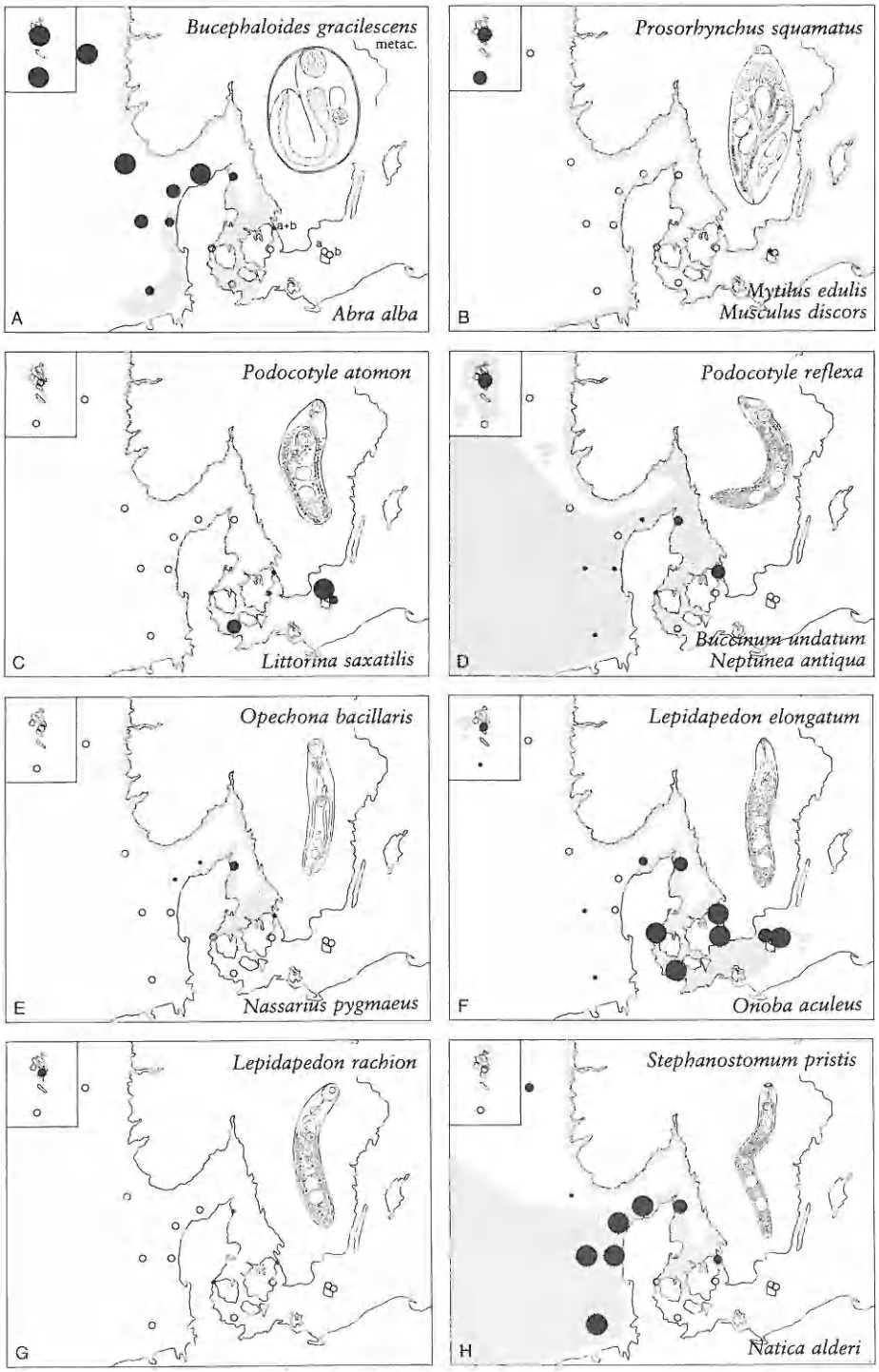
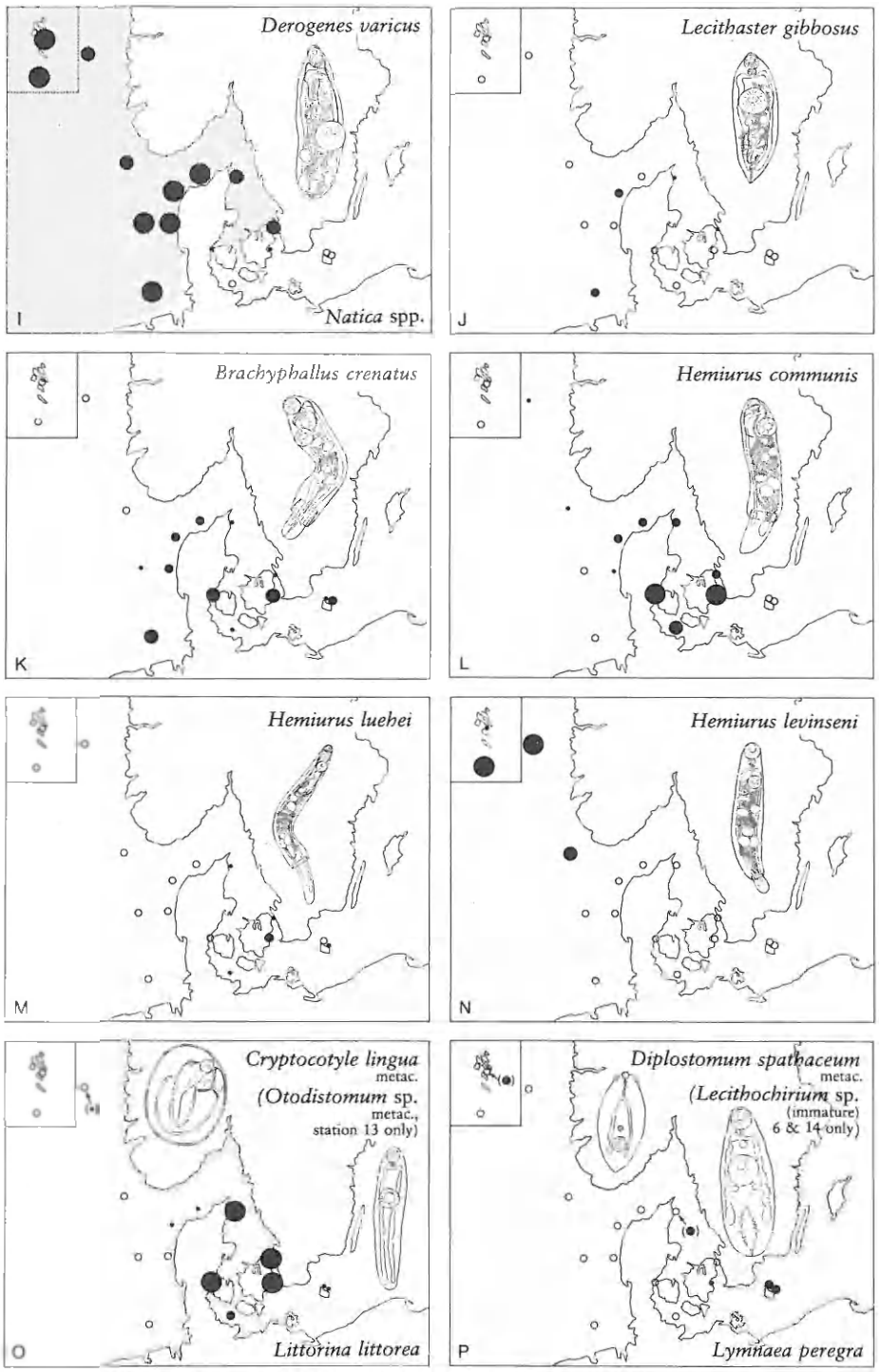


FIG. 2. Geographical distribution of cod digeneans (incidence of infestation) and of their first intermediate hosts (see lower right corner) in Danish and adjacent waters.



· : 0.1-9.9 % • : 10.0-29.9 % ● : 30.0-59.9 % ⬤ : 60.0-100 % ○ : no record.

: distribution of hosts

does not occur in the Baltic and in the Øresund south of Copenhagen, which may explain the absence of the metacercariae in the cods from these areas.

B. gracilescens is a common parasite in the cod (see Dollfus 1953, Johnston & Halton 1981). Thulin (1971) found it in cods from western Sweden. Joensen & Tåning (1970) found a high proportion of Faroese cods with a *Gasterostomum* infection in their brain. *B. gracilescens* has the same geographical distribution as its final host *L. piscatorius*, i.e. the Atlantic Ocean and adjacent seas including the Barents Sea and the Mediterranean Sea.

Prosorhynchus squamatus Odhner, 1905

P. squamatus was found in the stomach, pyloric caeca and intestine of cods from north of Bornholm, the northern Øresund and Faroese waters (Table 1, Fig. 2B).

The life-cycle was elucidated independently by Odhner (1905) and Chubrik (1952) (Table 2). The cercaria was redescribed by Matthews (1973).

The cercaria of *P. squamatus* was found in *Musculus discors* and *Mytilus edulis* from the northern Øresund, and in *M. edulis* from Bornholm and the western Kattegat. In Danish waters *Liparis* spp. are the main second intermediate hosts. *Liparis* spp. from Bornholm, the Øresund, the western Kattegat and Faroese waters were heavily infested with immature and progenetic specimens, which occur in all tissue of the fish body and also occasionally free in the intestinal lumen. In Danish and adjacent waters species belonging to the Cottidae function as main final hosts.

In one cod from Bornholm and in one from station 14, the Faroes, immature and mature *P. squamatus* were found together with remains of *Liparis* sp., and it is evident that cods become infested by eating *Liparis* sp. *L. liparis* (L.) lives at the Faroes from the tidal zone to several hundred metres depth (Joensen & Tåning 1970). About half of the infested cods from the Faroes had *P. squamatus* in the intestine, where they have no possibility to attach. Matthews (1973) mentions that *P. squamatus* has a comparatively small rhynchus and that it may be significant that the site of infection of this parasite in Cottidae, cod and whiting is the pyloric caecum, where it will be less likely to be dislodged by the passage of food through the intestine. He further writes that as some metacercariae are progenetic the finds of adults in the intestine of predatory fish might not indicate that these were normal hosts, although predation would be an important mechanism in the release of eggs from metacercariae in the tissue of intermediate hosts.

To show whether the cod is a suitable host for this parasite, four cods (about 30 cm long) were kept in individual tanks. 10 *Liparis* sp. were added to each tank. Ten control *Liparis* each contained 40-100 *P. squamatus* of different developmental stages. All the *Liparis* were eaten within a few hours. Two days

later one cod had 10 mature specimens scattered throughout the intestine. Six days after the ingestion of the *Liparis* two cods were without parasites. The fourth cod harboured two specimens; they were found in the apical end of different pyloric caeca. The parasites contained several hundreds eggs and were identical with the most developed specimens found in the second intermediate host. This experiment shows that the cod is an unsuitable host for this parasite. Only if progenetic specimens happen to enter a pyloric caecum do they become established and survive.

P. squamatus (as *P. grandis*) has previously been reported from cods from English waters by Lebour (1908), who found four cods infested, each with one specimen. *P. grandis* Lebour, 1908 was regarded as a valid species by Dollfus (1953), but other authors, e.g. Shulman & Shulman-Albova (1953) and Matthews (1973) consider *P. grandis* as a synonym of *P. squamatus*. Shulman & Shulman-Albova (1953) found two specimens in one of 83 cods from the White Sea. Up to 44 % of cods from Canadian Atlantic waters had a mean intensity of 6 (Appy & Burt 1982).

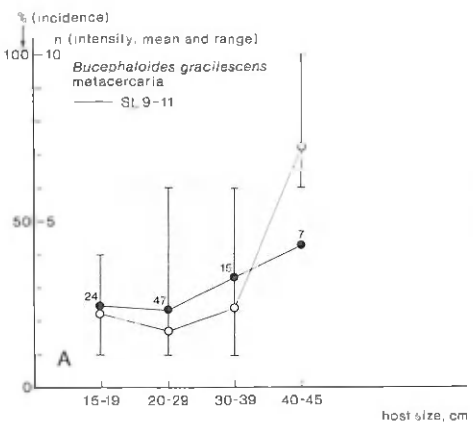
P. squamatus has an arctic-boreal distribution and is found in Cottidae, Pleuronectidae and occasionally in other fish families from the north Atlantic Ocean, the Arctic Ocean and the north Pacific Ocean.

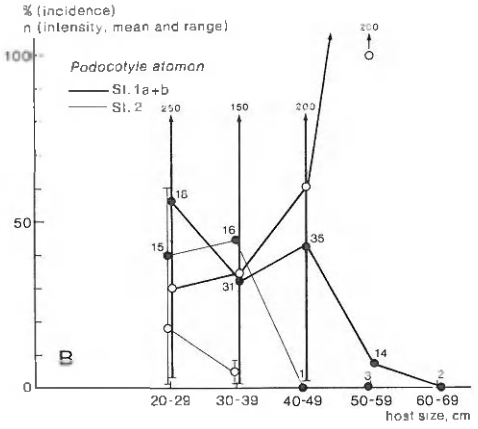
OPECOELIDAE Ozaki, 1925

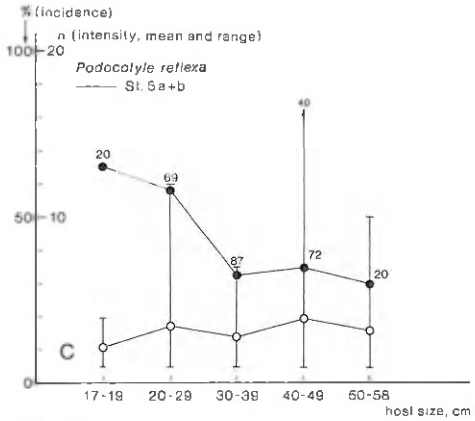
Podocotyle atomon (Rudolphi, 1802) Odhner, 1905

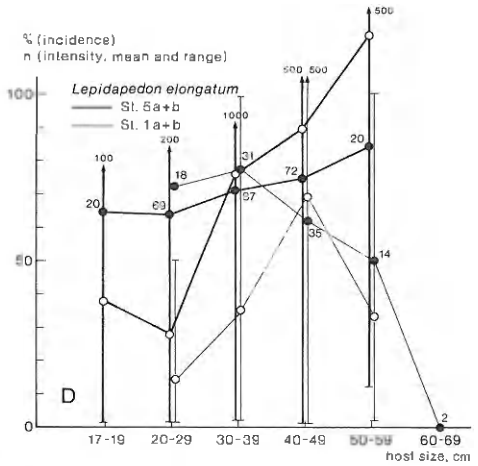
P. atomon was found in the pyloric caeca and the anterior part of the intestine of cods from stations 1-5 (Table 1, Fig. 2C).

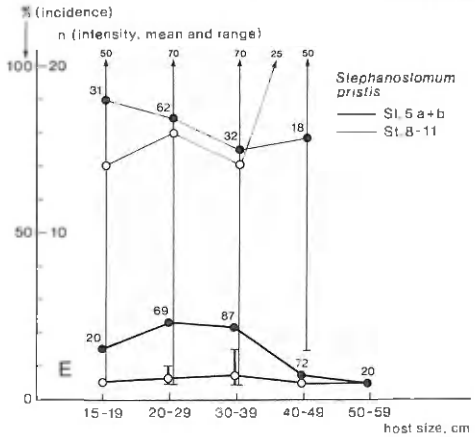
The first host is the littoral snail *Littorina saxatilis* which has been found infested on the rocky shores of northern Bornholm and in the northern Øresund (Køie 1981, 1983). The *L. saxatilis* from Bornholm was more heavily infested than the snails from the northern Øresund, which is in accordance with the higher incidences and intensities of infestation in the cods caught in the coastal area north of Bornholm compared with those from the northern Øresund. Small specimens were found from autumn and spring (station 1) and throughout the year (station 5) showing that the cods become infested all the year round. The second intermediate host of *P. atomon* at Bornholm, *Gammarus* sp., was found in both small and large cods (Fig. 3B) together with free metacercariae and metacercariae embedded in the transformed amphipod muscles (see Køie 1981). In the northern Øresund *P. atomon* was only found in cods less than 32 cm long. At stations 2 & 3, *P. atomon* only occurred in cods less than 40 cm (Fig. 3B). Polyanski (1955) found that *P. atomon* dominated in cods less than two years old, and Karasev (1983) found only the fingerlings from coastal areas infested.

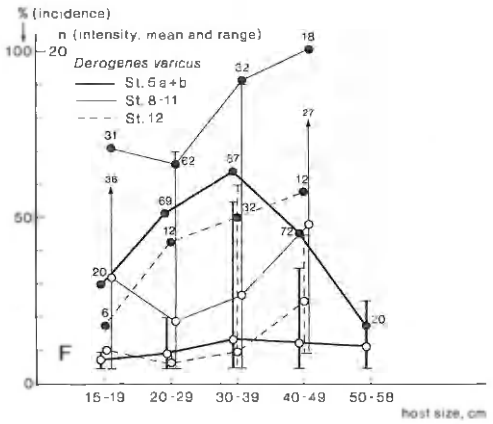

% (incidence)
n (intensity, mean and range)
Bucephaloides gracilescens
metacercaria
St. 9-11
A
15-19
20-29
30-39
40-45
host size, cm


% (incidence)
n (intensity, mean and range)
Podocotyle atomon
St. 1a+b
St. 2
B
20-29
30-39
40-49
50-59
60-69
host size, cm


% (incidence)
n (intensity, mean and range)
Podocotyle reflexa
St. 5a+b
C
17-19
20-29
30-39
40-49
50-58
host size, cm


% (incidence)
n (intensity, mean and range)
Lepidapedon elongatum
St. 5a+b
St. 1a+b
D
17-19
20-29
30-39
40-49
50-59
60-69
host size, cm


% (incidence)
n (intensity, mean and range)
Stephanostomum
pristis
St. 5a+b
St. 8-11
E
15-19
20-29
30-39
40-49
50-59
host size, cm


% (incidence)
n (intensity, mean and range)
Derogenes varicus
St. 5a+b
St. 8-11
St. 12
F
15-19
20-29
30-39
40-49
50-58
host size, cm

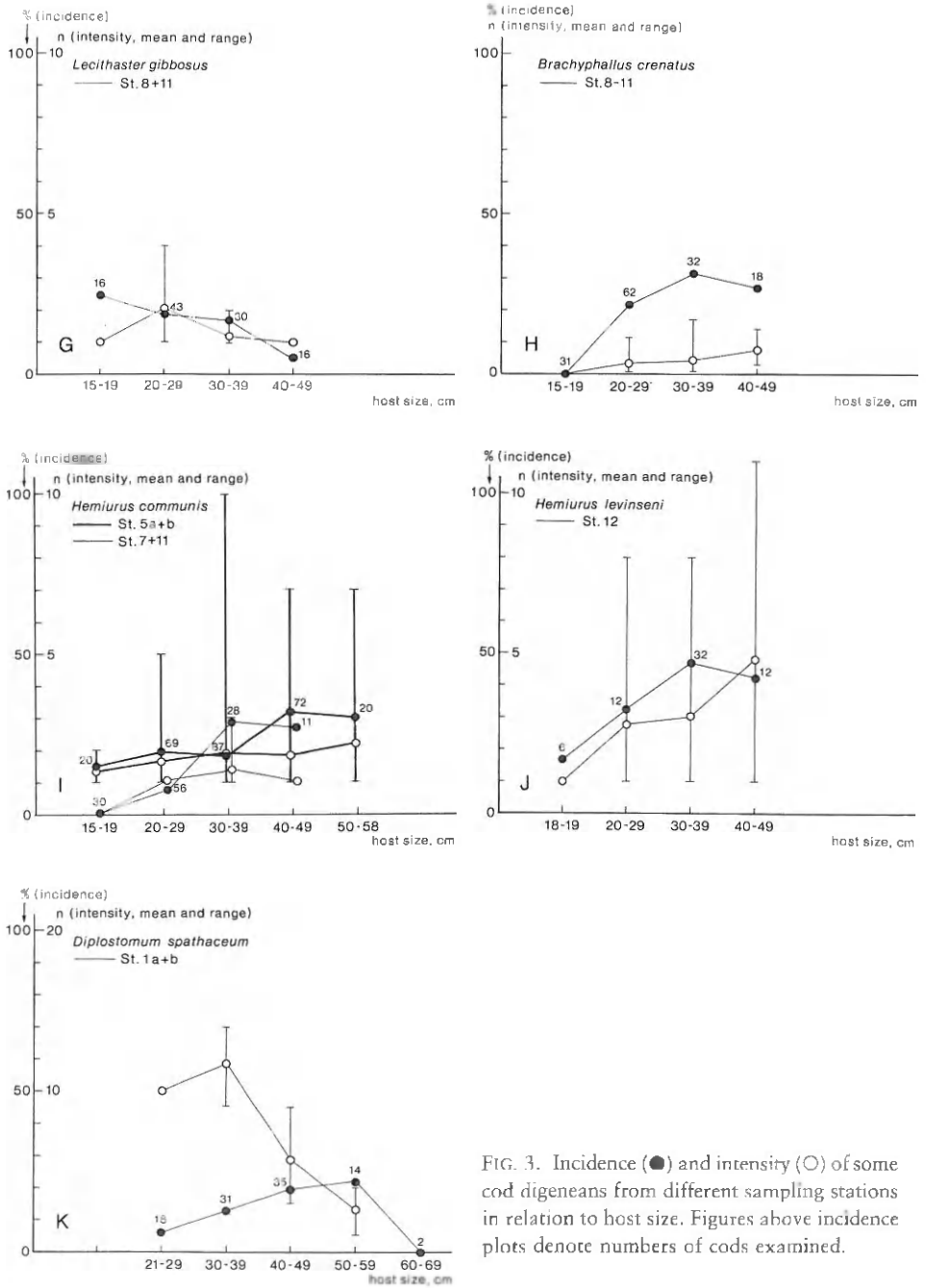


FIG. 3. Incidence (●) and intensity (○) of some cod digeneans from different sampling stations in relation to host size. Figures above incidence plots denote numbers of cods examined.

P. atomon has been recorded from a large number of fish families; it is most common in sheltered areas with reduced salinity (see Køie 1981, 1983). This fact and the fact that the cods from most stations were caught at depths where the intermediate hosts do not live may explain the absence of *P. atomon* at all the euhaline stations (S> 30‰) (stations 6-15).

P. atomon is reported from the cod from Canadian Atlantic waters (Heller 1949, Appy & Burt 1982), from the White Sea (Shulman & Shulman-Albova 1953), from the Barents Sea (Polyanski 1955, Karasev 1983), and from the western Baltic (Möller 1975). *P. atomon* has an arctic-boreal distribution and has been recorded from the north Atlantic Ocean, and the north Pacific Ocean.

Podocotyle reflexa (Creplin, 1825) Odhner, 1905

P. reflexa was found in the pyloric caeca of cods from the northern Øresund, the Lillebælt, the western Kattegat, the Skagerrak, three stations in the North Sea and in Faroese coastal waters (Table 1, Fig. 2D).

The distribution of the infested cods nearly coincides with the geographical distribution of the first intermediate hosts (Table 2, Fig. 2D). Immature *P. reflexa* were found throughout the year, and no seasonal variation in incidence was found in the northern Øresund. Cods were not found infested with *P. reflexa* in the western Baltic, probably because the snail hosts are rare in this area with reduced salinity. In coastal Faroese waters (station 14) only cods less than 42 cm were infested. Most cods from deep Faroese water (station 15) were more than 42 cm. This and the fact that *N. antiqua* and *B. undatum* at the Faroes principally live at depths of 5-40 m may explain the absence of *P. reflexa* at station 15.

The decreasing incidence with increasing host size (Fig. 3C) is in accordance with e.g. the results of Daan (1973) who found that the number of Crangonidae and Pandalidae in the stomachs of North Sea cods decreased in cods longer than 30 cm. Polyanski (1955) found that *P. reflexa* dominated in cods less than two years old.

P. reflexa has been recorded from cods from the Atlantic coast of North America (often under its synonym *P. olssoni* Odhner, 1905, see Dollfus 1953), and in addition from western Greenland (Brinkmann 1975), the Barents Sea (Polyanski 1955) and Canadian Atlantic waters (Appy & Burt 1982). *P. reflexa* has an arctic-boreal distribution and is found in Gadidae from the north Atlantic Ocean, the Arctic Ocean, and the north Pacific Ocean.

LEPOCREADIIDAE Nicoll, 1935

Opechona bacillaris (Molin, 1859) Looss, 1907

O. bacillaris was found in the pyloric caeca of cods from the northern Øresund, the western Kattegat, the Skagerrak and one station in the North Sea (Table 1, Fig. 2E).

Infested cods were found in all size groups. The finds of immature worms and worms with a few eggs only indicate that the cods are infested by ingesting the intermediate hosts (Table 2) and not e.g. whitings, which together with the mackerel are the main final hosts of *O. bacillaris* in Danish and adjacent waters. In the northern Øresund it was only found in June-August. The distribution of infested cods in Danish and adjacent waters coincides with the distribution of the snail host (Fig. 2E). *O. bacillaris* has not previously been recorded from the cod. It has a lucitanian-boreal distribution, being recorded mainly from the coast of western Europe and the Mediterranean Sea.

Lepidapedon elongatum (Lebour, 1908) Nicoll, 1910

L. elongatum occurred in the pyloric caeca and, in heavily infested cods, also in the anterior part of the intestine. It was found at all stations apart from four in the North Sea (Table 1, Fig. 2F).

The cercaria of *L. elongatum* was found in August 1984 in the rissoid snail *Onoba aculeus* (Gould). *Nereis diversicolor* Müller and other polychaetes were used as experimental second intermediate hosts (Køie 1985). Metacercariae identical with those obtained from experimentally infected polychaetes have been found in *N. pelagica* L. from the littoral zone in the Barents Sea (recorded as *L. gadi* (Yamaguti, 1934)) (Amosova 1955).

The distribution of the snail host nearly coincides with that of infested cods (Fig. 2F). *O. aculeus* has been found at Bornholm (as *O. striata* (Adams), a synonym of *O. semicostata* (Montagu), with which it often has been confused) (Jaeckel 1952), but it does apparently not extend further into the Baltic. *L. elongatum* has not been found in cods off Poland (Markowski 1933, Studnicka 1965, Rokicki 1975) indicating that these cods do not migrate to the area around Bornholm or west of Bornholm. The few infested cods caught at stations 8 & 10 must have acquired the infestation in an area where the snail host lives. *O. aculeus* has not been recorded at the Faroes, but *O. striata*, with which it might have been confused, lives at the Faroes to a depth of about 40 m. *L. elongatum* was common in coastal, shallow-water cods caught off Bergen (own observations, August 1975).

In the northern Øresund recently excysted worms were found in all size groups of cods and throughout the two-year period. Here the incidence and mean intensity increased with increasing host size (Fig. 3D). At stations 1-4 the

incidence decreased slightly with increasing host size. Polyanski (1955) found that *L. elongatum* (as *L. gadi*, see below) dominated in cods less than two years old.

Specimens apparently identical with *L. elongatum* have been described, e.g. *L. microcotyleum* Odhner (in Dollfus 1953) and *L. gadi* (Yamaguti, 1934) and others. Based on descriptions and figures in the literature it seems reasonable to consider *L. microcotyleum* and *L. gadi* to be synonyms of *L. elongatum*, as most authors do, although nobody has proven the synonymity of these forms. In addition to the records mentioned by Dollfus (1953), *L. elongatum* has been reported from cods from the Barents Sea (Polyanski 1955, as *L. gadi*, and Karasev 1983, as *L. elongatum*), from the White Sea (Shulman & Shulman-Albova 1953, as *L. gadi*), from Scottish waters (Williams *et al.* 1970, as *L. microcotyleum*), from the east coast of Greenland, the Atlantic coast of Canada, and the west coast of Sweden (Brinkmann 1975, Bray 1979, Appy & Burt 1982, and Thulin 1971, all as *L. elongatum*). It was found in cods from coastal, shallow water off Holsteinsborg, western Greenland (own observations, August 1984).

L. elongatum has an arctic-boreal distribution, as it is recorded mainly from Gadidae from the north Atlantic Ocean, the Arctic Ocean, and the north Pacific Ocean.

Lepidapedon rachion (Cobbold, 1858) Stafford, 1904

L. rachion was found in the intestine of cods from the northern Øresund, the Lillebælt, the western Kattegat and Faroese coastal waters (Table 1, Fig. 2G).

The life-cycle is unknown. Lebour (1908) suggested that a cercaria developing in the bivalve *Cardium* (= *Cerastoderma*) *edule* L. was that of *L. rachion*, but this cercaria has recently been shown to belong to the Monorchiidae (see Sannia *et al.* 1978).

The cod is an accidental host. The main host in Danish waters is the haddock *Melanogrammus aeglefinus* (L.). In the northern Øresund the few infested cods were found evenly distributed throughout the period of investigation. The smallest specimens, which measured 300 μm in length, were found in a cod from this area. The three infested cods from stations 3 & 6 were 23, 26 and 47 cm long. However, in the northern Øresund 4.5% of the cods ≦39 cm were infested, whereas 10.9% of the cods ≧40 cm had this parasite. In Faroese coastal waters (station 14) only cods ≦39 cm were infested. Most cods from Faroese deep water (station 15) were more than 40 cm long; this may explain the different degrees of infestation at these stations.

L. rachion has often been recorded from the cod (see Dollfus 1953). Later it has been found in this host by Williams *et al.* (1970) from Scottish waters, by Thulin (1971) from the Swedish west coast, and by Bray (1979) and Appy & Burt (1982) from the Atlantic coast of Canada. *L. rachion* has been recorded mainly in Gadidae from the north Atlantic Ocean, and in addition from the Barents Sea and the Black Sea.

ACANTHOCOLPIDAE Lühe, 1909

Stephanostomum pristis (Deslongchamps, 1824) Looss, 1899

S. pristis was found in the pyloric caeca of cods from all stations except those at the Faroes, the Baltic, the Lillebælt, and the southern Øresund (Table 1, Fig. 2H).

The life-cycle and different developmental stages were described by Køie (1978) on basis of specimens from the northern Øresund. All the examined specimens (metacercariae and adults) had 24-25 oral spines in each of the two rows, and the worms were therefore classified as *S. caducum* (Looss, 1901), which only differs from *S. pristis* by the number of oral spines. *S. pristis* is recorded to have 2×18 or 36 oral spines (see Køie 1978). Examination of hundreds of adult specimens from the western Kattegat and the North Sea revealed that the number of oral spines ranged from 2×18 to 2×26, with a dominance of specimens with 2×23-25, however. Although 2×18 oral spines rarely were found it is concluded that *S. caducum* probably is a synonym of *S. pristis*.

The distribution of the infested cods nearly coincides with the geographical distribution of the snail host (Fig. 2H). *N. alderi* is rare at the Faroes, which may explain the absence of *S. pristis* in the cods from this area. The absence of *S. pristis* in the cods from the Lillebælt (station 3) may indicate that these cods had spent the previous time in the western Baltic where *N. alderi* does not live.

In the northern Øresund small and mature specimens were found throughout the two-year period. The incidence of *S. pristis* in the cods from the northern Øresund has a maximum in the intermediate size groups (Fig. 3E) in accordance with, e.g. the results by Arntz (1974) who found that gobies were preferred by cods between 21 and 30 cm long but were replaced by other prey fishes by larger cods. However, the incidence in the cods from the North Sea did not reveal such a maximum (Fig. 3E).

S. pristis is recorded from cods from English and Scottish waters and the west coast of Sweden (see Dollfus 1953, Williams *et al.* 1970, Thulin 1971). The report of *S. pristis* in cods from the Kiel Fjord (western Baltic) (Möller 1975) needs confirmation. *S. pristis* has a lusitanian-boreal distribution and has been recorded mainly in Gadidae from the European west coast from Scandinavia to the Mediterranean Sea.

AZYGIIDAE Lühe, 1909

Otodistomum sp.

Metacercariae of *Otodistomum* sp. occurred free or encapsulated in the stomach wall of cods from station 13 only (Table 1, Fig. 2O).

The first host is unknown. The smallest specimen, which occurred free in the stomach of a 21 cm long cod, measured 780 μm in length and probably represents the body of a recently ingested cercaria (see Køie 1983). Similar worms, but 2 and 3 mm long, were found encapsulated in the stomach wall of five cods. Identical metacercariae were commonly found in flatfishes from localities between stations 12 & 13. The metacercariae from the flatfishes and the cod probably belong to O. *veliporum* (Creplin, 1837) (see Køie 1983).

Immature *Otodistomum* sp. has previously been recorded from cods from Canadian Atlantic waters only (Appy & Burt 1982).

Hemiuridae Looss, 1899

Derogenes varicus (Müller, 1784) Looss, 1901

D. varicus was found in the oesophagus and the very first part of the stomach of cods from all stations except the two in the Baltic (Table 1, Fig. 2I).

The distribution of the infested cods nearly coincides with the geographical distribution of the first host *Natica* spp. (Fig. 2I). As the cod may become infested by ingesting other fishes, e.g. herrings (Køie 1979) which migrate over long distances, it is not unexpected to find *D. varicus* in a cod from station 4 where the snail hosts do not occur. The incidence of infestation in relation to the size of the cods from the northern Øresund shows a maximum in the intermediate size groups (Fig. 3F), which gives no clue to which animals function as intermediate host or transport host in this area. In the North Sea, however, the incidence increased with increasing host size (Fig. 3F). In the Barents Sea *D. varicus* was more common in cods older than two years than in smaller cods (Polyanski 1955). Meskal (1967) found that the largest cods off the west coast of Norway harboured more *D. varicus* than small cods (<60 cm). In these areas, as well as in the North Sea, it is most likely that the cod acquires the parasite by preying upon fishes.

In the northern Øresund small specimens were found throughout the two-year period, and no seasonal variation in incidence was found.

D. varicus is a common cod parasite (see Dollfus 1953). Later it has been found in cods from the west coast of Greenland (Brinkmann 1975), Canadian Atlantic waters (Gaevskaya & Umnova 1977, Bray 1979, Appy & Burt 1982), Scottish waters (Williams 1959, Williams *et al.* 1970), the Barents Sea (Polyanski 1955, Karasev 1983), the White Sea (Shulman & Shulman-Albova 1953), the west coast of Sweden and Norway (Thulin 1971, Meskal 1967), and the Kiel Fjord in the western Baltic (Möller 1975). *D. varicus* has a bipolar distribution and is found in several fish families.

Lecithaster gibbosus (Rudolphi, 1802) Lühe, 1901

L. gibbosus occurred in the intestine of cods from the northern Øresund, the western Kattegat and two stations in the North Sea (Table 1, Fig. 2J).

The life-cycle has not been worked out experimentally, but the parasitic snail *Odostomia* spp. probably function as first host (see Køie 1983). The few infested cods from the northern Øresund and the western Kattegat occurred throughout the size range of the host. The incidence in relation to the size of the cods from the North Sea decreased with increasing host size (Fig. 3G), indicating that the cods probably become infested by eating copepods (or planktonic invertebrate transport hosts). In the northern Øresund *L. gibbosus* was only found in spring, but the finds are so few that nothing can be said concerning a possible seasonal variation in infestation.

L. gibbosus has only been recorded from the cod from Scottish waters (Williams *et al.* 1970) and Canadian Atlantic waters (Bray 1979, Appy & Burt 1982). Polyanski (1955) found a juvenile unidentified *Lecithaster* in a small cod from the Barents Sea. *L. gibbosus* has an arctic-boreal distribution and has been found in several fish families from the north Atlantic Ocean, the Arctic Ocean, and the north Pacific Ocean.

Brachyphallus crenatus (Rudolphi, 1802) Odhner, 1905

B. crenatus was found in the stomach of cods from all stations, apart from two stations in the northern North Sea and in Faroese waters (Table 1, Fig. 2K).

The life-cycle has not been worked out experimentally, but the small snails *Rissoa* spp. are likely to function as first intermediate hosts (see Køie 1983). The incidence in relation to the size of cods from the North Sea (Fig. 3H) indicates that the cods may become infested by eating small fishes, e.g. clupeids, which are common hosts for this parasite.

B. crenatus has previously only been found in cods from the White Sea (Shulman & Shulman-Albova 1953) and Canadian Atlantic waters (Appy & Burt 1982). This arctic-boreal species occurs in various fish families from the north Atlantic Ocean, the Arctic Ocean, and the north Pacific Ocean.

Hemiurus communis Odhner, 1905

H. communis was found in the stomach of cods from all localities, apart from the Baltic off Bornholm, Faroese waters and two stations in the North Sea (Table 1, Fig. 2L).

The molluscan host is unknown, but the metacercariae have been recorded from copepods, chaetognaths and ctenophores (see Køie 1983). *H. communis* occurred throughout the two-year study period in the northern Øresund with

no obvious seasonal variation. The increasing incidence with increasing host size (Fig. 3I) suggests that the cod acquires the parasite by eating fishes. However, the low intensity found in most cods compared with the importance of fish, e.g. small gadoids, in the cod diet indicates that some of the parasites are digested together with the prey fish. The parasites are apparently not expelled as *H. communis* was found only in the stomach. In other areas, e.g. in coastal waters off Bergen, Norway, most cods (<60 cm) contained 10-100 *H. communis* (Meskal 1967, 120 cods investigated throughout one year; own observations, August 1975). With one exception, none of the cods from station 13 contained *H. communis*. Thus the deep-water, offshore cods off Bergen (station 13) apparently do not intermingle with the inshore, shallow-water cods caught close to Bergen. The stomach of the large coastal cods from Bergen, August 1975, were filled with calanoid copepods, some of which were infested with metacercariae of *H. communis*. It thus appears that the cods also may become infested by preying upon the second intermediate host.

H. communis has a boreal distribution, being common in several fish families from Scandinavian and northwest European coastal waters. It has previously been recorded from the cod (see Dollfus 1953, and in addition, Williams 1959, Williams *et al.* 1970, Meskal 1967, Thulin 1971, and Möller 1975).

Hemiurus luehei Odhner, 1905

This species was found in the stomach of cods from the Øresund, the Baltic and the western Kattegat (Table 1, Fig. 2M).

The life-cycle is unknown, but pelagic copepods are suggested to function as second intermediate hosts. The main final hosts in Danish waters are clupeid fishes (herring and sprat), and it is obvious that the cod become infested by feeding upon these fishes. Clupeid remains were often found in the stomachs of infested cods. It appears that the cod is an unsuitable host as a higher incidence and intensity should be expected considering the importance of clupeid fishes in the cod diet.

H. luehei has not previously been recorded from the cod. It has a mainly lusitanian distribution and is especially common in clupeid and salmonid fishes from the Atlantic Ocean and the Mediterranean Sea.

Hemiurus levinseni Odhner, 1905

H. levinseni was found in the stomach of cods from the northern North Sea and Faroese waters (Table 1, Fig. 2N).

The molluscan host is unknown. Pelagic copepods are suggested to function as second intermediate hosts. *Sagitta elegans* Verril may act as transport host as metacercariae have been found in this chaetognath from the White Sea and

Canadian Atlantic waters (Kulachkova 1972, Weinstein 1974). Only one worm was found in the cods from Faroese shallow, coastal waters, whereas all the deep-water, offshore cods were infested. The increasing incidence and intensity with increasing host size (Fig. 3J) indicate that the cod becomes infested by eating fishes. Partly digested small gadoids containing *H. levinseni* in their stomachs were commonly found in the cods from stations 12, 13 and 15. However, most worms are apparently digested as a much higher intensity should be expected considering the large number of infested prey fishes. Polyanski (1955) found that *H. levinseni* was common in older cods but relatively rare in cods less than two years old.

H. levinseni is a common cod parasite (Dollfus 1953). It has later been recorded from cods from western Greenland (Brinkmann 1975), the Barents Sea (Polyanski 1955, Karasev 1983), the White Sea (Shulman & Shulman-Albova 1953), and north of Scotland (Williams 1959). *H. levinseni* has an arctic-boreal distribution as it occurs in several fish families from the north Atlantic Ocean, the Arctic Ocean, and the north Pacific Ocean.

Lecithochirium sp.

The immature encapsulated specimens found in the external wall of the pyloric caeca of cods from Faroese coastal waters and the western Kattegat (Table 1, Fig.2P) probably belong to *L. rufoviride* (Rudolphi, 1819) Lühe, 1901. Identical worms were common in the mesenteries and external wall of the alimentary tract of the goldsinny *Ctenolabrus rupestris* (L.). Mature *L. rufoviride* were common in eel *Anguilla anguilla* (L.) caught in the same trap as the cods (station 6). Only one worm was found in each infested cod, but as the mesenteries and the external wall of the alimentary tract were examined only superficially the number of worms is probably much higher. The cod is presumably an accidental host. The molluscan host is unknown. Copepods are supposed to act as second intermediate host, and small fishes as goldsinny, as third intermediate host. Eel, conger and angler are final hosts. The infested cods were all less than 37 cm long and may have become infested by ingesting copepods. Immature *Lecithochirium* sp. has not previously been recorded from the cod.

HETEROPHYIDAE Odhner, 1914

Cryptocotyle lingua (Creplin, 1825) Fischoeder, 1903

Metacercariae of *C. lingua* were found under the skin throughout the body of cods from all stations except five in the North Sea and the two in Faroese waters (Table 1, Fig. 2O).

The littoral snail *Littorina littorea* acts as first host. The absence of *C. lingua* in the cods caught in the North Sea shows that these cods did not spend their first years in coastal, shallow water, but the fact that the snail host is rarer on the sandy beaches of western Jutland than in stony sheltered areas may also play a role. *L. littorea* is infested with *C. lingua* in the German Bay (see Køie 1983). *C. lingua* is common in cods from coastal waters off Bergen, western Norway (own observations, August 1975), indicating that these coastal cods do not mix with the offshore, deep-water cods (station 13). *L. littorea* does not live at Bornholm, so the cods caught there must have acquired the infestation in more saline areas, e.g. the western Baltic or the Øresund.

The few infested cods from stations 7 & 11 were between 18 and 30 cm long, with the greatest intensity occurring in the smallest cods. The four infested cods from the Baltic, north of Bornholm, were all more than 45 cm long, and apparently harboured old metacercariae only. In the western Baltic, the Lillebælt, the Øresund and the western Kattegat both small and large cods were infested, with only a slight tendency to accumulate in the largest (oldest) cods.

Metacercariae of *C. lingua* have been recorded from cods from North American Atlantic waters (see Dollfus 1953), Denmark (Christensen & Roth 1949), Sweden (Thulin 1971), the western Baltic (Möller 1975) and Canadian Atlantic waters (Appy & Burt 1982). *C. lingua* has an arctic-boreal distribution and is especially common in shallow-water fishes from the north Atlantic Ocean, the Barents and White Seas, and the north Pacific Ocean.

DIPLOSTOMATIDAE Poirier, 1886

Diplostomum spathaceum (Rudolphi, 1819) Olsson, 1876

The metacercariae of *D. spathaceum* were found in the eye lens of cods from stations 1 & 4 (Table 1, Fig. 2P).

The snail host in the Baltic and adjacent areas is the pulmonate snail *Lymnaea peregra* (Müller). About 10 % of the *L. peregra* living on the northern coast of Bornholm were infested with *D. spathaceum* (October 1980). The infested cods caught north of Bornholm may have acquired the infestation at Bornholm or east and northeast of Bornholm, as *L. peregra* is rare in the Baltic west of Bornholm due to the higher salinity there. Small specimens were found in cods less than 49 cm long caught in both May and October. Dead metacercariae were found in cods longer than 40 cm. These results and the slightly increasing incidence and decreasing intensity with host size (Fig. 3K) indicate, although based on only a few infested cods, that the metacercariae apparently do not survive for years in this host. In freshwater fishes *D. spathaceum* has a tendency to accumulate throughout the life of the fish host, and there they have been reported to live for up to four years (Burrough 1978).

D. spathaceum has previously been found in the cod from the Baltic only. Shulman (1949, cited by Polyanski 1958) found that the infestation increased northeasterly from Kaliningrad to the Gulf of Finland. *D. spathaceum* is a common freshwater fish parasite in Europe.

Comparison of the incidences at different stations

A relative measure of the similarities of the sampling stations was obtained using data of the incidences of the 18 digenean species (Table 1). The data from stations 3 & 4 are not included. The samples from the northern Øresund and the Baltic north of Bornholm (stations 5 & 1) were both divided into two periods, thus giving 15 'stations' in all. The incidences were compared using principal coordinate analysis. The variability accounted for in the first two axes was 45 %, and the first three axes 63 % (Fig. 4). No confidence limits can be put around the points because the analysis used did not take into account the variability within the 'stations'.

Not taking into account that the cods, except those from stations 7-13 which were collected within a period of one month, were caught at different seasons and years, and that the mean size and the numbers of the cods differed from station to station, the results were as follows: The two samples from the Baltic

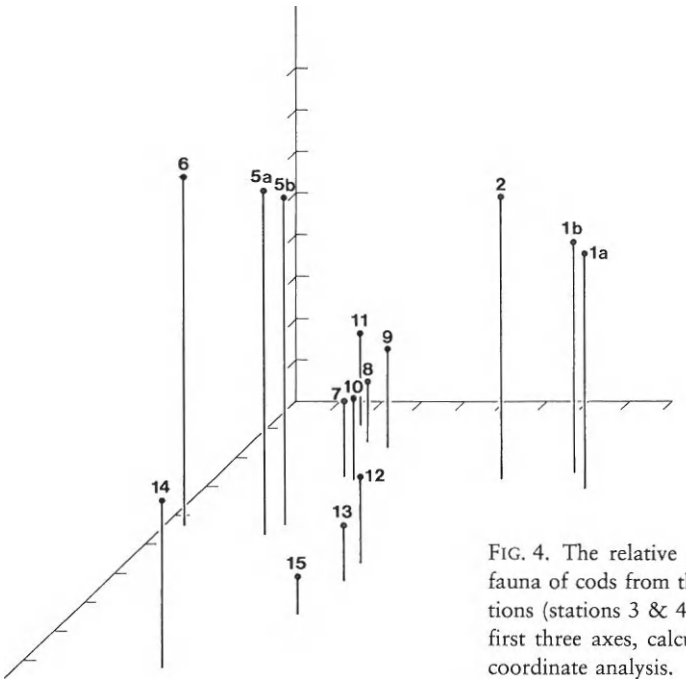


FIG. 4. The relative position of the digenean fauna of cods from the different sampling stations (stations 3 & 4 are not included) on the first three axes, calculated from the principal coordinate analysis.

north of Bornholm (1A, 1B) fall close together. Their closest neighbour is station 2, also in the Baltic. Similarly stations 5A & 5B fall close together; their closest neighbour is station 6. Stations 7-11 form a distinct group, indicating a similar parasitological fauna. The deep-water stations 12, 13 and 15 also form a distinct group. Station 14 is separate from all other stations, but its closest neighbour is station 15, also in Faroese waters.

DISCUSSION

Compared with other marine fishes from the north Atlantic Ocean and adjacent seas, the cod has an extremely rich parasite fauna, both in numbers of species and intensities of infestation (see Polyanski 1955, Appy & Burt 1982). According to Polyanski (1955) this may be explained by a) the great variety of food items consumed by the cod, b) the longevity of the cod, and c) the migration of the cod which facilitates food utilization at different depths and regions.

The stomach contents of cods from Danish and adjacent waters have been studied by, e.g. Blegvad (1916), Poulsen (1931), Hertling (1940), Rae (1967a, b), Daan (1973), and Arntz (1974, 1978). It appears that the cod feeds on nearly everything digestible, but that, in most areas, crustaceans appear to be the dominating food items in their first years of life, whereas fishes dominate in the older cods. Polychaetes, echinoderms and molluscs play a minor role in the diet.

Schultz (1911) and Nordenberg (1963) compared the food of the cod with its parasite fauna. Unfortunately they did not find (Schultz 1911), or ignored, (Nordenberg 1963) the digeneans.

The cercariae of *B. gracilescens*, *C. lingua* and *D. spathaceum* penetrate the cod, and the cercaria of *Otodistomum* sp. is probably ingested directly. The cod become infested with *P. atomon* and *P. reflexa* and probably with *Lecithochirium* sp. and *L. gibbosus* by eating crustaceans, with *O. bacillaris* by eating planktonic invertebrates, with *L. elongatum* by eating polychaetes, and with *P. squamatus* and *S. pristis* by ingesting fishes. It is unknown whether a hemiurid as *L. gibbosus*, which does not occur in the stomach, may be transferred from one fish to another, but all the remaining cod hemiurids, *D. varicus, B. crenatus* and *Hemiurus* spp., may be transmitted to the cod both through pelagic invertebrates and fishes. Of the cod digeneans, only the second intermediate host of *L. rachion* is unknown. Thus the great variety of food items does not appear to explain the rich digenean fauna of the cod, as all the digeneans which use the cod as final host, except the lepocreadiids, enter the cod via crustaceans and fishes.

Most cods from stations 1-6 belong to age groups I-III; the largest from the Bornholm samples may belong to age group IV (Poulsen 1931), whereas most cods from the North Sea samples belong to age groups I-II (Daan 1974). The

cods from the Faroes belong to age groups II-IV (Joensen & Tåning 1970). As most digeneans in the final host are supposed to survive for one to two years only, the longevity of the cod may not explain the high incidence and intensity of adult digeneans in Danish cods. Only the metacercariae of *C. lingua* – and probably also of *B. gracilescens* – may accumulate in large (old) cods.

The salinity at the sampling stations ranges from 8 ‰ (station 1) to 35 ‰ (stations 7-15), and the depths from 5 to 230 m. This may explain the high number of digenean species, as different species replace each other at the different localities and depths.

The number of digenean species at the different sampling stations varied between 5 and 14. Most digeneans were found at station 5 which, however, also was the station from which the largest number of cods was examined. None of the cods harboured more than seven species. No cods were completely without digeneans.

The low number of digeneans found in the cods from stations 1 & 2 (7 and 6 species, respectively) may be explained by the reduced salinity in the Baltic, with a concurrent decrease in number of benthic invertebrates and thus of intermediate host. Apart from *D. spathaceum* the Bornholm cods must have acquired their digeneans close to Bornholm or west of Bornholm. A large number of cods from the Baltic have previously been examined for parasites (Markowski 1933, 4 cods; Studnicka 1965, 290 cods; Rokicki 1975, 7 cods; all from off Poland, and Schultz 1911, 17 cods, from Kiel Bay to south of Bornholm), but no digeneans were found (the eyes were apparently not examined). Eight species were found in the transitional areas between the Baltic and the more marine localities (stations 3 & 4).

13 and 14 species were found in the western Kattegat and the northern Øresund (stations 6 & 5, respectively). The rich digenean fauna in these cods reflects the diverse benthic invertebrate fauna in these areas. 6-8 species were found in the samples from the Skagerrak and the North Sea, 17-40 m (stations 7-11), whereas only 5 and 6 species were found at the deep-water localities in the North Sea and Faroese waters (stations 12, 13 and 15). The number of molluscan intermediate hosts decreases with increasing depths, which explain the low diversity of cod digeneans at the three deepest stations. The shallow-water Faroese cods (station 14) had 8 species.

The absence of a seasonal variation in incidence and intensity of digeneans in the cods from the northern Øresund does not necessarily indicate that a seasonal variation is absent in other areas as, e.g. Möller (1975) found that both the incidence and intensity of *P. atomon* in cods from the Kiel Fjord, 1-3 m, the western Baltic, were highest in late summer and autumn. A seasonal variation is most likely to occur in shallow-water areas with great seasonal fluctuations in temperature. The migration of cods may also cause a seasonal variation within a limited area, if the cods belong to different stocks.

Only *P. atomon, P. reflexa, L. elongatum, C. lingua* and *D. spathaceum* fulfil the criteria mentioned by Køie (1983) for digeneans to be suitable as indicator species (natural tags). However, even though the remaining cod digeneans have unknown life-cycles, or have a previous host in their life-cycles which is planktonic or free-swimming, their different incidences and intensities at the different stations may serve to discriminate cod stocks.

REFERENCES

AMOSOVA, I.S., 1955. On the occurrence of trematode metacercariae in some polychaetes of the Barents Sea. – Zool. Zh. **34**: 286-290. (In Russian.)

ANKEL, W.E., 1936. Prosobranchia. – Tierwelt N.-u. Ostsee 9(b): 1-240.

APPY, R.G. & M.D.B. BURT, 1982. Metazoan parasites of cod, *Gadus morphua* L., in Canadian Atlantic waters. – Can. J. Zool. **60**: 1573-1579.

ARNTZ, W.E., 1974. Die Nahrung juveniler Dorsche (*Gadus morhua* L.) in der Kieler Bucht. – Ber. dt. wiss. Kommn Meeresforsch. **23**: 97-120.

ARNTZ, W.E., 1978. The food of adult cod (*Gadus morhua* L.) in the western Baltic. – Meeresforsch. **26**: 60-69.

BLEGVAD, H., 1916. *On the food of fish in the Danish waters within the Skaw.* – Rep. Dan. biol. Stn **24**: 19-72.

BRAY, R.A., 1979. Digenea in marine fishes from the eastern seaboard of Canada. – J. nat. Hist. **13**: 399-431.

BRINKMANN, A., JR., 1975. Trematodes from Greenland. – Meddr Grønland **205**(2): 1-88.

BURROUGH, R.J., 1978. The population biology of two species of eyefluke, *Diplostomum spathaceum* and *Tylodelphys clavata*, in roach and rudd. – J. Fish Biol. **13**: 19-32.

CHRISTENSEN, N.O. & H. ROTH, 1949. Investigations on internal parasites of dogs. – K. Vet.- og Landbohøjsk. Aarsskr. 1949: 1-73.

CHUBRIK, G.K., 1952. On the life cycle of the fish trematode *Prosorhynchus squamatus* Odhner, 1905. – Dokl. Akad. Nauk SSSR **83**: 327-329. (In Russian.)

DAAN, N., 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. – Neth. J. Sea Res. **6**: 479-517.

DAAN, N., 1974. Growth of North Sea cod, *Gadus morhua*. – Neth. J. Sea Res. **8**: 27-48.

DAVIS, F.M., 1925. Quantitative studies on the fauna of the sea bottom. No. 2. Results of the investigations in the southern North Sea, 1921-24. – Fishery Invest., Lond., Ser. 2. **8**(4): 1-50.

DOLLFUS, R.P., 1953. Aperçu general sur l'histoire naturelle des parasites animaux de la morue Atlanto-Arctique, *Gadus callarias* L. (=*morhua* L.) et leur distribution geographique. – *In* P. Lechevalier (ed.): Encyclopedie Biologique, Vol. 43, 423 pp. L. Moulin, Paris.

GAEVSKAYA, A.V. & B.A. UMNOVA, 1977. On the parasite fauna of the principal commercial fishes of the northwest Atlantic. – Biol. Morya (Vladivostok) **4**: 40-48. (In Russian.)

HELLER, A.F., 1949. Parasites of cod and other marine fish from the Baie de Chaleur region. – Can. J. Res., Sect. D, **27**: 243-264.

HERTLING, H., 1940. Untersuchungen über die Ernährung von Meeresfischen. II. Quantitative Nahrungsuntersuchungen an Schellfischen (*Gadus aeglefinus*), Wittlingen (*G. merlangus*) und Dorschen (*G. morhua*) aus der Nordsee unter besonderer Berücksichtigung des Wärmwertes der Nahrung. – Ber. dt. wiss. Kommn Meeresforsch. **9**: 274-323.

HUNNINEN, A.V. & R.M. CABLE, 1943. The life history of *Podocotyle atomon* (Rudolphi) (Trematoda: Opecoelidae). – Trans. Am. microsc. Soc. **62**: 57-68.

JAECKEL, S., 1952. Zur Oekologie der Molluskenfauna in der westlichen Ostsee. – Schr. naturw. Ver. Schlesw.-Holst. **26**: 18-50.

JENSEN, A.S. & R. SPÄRCK, 1934. Bløddyr II. Saltvandsmuslinger. – Danm. Fauna 40: 1-208.

JOENSEN, J.S. & Å. VEDEL TÅNING, 1970. Marine and freshwater fishes. – Zoology Faroes 62-63: 1-241.

JOHNSTON, B.R. & D.W. HALTON, 1981. Occurrence of *Bucephaloides gracilescens* metacercariae in three species of gadoid fish. – J. Fish Biol. 18: 685-691.

JÄGERSKIÖLD, L.A., 1971. A survey of the marine benthonic macro-fauna along the Swedish west coast 1921-1938. – GöteborgsK. Vetensk.- o. VitterhSamh. Handl., Zool. 6: 1-146.

KARASEV, A.B., 1983. Parasitological investigations on 0-group cod in the Barents Sea in the autumn and winter of 1979/1980. – Annls biol., Copenh. 37: 126-127.

KULACHKOVA, V.G., 1972. Helminths of *Sagitta elegans* from the White Sea. – Parazitologiya 6: 297-304. (In Russian.)

KØIE, M., 1975. On the morphology and life-history of *Opechona bacillaris* (Molin, 1859) Looss, 1907 (Trematoda, Lepocreadiidae). – Ophelia 13: 63-86.

KØIE, M., 1978. On the morphology and life-history of *Stephanostomum caducum* (Looss 1901) Manter 1934 (Trematoda, Acanthocolpidae). – Ophelia 17: 121-133.

KØIE, M., 1979. On the morphology and life-history of *Derogenes varicus* (Müller, 1784) Looss, 1901 (Trematoda, Hemiuridae). – Z. ParasitKde 59: 67-78.

KØIE, M., 1981. On the morphology and life-history of *Podocotyle reflexa* (Creplin, 1825) Odhner, 1905, and a comparison of its developmental stages with those of *P. atomon* (Rudolphi, 1802) Odhner, 1905 (Trematoda, Opecoelidae). – Ophelia 20: 17-43.

KØIE, M., 1983. Digenetic trematodes from *Limanda limanda* (L.) (Osteichthyes, Pleuronectidae) from Danish and adjacent waters, with special reference to their life-histories. – Ophelia 22: 201-228.

KØIE, M., 1985. On the morphology and life-history of *Lepidapedon elongatum* (Lebour, 1908) Nicoll, 1910 (Trematoda, Lepocreadiidae). (In preparation.)

LEBOUR, M., 1908. Fish trematodes of the Northumberland coast. – Rep. scient. Invest. Northumb. Sea Fish Comm. (1907): 23-67.

MARKOWSKI, S., 1933. Die Eingeweiderwürmer der Fische des Polnischen Balticums. – Archwm Hydrobiol. Ryb. 7: 1-58.

MATTHEWS, R.A., 1973. The life-cycle of *Prosorhynchus crucibulum* (Rudolphi, 1819) Odhner, 1905, and a comparison of its cercaria with that of *Prosorhynchus squamatus* Odhner, 1905. – Parasitology 66: 133-164.

MATTHEWS, R.A., 1974. The life-cycle of *Bucephaloides gracilescens* (Rudolphi, 1819) Hopkins, 1954 (Digenea: Gasterostomata). – Parasitology 68: 1-12.

MESKAL, F.H., 1967. Seasonal fluctuation in the population of two common trematode species from the stomach of the cod. – Sarsia 26: 13-20.

MUUS, B.J. & P. DAHLSTRØM, 1964. Havfisk og Fiskeri. G.E.C. Gads Forlag, København. 244 pp.

MÖLLER, H., 1975. Die Parasiten des Dorsches (*Gadus morhua* L.) in der Kieler Förde. – Ber. dt. wiss. Kommn Meeresforsch. 24: 288-294.

NORDENBERG, C.B., 1963. Studies on the relations of fish, food, intestinal parasites in cod, whiting and haddock. – Acta Univ. lund. N.F. Avd. 2, 58(14): 1-54.

ODHNER, T., 1905. Die Trematoden des arktischen Gebietes. – Fauna arct. 4: 291-372.

PETERSEN, G.H., 1968. Marine Lamellibranchiata. – Zoology Faroes 55: 1-80.

PETERSEN, G.H., 1977. The density, biomass and origin of the bivalves of the central North Sea. – Meddr Danm. Fisk.- og Havunders. N.S. 7: 221-273.

POLYANSKI, Y.I., 1955. Parasites of the fish of the Barents Sea. – Trudy zool. Inst. Leningr. 19: 5-170. (English translation: I.P.S.T. 1966, 158 pp.)

POLYANSKI, Y.I., 1958. Ecology of parasites of marine fishes. – *In* V.A. Dogiel, G.K. Petruchevski & Y.I. Polyanski (eds): Parasitology of Fishes, 363 pp. Leningrad Univ. (English translation, Oliver & Boyd, London. 1961. 384 pp.)

POULSEN, E.M., 1931. Biological investigations upon the cod in Danish waters. – Meddr Kommn Danm. Fisk.- og Havunders. Fiskeri **9**(1): 1-148.

RAE, B.B., 1967a. The food of cod in the North Sea and on west of Scotland grounds. – Mar. Res. 1967, **1**: 1-68.

RAE, B.B., 1967b. The food of cod on Faroese grounds. – Mar. Res. 1967, **6**: 1-23.

ROKICKI, J., 1975. Helminth fauna of fishes of the Gdańsk Bay (Baltic Sea). – Acta parasit. pol. **23**: 37-84.

SANNIA, A., B.L. JAMES & E.A. BOWERS, 1978. The morphology of *Cercaria cerastodermae* I nom. nov. (Monorchiidae) (= *Cercaria lepidapedon rachion* (Cobbold, 1858) *sensu* Lebour, 1908) a rare digenean parasite of the cockle in Britain. – J. nat. Hist. **12**: 487-500.

SCHULTZ, G., 1911. Untersuchungen über Nahrung und Parasiten von Ostseefischen. – Wiss. Meeresunters. Abt. Kiel **13**: 285-312.

SHULMAN, S.S. & R.E. SHULMAN-ALBOVA, 1953. Parasites of fishes of the White Sea. – Trudy Karel.-Fin. Fil. Acad. Nauk SSSR, Moskva, Leningrad. 198 pp. (In Russian.)

SPÄRCK, R. & G. THORSON, 1933. Marine Gastropoda Prosobranchiata. – Zoology Faroes **52**: 1-56.

STUDNICKA, M., 1965. Internal parasites of the cod, *Gadus callarias* L., from the Gdańsk Bay of the Baltic Sea. – Acta parasit. pol. **13**: 283-290.

STUNKARD, H.W., 1930. The life history of *Cryptocotyle lingua* (Creplin), with notes on the physiology of the metacercariae. – J. Morph. **50**: 143-191.

SZIDAT, L., 1924. Beiträge zur Entwicklungsgeschichte der Holostomiden. II. – Zool. Anz. **61**: 249-266.

TEBBLE, N., 1966. British Bivalve Seashells. – The British Museum (Natural History). London. 212 pp.

THULIN, J., 1971. Parasitic platyhelminths in cod (*Gadus callarias*). – Zool. Revy **33**: 76-84.

WEINSTEIN, M.S., 1974. Studies on the relationship between *Sagitta elegans* Verrill and its endoparasites in the southwestern Gulf of St. Lawrence. – Diss. Abstr. **34B**(10): 5062.

WILLIAMS, H.H., 1959. A list of parasitic worms, including 22 new records, from marine fishes caught off the British Isles. – Ann. Mag. nat. Hist., Ser. 13, **2**: 705-715.

WILLIAMS, H.H., A.H. MCVICAR & R. RALPH, 1970. The alimentary canal of fish as an environment for helminth parasites. – Symp. Br. Soc. Parasit. **8**: 43-77.

B1289