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The life cycle of *Dichelyne* (*Cucullanellus*) *minutus* (Nematoda: Cucullanidae)

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Abstract. Mature specimens of the nematode *Dichelyne* (*Cucullanellus*) *minutus* (Rudolphi, 1819) (Ascaridida, Cucullanidae, Seuratoidea) were obtained from the intestine of flounder *Platichthys flesus* (L.) caught in the Øresund, Denmark. Plaice *Pleuronectes platessa* L. and common goby *Pomatoschistus microps* (Kröyer) also harbour this species. The eggs embryonate on the seabottom. Larvae about 440 µm long, and believed to be in their third stage, hatch from the eggs. These larvae are not directly infective to flounders or gobies. The polychaete *Nereis diversicolor* O.F. Müller acts as obligatory intermediate host. Experimental infections showed that larvae >600 µm long and provided with a chitinous tooth survived in flounder and common goby. The third-stage larvae moult to fourth-stage larvae in the fish gut wall. Mature worms occur in the lumen of the anterior part of the intestine. All developmental stages may be transferred from one flounder to another; thus the flounder may acquire the parasite also by devouring infected gobies.

Dichelyne (*Cucullanellus*) *minutus* (Rudolphi, 1819) (Nematoda, Ascaridida, Seuratoidea, Cucullanidae) is a small fusiform nematode. Flounder *Platichthys flesus* (L.) is the type host and the type locality is the Baltic area. It has been recorded from off the northwestern Europe, from the Baltic Sea, the Mediterranean and the Black Sea area (Gibson 1972, Fagerholm 1982). The morphology of the adult worm has been described by Gendre (1926), Törnquist (1931), Berland (1970), MacKenzie and Gibson (1970) and Fagerholm (1982). The morphology of the third- and fourth-stage larvae from the intestinal wall of flounder has been described by Janiszewska (1939) and Gibson (1972). The life cycle has not been worked out experimentally. In the Caspian Sea, larvae of *D. minutus* have been reported in the polychaete *Nereis diversicolor* O.F. Müller and in the bivalve *Abra ovata* (Philippi) (Ivashkin and Khromova 1975, Nikitina 1979, 1985, 1991).

MATERIALS AND METHODS

Study of eggs and free-living larvae. Eggs were obtained from gravid female *Dichelyne* (*Cucullanellus*) *minutus* removed from the intestine of naturally infected flounders *Platichthys flesus* (L.) captured in the Øresund at a depth of 10-20 m. Naturally released eggs and eggs from dissected worms were placed in seawater (30‰ S) at 15°C and 20°C to obtain larvae for descriptions and for experimental infections. Live eggs and larvae of different developmental stages were released artificially from eggs by coverglass pressure.

Collection and study of invertebrates. The following laboratory-reared invertebrates were used for experimental infections: the calanoid copepod *Acartia tonsa* Dana and the harpacticoid copepod *Tisbe furcata* Baird, the polychaetes *Capitella* sp. (Capitellidae) and *Cirratulus* sp. (Cirratulidae) and the oligochaete *Heterochaeta costata* Claparède (syn.: *Tubifex costatus*). The following species collected in the Øresund were used for experimental infections: the polychaete *Nereis diversicolor* (Nereididae) and the bivalve *Macoma balthica* (L.) (Tellinidae). Fifty specimens of the copepods and about 20 specimens of the remaining genera/species were used for experimental infections. Twice the number of each genus/species were used as controls. Over a period of one week the potential invertebrate hosts were repeatedly exposed to hundreds of free-swimming larvae of *D. minutus*, in glass containers up to 10 cm in diameter, together with laboratory-reared algae (calanoid copepods) or chopped, defrosted mysids and boiled mussels (the remaining invertebrates) (all at 15°C). About one week after the last exposure/feeding the bottom of the containers was examined to observe whether larvae remained uneaten. The *N. diversicolor* used as intermediate hosts were exposed to hundreds of free-swimming larvae within a period of one week and then removed to another container with clean sand.

Experimental infection of fish. All fish used for experimental infections were dredged in the Øresund and kept in aquaria (30‰ S, 10°C) for at least four months before they were used. During this period they were fed on defrosted mussels, mysids and prawns only. The experimental infections were carried out at 15°C and the exposed fish were kept at this temperature. Within a one-week period four 0-group flounders and four adult common gobies *Pomatoschistus microps* (Kröyer) (all 4-6 cm long) were exposed to hundreds of free-swimming larvae together with chopped, defrosted mysids. The exposed fish were examined four weeks after initial exposure.

Three times within a one-week period five common gobies (4-6 cm long) and five 0-group flounders (5-7 cm long) were exposed to live *N. diversicolor* that had been experimentally infected with larvae of *D. minutus* of different ages. The fish

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were examined one week and eight weeks after initial exposure. Two 1-group flounders (15 cm long) were each exposed to about 20 specimens of mature males of *D. minutus* placed in pieces of defrosted prawns and mussels. The flounders were examined two weeks after exposure.

Study of parasitic stages. Eggs and larvae from spontaneously hatched eggs, and larvae from naturally and experimentally infected hosts, were studied live and after fixation in Berland's fluid (glacial acetic acid : 40% formalin, 19 : 1), cleared in lactic acid and mounted in glycerol jelly. Measurements (in µm) are based on 10 specimens of live worms slightly flattened under coverglass pressure.

RESULTS

Eggs and free-living third-stage larvae. Most eggs are uncleaved when released from the female worm. However, at least two females removed from a recently caught flounder (August) harboured cleaved eggs, and those close to the vulva were apparently fully embryonated. Most naturally released eggs started spontaneous hatching within one week at 20°C and two weeks at 15°C. The thin-shelled fully-embryonated eggs (Figs. 1, 10) are spherical to ovoid, 60-70 long and 50-60 wide (Table 1). The larva and two empty cuticles may be pressed out from the egg shortly before spontaneous hatching (Figs. 2, 3). One of the cuticles is thin and without structure, that below is thicker and anteriorly provided with amphids (Fig. 3, inset, top) and posteriorly with the lining of the rectum (Fig. 3, inset, bottom). Most larvae forced out of eggs shortly before spontaneous hatching are partly enclosed in the cuticle of the previous larval stage (Fig. 4). Larvae emerging from spontaneously hatched eggs (Fig. 5) were not surrounded by a moulted cuticle. These larvae are very active and capable of swimming.

Live larvae from naturally hatched eggs were 420-460 (440) long. The nerve-ring was difficult to distinguish. The excretory system includes two anterior and two posterior lateral canals. Two deirids are associated with the lateral alae. Numerous droplets occur in the posterior two thirds of the body. The tail tip is extremely pointed.

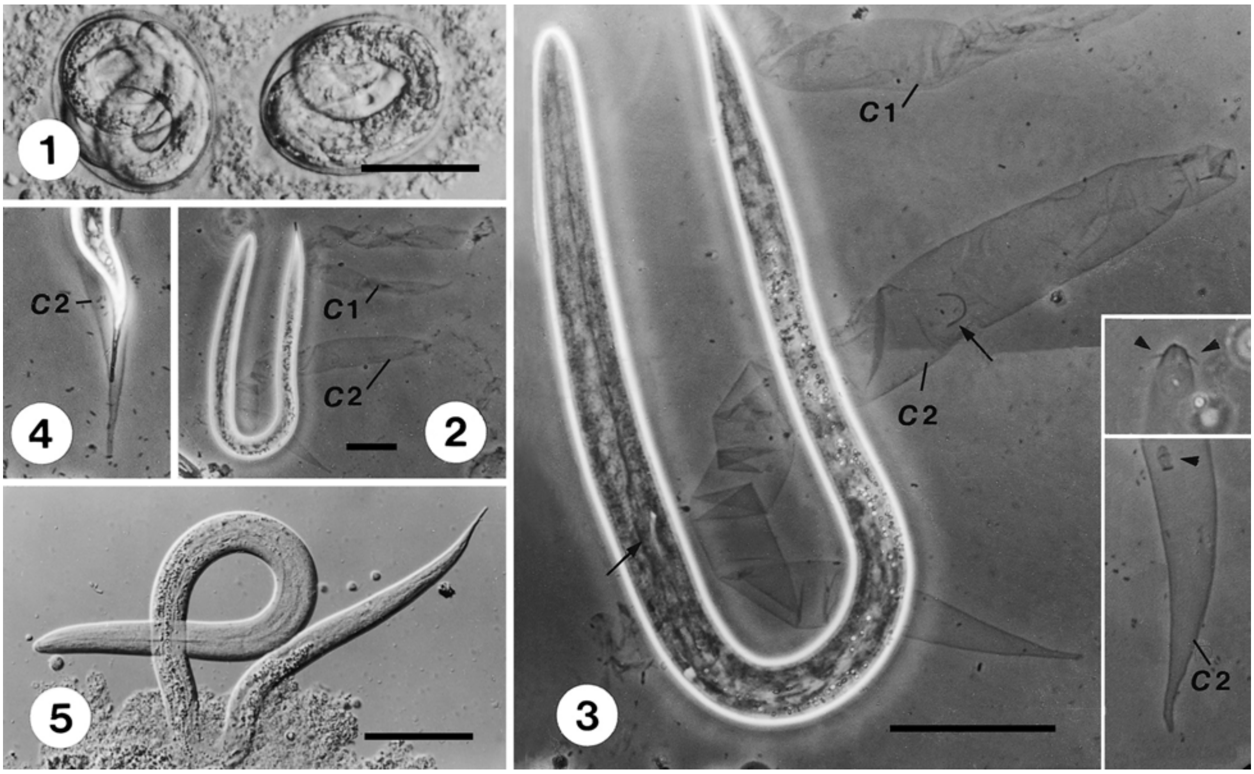
Experimental infections of invertebrates. All control invertebrates were uninfected. Exposure of copepods, bivalves and annelids other than *Nereis diversicolor* to free-swimming larvae of *D. minutus* did not result in infections, even though the larvae were ingested by the invertebrates. The larvae were found throughout the tissue of *N. diversicolor* (Fig. 6). In this host the larvae grow to infectivity (600 long) within 8 weeks. Maximum length obtained within this period was 800 (Table 1). No moult was observed in the intermediate host. The infective larva has a prominent oesophagus. The content of the oesophageal gland is dark in transmitted light. A cuticular two-pointed, tooth-like structure occurs anteriorly (Fig. 10).

Experimental infection of fish. Neither gobies nor 0-group flounders became infected by ingesting free-swimming larvae of *D. minutus*. However, both gobies and flounder became infected by devouring *N. diversicolor* with third-stage larvae >600 long. One week postinfection (p.i.) 600-long larvae were migrating in the intestinal wall or coiled within thin-walled cysts in the mucosa of the intestine of gobies and flounders. In transmitted light the live third-stage larvae are easily distinguished due to the dense glandular contents of the oesophageal gland (Fig. 7). A cuticular tooth-like structure occurs anteriorly (Fig. 8). Eight weeks p.i. about half the larvae had moulted into fourth-stage larvae (Fig. 9) within the thin-walled cyst.

Table 1. Size in µm (l – length, w – width) of different developmental stages of *Dichelyne minutus*.

Egg, l × w*	Free L3, l × w	L3 in *Nereis*, l × w	L3 in fish, l × w	L4 – imm. adult, l	Mature adult, l	References
			750-1,430	760-1,200	- 4,000	Janiszewska 1939
61-68 × 34-38	304-374		600-1,237 × 40-80	720-1,210	2,000-3,800	Gibson 1972
		770-1,043 × 57-68				Ivashkin and Khromova 1975
		790-1,148 × 41-99				Nikitina 1979
60-70 × 50-60	420-460 × 10-15	420-800 × 15-40**	600-1,200 × 45-80**	720**-		present study

* Other measurements of eggs of *D. minutus* from flounder: 68-92 × 41-54 (Markowski 1933) and 45-50 × 41-45 (Fagerholm 1982).
** Experimental infections.



Figs. 1-5. Live eggs and third-stage larvae of *Dichelyne minutus*. Figs. 1 and 5, interference contrast, Figs. 2-4, phase contrast, Figs. 3 and 4 to same scale. **Fig. 1.** Embryonated eggs. **Fig. 2.** Larva and two empty cuticles pressed out of egg shortly before natural hatching. **Fig. 3.** Detail of Fig. 2 showing excretory ducts of larva and empty cuticle (arrows). Inset (top) shows anterior end of empty cuticle with everted amphids (arrowheads). Inset (bottom) shows posterior end of cuticle with cuticular lining of the rectum (arrowhead). **Fig. 4.** Posterior end of larva forced out of egg shortly before natural hatching. A loose cuticle ensheathes the tail. **Fig. 5.** Naturally released larva. C1 – cuticle of first-stage larva; C2 – cuticle of second-stage larva. Scale bars = 50 µm.

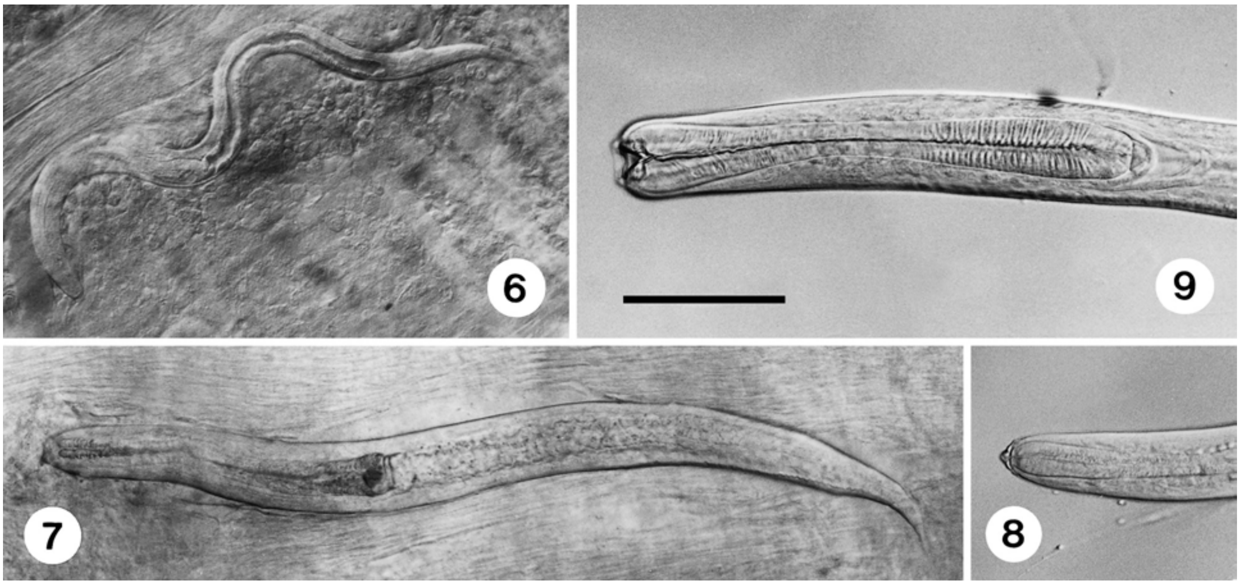
Natural infection of fish. *Dichelyne minutus* occurred in 5-10% of flounders and in 2-3% of plaice *Pleuronectes platessa* L. (15-25 cm long) caught in the Øresund from August to November at a depth of 10-20 m. The intensity varied between 1 and 7, most often 1-3. Third-stage larvae were found in 0-group flounders (5-7 cm long) in October, and in large flounders (>15 cm long) in January and May. Mature specimens were found from June to November. Small immature adult worms (>1.5 mm long) and mature worms were found free in the lumen or attached to the intestinal mucosa by their pseudobuccal capsule. Adult worms were found most commonly in the first half of the intestine. One adult unfertilised female and one adult male were found in two specimens of common goby *Pomatoschistus microps* (5-6 cm long) from 0.5 m, Nivå Bay, the Øresund (among 100-200 common gobies examined throughout the year).

Life cycle. The life cycle based on experimental infections is shown in Fig. 10.

DISCUSSION

The present species was originally described as *Cucullanus minutus* Rudolphi, 1819. Törnquist (1931) placed the species in a new genus *Cucullanellus* because of the presence of an intestinal caecum. Berland (1970) argued for keeping the species in the genus *Cucullanus* Müller, 1777 and several authors, such as MacKenzie and Gibson (1970) and Gibson (1972), placed it in the genus *Cucullanus*. Petter (1974) considered *Cucullanellus* a subgenus of *Dichelyne* Jägerskiöld, 1902. Fagerholm (1982), Moravec (1994) and Anderson (1992) placed it in the genus *Dichelyne*.

Rădulescu and Vasiliu (1951) described *Cucullanellus gobii* from a gobiid from the Black Sea, but a comparison between their description and the present species shows that *C. gobii* is a synonym of *D. minutus*. The description by Rădulescu and Vasiliu (1951) has apparently been overlooked by later researchers. Specimens found in



Figs. 6-9. *Dichelyne minutus* in *Nereis diversicolor* and *Platichthys flesus*. Interference contrast. All to same scale. **Fig. 6.** Live non-infective, third-stage larva in *N. diversicolor* 3 weeks p.i. **Fig. 7.** Live third-stage larva in intestinal mucosa of flounder one week p.i. **Fig. 8.** Anterior end of fixed third-stage larva from flounder intestine one week p.i. **Fig. 9.** Anterior end of fixed fourth-stage larva 8 weeks p.i. Scale bar = 100 µm.

gobiids in the Black and Caspian Seas are mentioned as *Cucullanus minutus* by e.g. Naidenova (1974; for other records, see Gibson 1972 and Moravec 1994). For synonyms, see Törnquist (1931), Campana-Rouget (1957) and Moravec (1994). The first two did not mention cucullanids from the Gobiidae, whereas Moravec (1994) considered it likely that specimens found in the Gobiidae belong to another species. However, the present specimens from naturally infected common gobies were morphologically identical with *D. minutus* from flounder. Besides, common gobies were experimentally infected with larvae of *D. minutus* from flounder.

The type host of *Dichelyne minutus* is the flounder *Platichthys flesus* and the type locality is Scandinavian waters. In this area the flounder is the main final host. It has repeatedly been recorded in flounders from the Baltic Sea (see Fagerholm and Køie 1994). In the Baltic Sea, it has, as *Cucullanus fusiformis* (Molin, 1860), been recorded from plaice by Markowski (1933), and, as *Cucullanellus minutus*, from dab *Limanda limanda* (L.) by Rokicki (1975). In the Black Sea and Azov Sea the nematode is recorded as occurring in several fish families including the Gasterosteidae, Carangidae, Callionymidae, Gobiidae, Pleuronectidae (flounder) and Soleidae (Greze et al. 1975). The most important final hosts in this area are probably members of the Gobiidae. Rădulescu and Vasiliu (1951) recorded it (as *Cucullanellus gobii* Rădulescu et Vasiliu, 1951) in 95% of *Gobius melanostomus* from the Black Sea. Naidenova (1974) found *D. minutus* in 13 species of gobiids with intensities higher than one hundred. Flounders *Platichthys flesus luscus* have been transferred from the Azov Sea to the Aral Sea in the years 1979-1987 to improve the fishery in this lake where the salinity has increased to 22-23‰. The nematode was introduced to the Aral Sea with introduced fish. Yusupov and Urasbaev (1994) reported it in 13 species of fishes, including flounder and gobiid species.

In northern Europe gobies may not be important as final hosts for *D. minutus* even though the nematode may develop to maturity in these fish. In the Baltic Sea, off the Polish coast, Markowski (1935) found 1-2 specimens in 8 of 520 examined specimens of the sand goby *Pomatoschistus minutus* (Pallas) and Groenewold et al. (1996) found one adult *D. minutus* among 194 specimens of *P. minutus* from the southeastern North Sea. In the Øresund it was found in *Pomatoschistus microps* only, a brackish goby mostly living at depth less than 10 m. It is replaced by *P. minutus* at deeper waters. Members of the Gobiidae acquire the infection by ingesting *N. diversicolor*. Gobies may act also as transport hosts. When a goby harbouring a single worm is ingested by a flounder, the parasite increases its possibility to find a mate.

Baker (1984) and Kuzia (1978, cited by Anderson 1992) found that it is the third-stage larvae that emerge from eggs of two freshwater species of *Dichelyne*. The present finding that the larva is extruded from the egg together with two empty cuticles also indicates that it is the third-stage larvae which emerge from the eggs of *D. minutus*. Larvae from spontaneous hatched eggs of *Cucullanus cirratus* Müller, 1777 and *C. heterochrous*

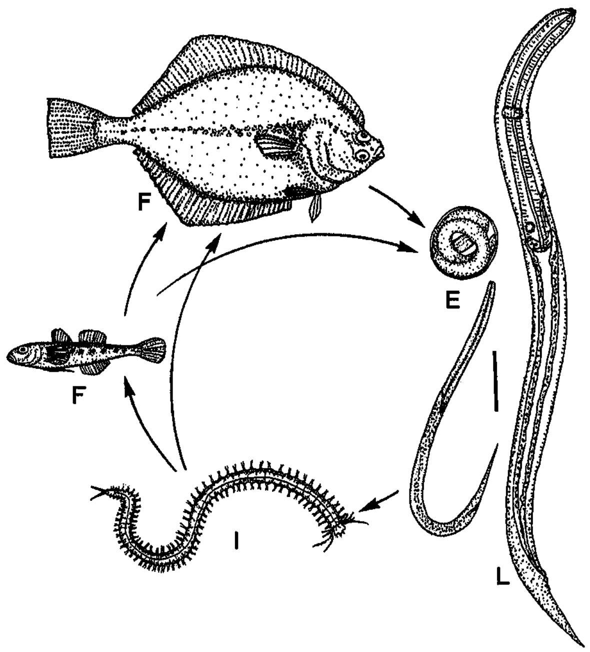


Fig. 10. The life cycle of *Dichelyne minutus.* E – egg in which two moults take place (first-stage larva→second-stage larva→ third-stage larva) and free-swimming third-stage larva; I – intermediate host *Nereis diversicolor* with third-stage larva; F – final hosts, flounder and gobies in which two moults take place (third-stage larva→fourth-stage larva→adult); L – infective third-stage larva from *N. diversicolor*. Scale bar: E, L = 50 µm.

Rudolphi, 1802 were also believed to be in their third stage (Køie 2000a, b). It is likely that this is a common feature of members of the Cucullanidae. The third-stage larvae of *D. minutus* in the intermediate host were identical with the small migrating larvae in the fish intestinal wall. Larvae believed to be fourth-stage were occasionally found slightly encapsulated in the intestinal wall, indicating that one moult has taken place inside the gut wall. It is likely that the last moult takes place in the intestinal lumen. However, the scarcity of worms for experimental infections prevented an examination of this question.

Cucullanus heterochrous, which has a very similar life cycle with polychaetes as the only intermediate host and various flatfish including flounder as final hosts, does not have a histotropic stage. The infective third-stage larvae in the intermediate host and the third-stage larvae in the fish host do not have a chitinous tooth (Køie 2000b). The chitinous tooth of *D. minutus* is probably used during penetration into and migration through the intestinal wall of the fish host.

Eggs and free-living third-stage larvae of *D. minutus* have been described by Gibson (1972). He found that very little of the internal anatomy was visible in the larvae, which he regarded as belonging to the second stage. The larva of *D. minutus* mostly differs from that of *Cucullanus heterochrous* by its extremely pointed posterior end. The anatomy of the present third-stage larvae from *N. diversicolor* and flounder is in accordance with the descriptions by Ivashkin and Khromova (1975) and Nikitina (1979, as *Anisakis* sp.) from *N. diversicolor* and with the descriptions from flounders by Janiszewska (1939, as first larval stage in the gut wall) and Gibson (1972). Janiszewska (1939) found mature females and eggs encapsulated in the liver of flounder in the Baltic. Larvae were described from capsules in the intestinal wall, in the mesenteries or in the liver. Those found encapsulated in the body cavity and liver were often decomposing (Janiszewska 1939). Also Schneider (1866, quoted by Janiszewska 1939) found it (as *Heterakis foveolata*) in the body cavity; he proposed it likely that the worm had penetrated the intestinal wall and entered the body cavity. Extraintestinal worms were not found in the present study.

Dichelyne minutus has repeatedly been found in Baltic flounders (see Fagerholm and Køie 1994). In November-December mature specimens of *D. minutus* were found in flounder caught at seven stations in the Baltic Sea from the Island of Rügen to the Estonian coast. No larval stages were found. Only the 25 flounders from the Mecklenburg Bight were not infected. The highest prevalence (72%) and intensity (30) occurred in flounders caught off the Latvian coast (Køie 1999). However, it was not known how the flounders acquire these larvae. Wülker (1930) suggested that small crustaceans such as cumaceans and decapods might act as intermediate hosts for members of *Cucullanus*, but attempts to infect such crustaceans including *Idotea* spp., *Mysis* sp., *Crangon crangon* and *Gammarus* sp. with *D. minutus* failed (Janiszewska 1939). Markowski (1966) proposed that *Nereis diversicolor* might act as its intermediate host, but experimental infections of this polychaete and various malacostracans were unsuccessful (Gibson 1972). No trace of larvae of *D. minutus* was found in various malacostracans and nereidids (MacKenzie and Gibson 1970). The fact that two-year-old flounders showed the highest prevalence, i.e., the about one-year-old flounders acquire the parasite, indicates according to Janiszewska (1939) that planktonic invertebrates may act as intermediate hosts.

Even though only *Nereis diversicolor* was experimentally infected it is possible that other polychaetes may act as intermediate hosts. Shortage of mature females and thus of larvae for experimental infections prevented a thorough investigation of potential intermediate hosts. However, the nearly exclusive occurrence in flounder and small plaice, which, similar to *N. diversicolor*, mostly live in shallow water, indicates that this polychaete is the most important intermediate host. The geographical distribution of *N. diversicolor* is much wider than that of *D. minutus* (Hartmann-Schröder 1996). *Cucullanus heterochrous,* which uses polychaetes belonging to several families as obligatory intermediate hosts (Køie 2000b), occurs as an adult exclusively in flatfishes (Moravec 1994). *Dichelyne minutus* apparently differs from this species by being hostspecific regarding the intermediate host, but non-specific regarding the final host.

Ivashkin and Khromova (1975) recorded larvae believed to be *D. minutus* in 7.7% of *N. diversicolor* from the Caspian Sea (intensity 1-2) (Table 1). Similar larvae in the same polychaete from the Caspian Sea and Azov Sea were suggested by Khromova (1975) to belong to *Cucullanus sphaerocephalus* (Rudolphi, 1809), a parasite of sturgeons (see Moravec 1994). Nikitina (1979) described and illustrated a larva believed to be *Anisakis* sp. found in *N. diversicolor* (prevalence 6.6%) and in the bivalve *Abra ovata* (prevalence 6.3%) from the Caspian Sea (Table 1). Later these larvae were identified as *Cucullanellus minutus* (Nikitina 1985, 1991). Yusupov and Urasbaev (1994) suggested that different polychaetes that have acclimated to the Aral Sea might take place in the life cycle. However, nobody has so far succeeded in infecting a polychaete or other invertebrates with *D. minutus*.

Dichelyne minutus is mostly a Lusitanean species with the North Sea and the Baltic Sea as its northern limit (Gibson 1972). In the North Sea and the Baltic Sea the temperature is so low that it cannot develop in winter. The rare occurrence of *D. minutus* in flounders in the Øresund prevented an examination of its seasonal dynamics in this area. Janiszewska (1939), Gibson (1972), Möller (1974) and Fagerholm (1982) recorded adult *D. minutus* in flounders only in summer and autumn. Third-stage larvae were found throughout the year (Gibson 1972). Flounder may become infected in the autumn (Janiszewska 1939), but most flounders are infected in spring when they return to shallow water from deeper water (Gibson 1972). Eggs shed during the summer may infect flounders during the autumn. Eggs shed in late autumn may survive unhatched on the seabottom, hatch and infect *N. diversicolor* and are swallowed by flounders the following spring.

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