The Helminth Fauna and Host-Parasite Relations of Squids *Sthenoteuthis oualaniensis* (Lesson) (Cephalopoda, Ommastrephidae) in the Indian Ocean and the Red Sea

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ABSTRACT

Nine species of helminths, including two species of trematodes, three of cestodes, two of nematodes, and one species of acanthocephalans, were found in the squid, *Sthenoteuthis oualaniensis*, from the Indian Ocean and the Red Sea. According to the incidence of infection and the degree of density of the parasite-host relationships, all of the helminths were distributed into three groups: Main, secondary, and accidental helminths [parasites]. The age and geographic changes of the helminth fauna of *S. oualaniensis* are presented. The significance of *S. oualaniensis* in the life cycle of helminths is discussed. The helminth fauna of the squids *S. oualaniensis* and *S. pteropus* from the Atlantic Ocean is compared. The principle resemblance of the helminth fauna of these species of squids is revealed. The possible reasons for the reduced diversity of species of helminths of *S. oualaniensis* are discussed.

INTRODUCTION

Many reports on the important role of squids in the life cycles of different systematic groups of helminths have been published recently (Gaevskaya and Nigmatullin 1975; Naidenova and Zuev 1978; Hochberg 1975; Stunkard 1977; and others).

In the eupelagic of the tropic zone of the World Ocean two species of the genus *Sthenoteuthis*—Atlantic *S. pteropus* (Steenstrump, 1855) and the Indo-Pacific *S. oualaniensis* (Lesson, 1830)—dominate the squids in terms of mass (numbers) and size. The role of the first species in the parasite fauna of the eupelagic of the Atlantic Ocean has been studied relatively well, but we have only fragmentary information about the helminth fauna of *S. oualaniensis*.

In this report we describe the results of a quantitative and qualitative study of the helminth fauna of *S. oualaniensis* in the tropical parts of the Indian Ocean and (partially) of the Red Sea.

The distributional area of *S. oualaniensis* includes the Indo-Pacific region from the west coast of Central and South America to the Cape of Good Hope and from Japan to northern Australia. Its numbers are dominant among the nektonic predators—consumers of the III to IV orders. The mantle length reaches 45 cm, but specimens larger than 25 cm are very rare. Males are smaller than females; their maximum length is 24.5 cm.

Considering certain morphophysiological and ecological features there are two well-differentiated forms within the species—a small early spawning form and a large late spawning one (the A and B forms mentioned in foreign literature) (Clarke 1966 and Nesis 1977).

According to our data the food links of these squids are various and change essentially in ontogenesis. The main food of young, 8 to 10 cm long, squids are large copepods, euphausiids, amphipods, young decapod crustaceans, chaetognaths, and fish larvae. The role of crustaceans in their food is reduced as the squids grow, and those > 13 to 15 cm long eat pelagic, open-ocean fish almost solely (Myctophidae in 60 to 80% of the cases) as well as small species and juvenile forms of squids—often of their own species. Sometimes they eat large crustaceans such as shrimps and blue swimming-crabs. At the same time mesoplanktonic organisms (copepods, amphipods, ostracods, chaetognaths, and others) are usual in the stomachs of even the largest squids. They are devoured with the main food organisms—Myctophidae. The food spectrums of the representatives of small and large forms are similar.

In their turn young squids serve as general food for many kinds of marine birds, dolphin fishes, snake mackerels, and lancetfishes. Middle-sized and large squids are eaten by yellowfin, longfin, and bluefin tunas; marlins; sailfishes; whitetip sharks; cachalots; and dolphins (Wormuth 1976; Young 1975; and our data). Thereby, *S. oualaniensis* is an important intermediate link between macroplankton and small fishes in the trophic structure of the eupelagic zone—planktophages on the one side and large predatory teleost fishes, sharks, marine mammals, and birds on the other side.

Our materials were taken in the tropical zone of the Indian Ocean and the Red Sea between May and August of 1978. Three hundred and thirty-seven squids were examined on board the ship *Professor Vodyanitsky*.

QUALITIES OF THE HELMINTH FAUNA

Examination of the squids disclosed nine species of helminths—trematodes [digeneids], cestodes, nematodes, and acanthocephalans.

About 2,000 metacercariae of Didymozoidae gen. and sp. were found in oval cysts with thin, transparent envelopes. They are located mainly in the external coverings of the stomach and less frequently in its muscular layer or caecum covers. The most compact accumulations of cysts were found in the forepart of the stomach, usually near a general [principal] blood vessel. From there they spread to the rest of its surface. Worms move in their

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cysts. The fact that upon fixation some larvae have long narrow bodies and others have wide flattened ones demonstrates this feature.

Judging from the morphology of the metacercariae they are of the *Monilicacecum* type, with a large muscular stomach situated above the level of the ventral sucker. The oral sucker is small. The pharynx is rather powerful and muscular. The acetabular sucker is small. The larvae differ by size and number of chambers per caecum. It should be noted that only large forms are registered [recorded] as being in the internal muscular layer of the stomach. Judging from the sizes of the metacercariae, they grow inside the squid. Upon reaching the maximum size, metacercariae live for a short time and perish, after which the cover of the cyst dissolves completely and the larvae become macerated. The same phenomenon was observed in didymozoid metacercaria from *S. pteropus* of the Atlantic. It usually occurs when the squid's mantle reaches 20 cm in length and the age is from about 6 to 8 mo. Since the beginning of mass infection occurs in 2- to 3-mo-old squids, the duration of metacercarial life in the squid does not exceed 4 to 6 mo.

Didymozoid metacercariae use a wide variety of hosts, such as different plankton organisms (i.e., copepods, euphausiids, and chaetognaths) and small teleost fish (Madhavi 1968; Reimer 1971; Overstreet and Hochberg 1975; Gaevskaya and Nigmatullin 1977). High indices of infection in the squid reflect the high intensity of feeding. According to our data, the daily diet of young squid constitutes 10 to 15% of the body mass and 4 to 5% of the body mass of adults.

At the same time, didymozoid cercariae are noted as independent components of the plankton. Carried by water currents into the mantle cavity of squids, these cercariae can actively penetrate into the squid through its coelomic coverings.

The enormous infection of squid by didymozoid metacercariae indicates an important role of squids in the life cycle of these trematodes. Heavy infection of the squids is a cause of the high infection of the final fish hosts, mainly tunas, scombroids, and xiphoids. In the Indian Ocean around 100% of wahoo and 50% of the tunas are infected by the adult stages of didymozoids, with an intensity of about 100 cysts/fish (Nikolaeva and Dubina 1978).

Immature stages of the trematode [digeneid] *Hirundinella ventricosa* are encountered singly in the coelomic cavities of squids. Large specimens, with the characteristic narrowing of the body behind the acetabular sucker, have pointed body extremities. Average dimensions of the trematodes are 6.5 × 1.5 mm. The oral sucker is 0.55 × 0.72 mm, the pharynx is 0.39 × 0.40 mm, and the acetabular sucker is 1.5 mm in diameter. The morphological characteristics of these trematodes are similar to those occurring in Atlantic squids.

Upon attaining large size, cercariae of azygiat trematodes enter into the plankton and can infect squid. They occur in the host's digestive organs with ingested food. The final hosts of *H. ventricosa* are predatory teleosts—dolphins and scombroids.

Larval *Nybelinia lingualis* (Cuvier, 1817)—the plerocercoids—localize in intestinal mesenteries, on the ovary, and on the external coverings of the stomach. They encyst also in the stomach. The scolex length is 1.6 to 1.65 mm; the bothrium portion is 0.94 to 1.1 mm long and 1.4 mm wide; the tentacular sheath is 0.52 to 0.55 mm long. Dimensions of the tentacular bulbs are 0.286 to 0.319 × 0.11 mm.

Nybelinia larvae are widely spread among teleost fishes of the World Ocean. Twelve species of cephalopods have them in the Atlantic and Pacific Oceans (Kurochkin 1972; Brown and Threlfall 1968; Dollfus 1964; and others). Dollfus (1967) discovered free-living *Nybelinia* larvae to be an organic [a regular] part of the plankton.

Indices of infection of squid by *Nybelinia* exceed those of the fishes. Thus, the extensiveness of the infection of squid reaches 90%. More than 200 plerocercoids may be found in one squid. In contrast, infection of fish seldom exceeds 40% and the intensity of infection constitutes 1 to 30 plerocercoids as a rule.

Probably, the squids acquire these parasites while ingesting their intermediate hosts—copepods and euphausiids, etc. However, considering the magnitude of the alteration of infection the second intermediate hosts—small teleost fishes—become the main source of infection. The latter circumstance promotes a second accumulation of *Nybelinia* plerocercoids in squids.

The final hosts of *Nybelinia* are large active sharks of the families Carcharhinidae, Isuridae, and others, which can ingest squids both alive and dead (after the period of spawning). In the life cycle of *Nybelinia*, the squid *S. oualaniensis* is an insert host [and may be a reservoir host] between small teleost fishes and selachians.

Larval *Tentacularia coryphaenae* Bosc, 1802 are registered [recorded] for the first time as parasites of squids of the Indian Ocean with 65% infection. Large (3.0 to 8.3 mm), mobile plerocercoids locate in the internal organs and the mantle cavity, especially in its posterior end. Plerocercoids can actively embed in the mantle wall of the squids. They are widely dispersed on marine teleosts and are recorded in four species of cephalopods of the Atlantic Ocean. The final hosts of these cestodes are sharks. The first intermediate hosts are planktonic crustaceans and the second are teleost fishes. Plerocercoids infect the squids when ingested by them.

Phyllobothrium sp. larvae, encountered rarely, usually locate in the caecum, more often in the rectum. After the squid die they can actively migrate into different portions of the body. The average length of the plerocercoids reaches 5 mm, the maximum width—1.2 mm, the apical sucker—0.143 to 0.176 mm in diameter. The dimensions of the lateral suckers are 0.275 to 0.297 × 0.352 mm. The bothridia are heart-shaped and measure 0.55 × 0.72 mm.

Plerocercoids of the genus *Phyllobothrium* are rather widely dispersed in the squids of the Atlantic Ocean (Stunkard 1977; Gaevskaya 1976; and others). As the work of American scientists (Brown and Threlfall 1968) showed, infection of the squids by plerocercoids experiences monthly and yearly variation. It is apparently connected with the short (1 yr) life cycle of these squids.

In the life cycles of the phyllobothriums, *S. oualaniensis* assumes the role of insert host [another host which is inserted] between small teleost fishes and squids and the final hosts—sharks.

Two types of *Porrocaecum* sp. larvae are recorded in 24 to 57 % of squids with an intensiveness of infection of 1 to 100 specimens. They are situated in connective tissue capsules in the body cavity. Small larvae (3 to 5 mm) localize on the external wall of the stomach; large ones (20 to 25 mm) on the internal mantle wall. Adentic nematodes were found also in squids of the Atlantic Ocean, but their infection was considerably higher (96%). It may be supposed that both forms are successive stages of the development of a single species of nematode, since their morphology is similar. However, the absence of transitional forms between the small and large larvae causes bewilderment.

The life cycle of *Porrocaecum* sp. is probably as follows: The first intermediate hosts are planktonic crustaceans (euphausiids), the second are teleost fishes, the third are squids, and the final hosts are mammals. It should be noted that *Porrocaecum caballero*, whose morphological features coincide with those of larvae registered [recorded] on the squids, has been described from *Makaira mitsukuri* from Mexican waters.

Anisakis sp. larvae are encountered relatively rarely (0.9 to 3.8%) with a low intensity of infection (one to two specimens). They locate in the ovary and coelomic membranes of the sexual cavity, rarely on the caecum walls. Ending their development in marine mammals, the larvae show great activity at high temperatures and retain their vitality for a long time. The life cycles of these larvae and the position the squids occupy in them are similar to those of the *Porrocaecum* species.

The Acanthocephala gen. and sp. I are very long and threadlike. They are found in sections of the pericardial coelom and usually attached to the mantle wall or liver with their probosces. Live worms measure from 10 to 20 cm. The morphometric characters of these acanthocephalans conform to those described from the squids of the Atlantic Ocean by Naidenova and Zuev (1978). Two mature females were found near Sokotra Island in 1964. Our most recent finds represent immature forms.

Acanthocephala gen. and sp. II were twice found in the stomach cavity of the large squids. They measured 1.0 to 1.3 cm. Their systematic identity was not determined because of poor preservation.

QUANTITATIVE INDICES OF INFECTION AND THEIR CHANGES

The total infection of the squids we examined was 98.4%. Eighty to 84% of the juveniles 2 to 8 cm long are infected with helminths. The extensiveness [prevalence] of infection of the larger squids is 100%.

According to the indices of extensiveness [prevalence] and intensity of infection, and the degree of narrowness of host-parasite relations of the squid, we may divide the helminths discovered into three groups: 1) Principal helminths (occurring at an extensiveness [prevalence] of infection of from 30 to 95% and an intensity from a few specimens to tens of hundreds of specimens)—metacercarial didymozoidae, *Porrocaecum* larvae, *Nybelinia*, and *Tentacularia*. 2) Secondary helminths (2.5 to 3.5%, single specimens)—cavital Acanthocephala gen. and sp. I, *Phyllobothrium* larvae, *Anisakis* larvae, and *H. ventricosa*. 3) Causal helminths ($<$ 1%)—small Acanthocephala gen. and sp. II from the stomach.

As the size of the squids increases, infection by various species of helminths changes unequally [disproportionately]. The poorest is the qualitative composition of helminths of the youngest squids 2 to 4 cm long. Only metacercarial didymozoidae have been found in them. Specimens of the next size group (4 to 12 cm) have *Nybelinia* larvae in addition. As squids attain a mantle size of 12 to 14 cm in length they have all species of helminths. From then on only an increase of infection by the principal species of helminths occurs. Three types of size-age dynamics of squid infection may be identified: 1) The first type is characteristic of the largest mass of parasites--the didymozoidae. The indices of extensiveness [prevalence] of infection are large for the squids of all size groups and are approximately at the same level (80.0 to 98.7). Only the intensity of infection changes noticeably. 2) In the second type, the change of infection by the other principal helminths—*Porrocaecum*, *Nybelinia*, and *Tentacularia* larvae—occurs. These parasites appear in squids 8 to 10 cm long, and when they are 14 to 18 cm long the indices of infection increase almost to the maximum. The secondary helminths—*Anisakis* and *Phyllobothrium* larvae—join this type. But the sharp rise of infection by these parasites takes place later, when the squids attain more than 20 to 22 cm in length. 3) In contradistinction to the other helminths, *H. ventricosa* and cavital acanthocephalans begin to infect specimens 10 to 12 cm long and maintain an essentially low level of infection index as the squids grow.

Infection by Didymozoidae occurs thanks to copepods, euphausiids, and chaetognaths—the principal food of the smallest squids. Further accumulation of these trematodes probably occurs when these invertebrates get into the stomachs of the squid. On the whole the formation of the helminth fauna coincides with the squid's attainment of adulthood when they become 10 to 14 cm long. This takes place when the adult squid begin to feed on adult specimens of small fishes and small squids, which are the suppliers [carriers] of cestodes, nematodes, trematodes, *H. ventricosa*, and probably of small acanthocephalans, as their principal source of nourishment. To judge from the special features of the size-age metamorphosis of the squid's infection, the majority of helminth species get into them with the representatives of different groups of fishes and small squids or with different age stages of one or another food object.

When comparing the qualities of helminth fauna and the indices of the early spawning and late spawning squids as a whole [all together], their main similarity is discovered. Their difference consists of a poorer species composition (five to nine) and low indices of infections of the early spawning forms by almost all helminths, with the exception of didymozoidae and *Nybelinia*. At the same time, all species of helminths found in early maturing squids are common for both forms, and the indices of infection of representatives of early and late maturing forms on the whole are connected with the difference of their dimensions (the length of early maturing specimens in our collections did not exceed 12.7 cm) and, in the end, of the length of life and food composition.

Within the late maturing forms the structure of the helminth fauna and the squid's infection may vary considerably depending on the geographical region of the research. In this respect the Red Sea region stands out for the paucity of its helminth fauna. It has only three species. Perhaps this is connected to an insufficient sample of squids examined from a single station. However, we do not exclude the possibility that the results obtained reflect the true situation only partially and may be a consequence of a scarcity of final hosts of the squid helminths. The high indices of infection of Red Sea squids by *Nybelinia* and the low indices of infection by didymozoidae attracted our attention.

DISCUSSION

We discovered that the chief factor leading to the infection of squids by helminths is food. As the ontogenesis of food links occurs, the helminth fauna and quantitative indices of infection also changes. The food factor promotes the transmission of these helminths to the final hosts. Xiphoid fishes, sharks, and [marine] mammals mainly use the most heavily infected medium- and large-sized squid. The latter become most accessible after spawning. Small and medium *S. oualaniensis* occur at the same time as large squids in the food of the tunas. Therefore, in this case we have full accordance between trophic and parasitic links.

Except for acanthocephalans and juvenile *H. ventricosa*, all helminths parasitizing squids represent larval forms. They have very wide [broad] specificity and use various invertebrates, teleost fishes, and squids at the same stages of their life cycles. Therefore, the use of other squids for food is the cause of the secondary accumulation of didymozoidae and different species of nematodes and cestodes in the squid. With the increase of age and size and transition to a higher trophic level, the number grows. In the life cycles of didymozoidae, cestodes, and nematodes, there is an insert host between the second intermediate hosts—planktonic invertebrates and micronekton (i.e., fish-planktophytes and small squids), and the final hosts—large nektonic predators, occupying the top of the food chains of the eupelagic zone. To speak of the squid's position in the life cycle of acanthocephalans at present would be premature. We may only suppose that the squids are their final hosts.

Considering the high indices of infection, which are not encountered in other hosts of these helminths, the high quantity, wide dispersion, and the variety and stability of trophic links we may consider *S. oualaniensis* to be one of the main obligatory hosts for didymozoidae, *Nybelinia*, *Tentacularia*, and *Porrocaecum*. *Stenotheuthis oualaniensis* is the vehicle for their transmission to the final hosts. Wide [broad] specificity and the "fish" larvae "aspect" of the helminth fauna of *S. oualaniensis* shows it to have been "acquired" by the squids relatively recently. The parasites have successfully acclimated and are incorporating this species of host, which occupies a key position in the pathway of circulation of helminths among oceanic pelagic communities [into their circle of hosts]. At present we find different species of helminths in different stages of forming parasite-host relationships. They are strongly expressed in didymozoidae, *Porrocaecum*, *Nybelinia*, *Phyllobothrium*, and *Tentacularia*. Though the food linkages of young squids are very close to marine birds, larvae of bird parasites are absent in squids.

The helminth fauna of *S. oualaniensis* represents (as a matter of fact) an impoverished version of that in the Atlantic vicariate of *S. oualaniensis*, i.e., 8 species as compared with 15. Moreover, the first species has no helminth which does not occur in the second one. The impoverishment of the species of their parasite fauna occurs primarily because of the disappearance [or lack] of the secondary and casual species of helminths.

At times the difference in the infection indices of the common species of helminths tends toward the side of a larger quantity in *S. pteropus*. In our opinion the causes of the main differences are related to the difference in the number of individuals examined (303 specimens of *S. oualaniensis* as compared with 2,200 specimens of *S. pteropus*) and in the dimension of the squids (*S. pteropus* are 2 to 50 cm in length with a mode of 20 to 30 cm). It naturally depends on the presence or absence of the secondary and, especially, of the casual species of helminths and the degree of accumulation of the principal helminths.

The main conclusion of this comparison is that both geographic vicariates have a similar position in respect to the parasite fauna of conformable [comparable?] associations of the tropical eupelagic. This is more indirect evidence that their econiches are almost identical, though that of *S. pteropus* is somewhat wider, due to its larger size.

The ancestor of *S. oualaniensis* penetrated into the Indo-Pacific from the Atlantic Ocean, rounding the southern extremity of Africa during one of the warming Pleistocene periods. During the ensuing drop in temperature and upon isolation two allopatric species were formed. Undoubtedly, the squids themselves could not have carried the helminths from the Atlantic to the Indo-Pacific, since they were only the intermediate hosts. Considering that these geographic vicariates occupy similar econiches in homologous associations of the World Ocean and considering their high ecological valency, the formation of the helminth fauna of both species evidently proceeded simultaneously.

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