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Dispersal of phytoplanktotrophic shipworm larvae (Bivalvia: Teredinidae) over long distances by ocean currents*

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Abstract

Shipworms or Teredinidae may be dispersed either as adults in floating wooden objects or as pelagic larvae drifting near the sea surface. Five shipworm species, i.e., half of those having an amphi-Atlantic geographical distribution, are known also to have pelagic phytoplanktotrophic larvae which can be carried by ocean currents. From a series of 742 plankton samples taken from throughout the temperate and tropical North Atlantic Ocean, it can be shown that shipworm larvae are not uncommon in the open sea. Teredinid veligers were found in 19 % of all samples taken. One species of larvae, identical in all details to that described by RANCUREL (1965), is particularly prevalent and is tentatively identified as *Teredora malleolus* (TURTON). A definitive identification will be possible only after the pelagic larvae of the other Atlantic species are known. The larvae of *Teredora malleolus* are found throughout the North Atlantic Gyre and the adjacent temperate and tropical seas, and from scattered records in the South Equatorial Current. Larvae of other unidentified Teredinidae species were also found. The distance that larvae may be transported depends upon the length of pelagic larval development and the velocity of the currents. From the known current velocities it can be shown that, even in a few weeks, larvae may be dispersed many hundreds of kilometers. The geographical distribution of shipworm larvae suggests that they are carried along the coasts of continents and even across ocean basins, and that this dispersal must be an important factor in the geographical distribution of the adult forms and in the maintenance of genetic continuity between populations otherwise isolated from one another.

Introduction

Shipworms or Teredinidae may be dispersed either as (1) adults in floating wooden objects, or (2) pelagic larvae drifting near the sea surface. The first mode of dispersal has been discussed recently by EDMONDSON (1962) and TURNER (1966). The transport of teredinid larvae by ocean currents has been largely overlooked (see, however, SCHELTEMA and TRUITT, 1954, pp 18 to 20; QUAYLE, 1959; NAIR, 1962; TURNER, 1965).

The family Teredinidae includes a total of about 66 species, 31 of which are known from the Atlantic Ocean (TURNER, 1966). Among the Atlantic species, one third have a wide geographical distribution and are found both in the eastern and western Atlantic Ocean.

Among the 10 amphi-Atlantic species, 5 are believed to be oviparous and to have long phytoplanktotrophic larval stages. These are *Teredora malleolus* (TURTON), *Psiloteredo megotara* (HANLEY), *Bankia carinata* (GRAY), *Bankia bipennata* (TURTON) (TURNER, 1966, p. 54), and *Nototeredo knoxi* (BARTSCH) (TURNER and JOHNSON, 1968). Three are larviparous, the larvae being retained in the mantle cavity for various lengths of time; these are *Teredo navalis* L. (LOOSANOFF and DAVIS, 1963, p. 127), *Teredo bartschi* CLAPP (TURNER, 1966, pp 54 to 55) and *Lyrodus pedicellatus* (QUATREFAGES) (ISHAM and TIERNEY, 1953). The first of these three species, *Teredo navalis*, has larvae which are released at the straight-hinge stage and consequently have a relatively longer duration of planktonic existence than the other two larviparous species (20 to 34 days; *vide*, IMAI et al., 1950; LOOSANOFF and DAVIS, 1963). The type of reproduction of the remaining two species is not yet known.

Shipworm species which lack long pelagic larval stages can only be dispersed in drifting wooden objects. For example, *Lyrodus pedicellatus* cannot possibly have achieved its very wide, nearly cosmopolitan, geographical distribution by any other means, as its larvae remain planktonic for only 24 h (ISHAM and TIERNEY, 1953). On the other hand, species with long free-swimming phytoplanktotrophic veliger stages have an opportunity to be dispersed by larval transport. In the following account the very wide geographical distribution of shipworm larvae in the North and Equatorial Atlantic Ocean is described, and conclusions drawn from these data regarding the importance of larvae for the dispersal of some teredinid species.

Methods

Between 1964 and 1969, a series of extended research cruises were made throughout the North and Equatorial Atlantic Ocean. Twenty-minute plankton tows were taken obliquely from approximately 150 m to the surface with a $^{3}/_{4}$ m net having a mesh size of 0.2 to 0.3 mm. Preliminary sorting was done at sea and larvae of all bivalve molluscs were preserved in

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70% alcohol. The remaining sample was kept in buffered, 4% formaldehyde, and final sorting was carried out after return to the shore laboratory. The cruises were made at various times of the year. Transatlantic sections were made at approximately 45°N (July-August), 39°N (July; September-October), 35°N (May-June), 25°N (January-February), 20°N (June), 10° to 15°N (February-March), and along the equator during spring and early summer. Samples also were taken in the Gulf of Mexico, the Caribbean Sea, and the Gulf Stream; along the northeastern coast of South America between the equator and 15°N; and along the West African coast from 5°S to the Canary Islands. A total of 742 samples were obtained on these expeditions; 445 from the Atlantic transects described above, 100 from shorter research cruises along the coast of North America (mostly in the Gulf Stream), 20 from the northwest African coast, and the remainder from the Caribbean and Mediterranean Seas, the Gulf of Mexico, and scattered points throughout the Atlantic Ocean. Bivalve larvae were found in 484 or 65.2% of all stations.

Description of larvae

Previous descriptions of teredinid larvae are restricted to only 9 species, although the adult affinities of some of these are quite uncertain. Only *Teredo navalis* L. has been reared from fertilization to settlement in the laboratory (IMAI et al., 1950, p. 202, Fig. 1a, b, c; LOOSANOFF and DAVIS, 1963, pp 127—129, Fig. 43; LOOSANOFF et al., 1966, pp 425—428, Figs. 57 to 58).

Other descriptions, mostly of larvae taken from the plankton are: *Teredo navalis* (MIYAZAKI, 1935, pp 4—5, pl. 2, Figs. 1—7 as *Teredo japonica*; JØRGENSEN, 1946, pp 309—310, Fig. 189; SULLIVAN, 1948, pp 12—13, pl. iv, Figs. 1—6; ZAKHVATKINA, 1959, pp 148—150, Figs. 55—56); *Bankia gouldi* (BARTSCH) (SIGERFOOS, 1908, pp 201—204, pl. vii, Fig. 1, pl. xi, Figs. 11—13); ? *Bankia bipennata* (TURTON) (REES, 1950, p. 100, pl. v, text-fig. 3); *Psiloteredo megotara* (HANLEY) (JÖRGENSEN, 1946, late larval stage, pp 308—309); *Nototeredo norvagica* (SPENGLER) (LEBOUR, 1938, pp 136—138, Fig. 4; JØRGENSEN, 1946, no Fig.); *Bankia setacea* (TRYON) (QUAYLE, 1953, pp 88—89, Figs. 1—8); *Lyrodus pedicellatus* (QUATREFAGES) (ROCH, 1940, pl. 8, Figs. 1—5; RANCUREL, 1951, pp 21—23, Figs. 1—3; ISHAM and TIERNEY, 1953, p. 581, Figs. 5—7); and *Bankia anechoensis* ROCH and *Teredo thomsonii* TRYON (RANCUREL, 1965, Figs. 1—4). Most of these descriptions are inadequate for the purpose of identifying unknown larvae from the plankton.

There are, in addition, a number of older references to teredinid larvae, chiefly of historical interest, in which the species are either not given or uncertain (QUATREFAGES, 1849; HATSCHEK, 1880; BORISIAK, 1905, p. 167, Fig. 11 (?), also p. 172, Fig. 17 in French translation; and NAKAZAWA, 1915).

Several species of Teredinidae veliger larvae are recognizable in the plankton of the North and tropical Atlantic Ocean. One, however, predominates in the samples taken, and this species is singled out for detailed consideration. This most often-found larva is tentatively identified as *Teredora malleolus* (TURTON) = *Teredo thomsonii* TYRON, *vide*, TURNER, 1966, p. 109, p. 125, because it very closely corresponds to the larval description of this species made by RANCUREL (1965) (compare Fig. 1 of present paper with Figs. 1 and 2, p. 104 of RANCUREL). The shell is nearly spherical, its height somewhat exceeding its length (Fig. 1 A); this shape is characteristic of larvae belonging to the Teredinidae. The shell color is amber, approaching brown. On intact larvae there is a clear area around the margin of the valves similar to that described on most other larval teredinids (SULLIVAN, 1948, p. 13; QUAYLE, 1953, p. 89, Figs. 3—5; LOOSANOFF and DAVIS, 1963, p. 128). This appears to be an optical illusion resulting from the spherical shape of the shell, and is not seen with a scanning-electron microscope which has greater depth of focus. The surface of each valve is sculptured with very marked concentric annuli. In addition, there are radial lines between annuli (Fig. 1 B) sculpturing similar to that described by RANCUREL (1965). There appears to be some variability in the distinctness of the radial sculpturing on different specimens. Shells of completely developed larvae are about 300 μ in height and 275 μ in length. (The dimensions given by RANCUREL in his text do not correspond with those obtained by using the scale in his Fig. 1, p. 104; the size of the larvae in his figure corresponds with the dimensions given above.) The hinge teeth are typical for the family, with 2 on the left and 3 on the right valve (Fig. 1 C, D). The dimensions of the teeth, described in detail by RANCUREL, which are seen only with difficulty under the high power (450 x) compound light microscope, are very easily observed and photographed with the electron-scanning microscope. Both shape and dimensions of the hinge teeth as given by RANCUREL (1965, pp 101—102) are identical to those of the present forms; there is no need, therefore, to repeat details of the hinge morphology here.

On living larvae there is a red circular pigmented area associated with the velum. This pigmentation is evident even on recently preserved specimens.

Although the specimens from our plankton tows are identical in all details to the larva described by RANCUREL (1965), a definitive identification is only possible when the larvae of all other teredinid species with long pelagic phytoplanktotrophic development in the Atlantic Ocean have been described.

Distribution of larvae

Shipworm larvae have been found distributed in surface waters throughout the North and Equatorial Atlantic Ocean, the Caribbean and Mediterranean Seas, and the Gulf of Mexico (Fig. 2). Indeed, 19% of

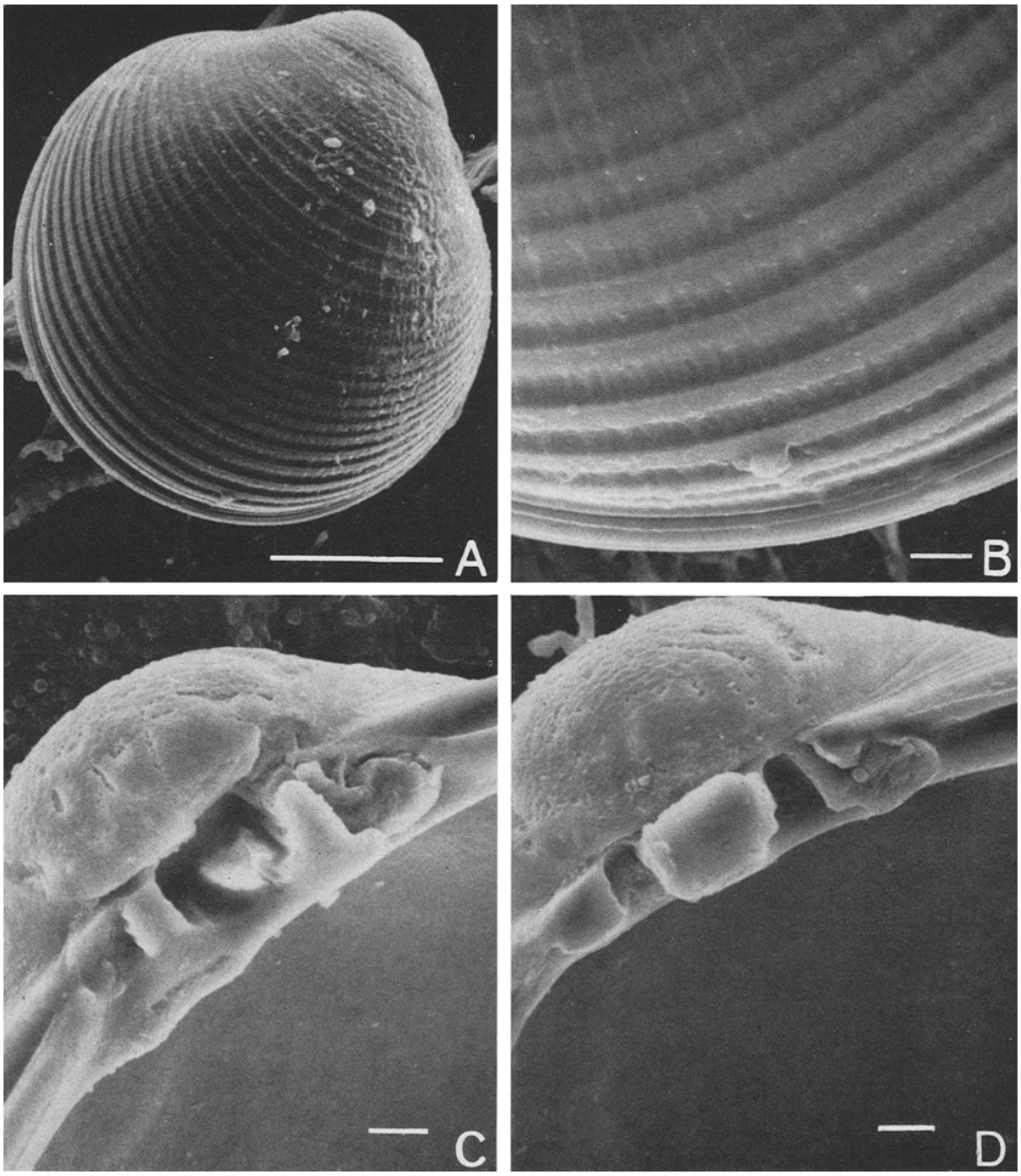

Fig. 1. *Teredora malleolus*. Larval-shell morphology of the provisionally identified species found in off-shore waters of the North Atlantic Ocean. The specimens shown in the photomicrographs are from a tow taken in the north-central Gulf of Mexico (27°01'N – 90°03'W) on June 21, 1966. (A) Whole larval shell showing concentric annuli and radial lines between annuli, scale: 100 μ; (B) detail of shell in (A) but greatly enlarged to show lines between annuli, scale: 10 μ; (C) details of hinge teeth, left valve. Large central depression will accommodate large tooth on right valve, the two small teeth will fit into the two slots in right valve, scale: 10 μ; (D) detail of hinge teeth, right valve. Two depressions accommodate teeth from left valve, scale: 10 μ. Specimens in (C) and (D) show slight damage resulting from preservation, even though larvae were kept in 70 % alcohol. The texture on the embryonic shell, however, is not artifact

all plankton samples taken contained larvae of Teredinidae. The veligers of *Teredora malleolus* (TURTON) are the most widespread of these open-ocean teredinid larvae, and were found in samples taken in the eastern Mediterranean Sea, the Canary Current, the North Equatorial Current, the western end of the South Equatorial Current, the Antilles Current, the Gulf Stream and the North Atlantic Drift between latitude

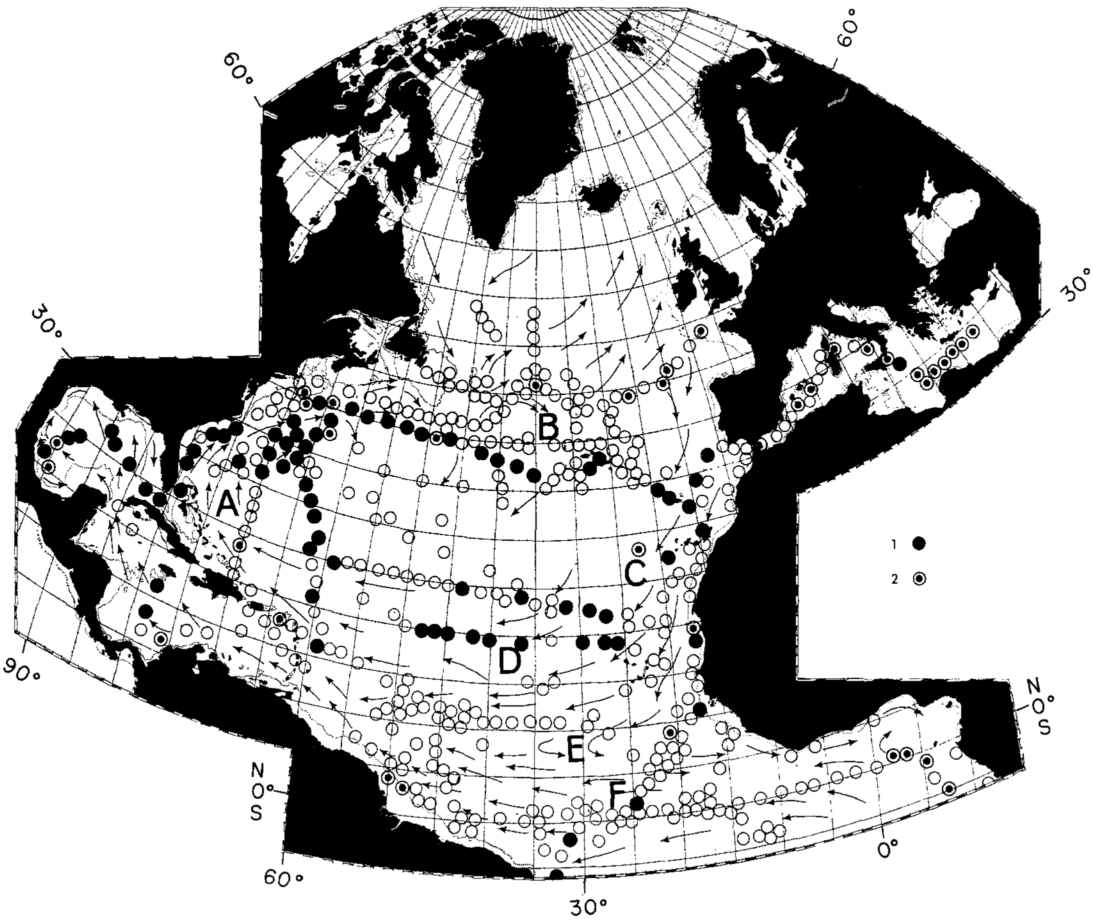

Fig. 2. Geographical distribution of shipworm larvae in the North and tropical Atlantic Ocean. (1) *Teredo malleolus* larvae: throughout North Atlantic Gyre, specifically in Gulf Stream, North Atlantic Drift, Canary Current and North Equatorial Current; scattered records also from western end of South Equatorial Current (from about 24°W to South American coast) and Caribbean and Mediterranean Seas; common in Gulf of Mexico. (2) Other species of teredinids: Mediterranean Sea, off the west coast of Africa, northeast coast of South America, Gulf and Caribbean, Antilles Current, Gulf Stream and North Atlantic Drift. Open circles: locations of plankton tows where no teredinid larvae were collected. Arrows: major ocean currents; *A* Gulf Stream; *B* North Atlantic Drift; *C* Canary Current; *D* North Equatorial Current; *E* Equatorial Countercurrent; *F* South Equatorial Current

37° and 41°N. If the major ocean currents are important in the dispersal of the larvae, one would expect shipworm veligers to be found primarily along the axes of these currents, and indeed this appears to be so. The larvae were found in surface waters at temperatures between 18° and 29 °C; they can be characterized, therefore, as belonging to a eurythermal, warm-temperate and tropical species. The known distribution of adult *T. malleolus*, which has been reported from the Mediterranean Sea, southern Europe, the northwest coast of Africa and the east coast of North America, is not inconsistent with the paths of larval dispersal demonstrated in the plankton.

Records of *Teredora malleolus* settlement on wooden test panels suspended from lightships anchored offshore confirm that larvae of this species are dispersed along the east coast of the United States by surface currents. *T. malleolus* specimens have been recovered in such panels from Fryingpan Lightship, 32 miles off Cape Fear, North Carolina; Diamond Shoals Lightship, 13 miles east of Cape Hatteras, North Carolina; and Nantucket Lightship, 40 miles southeast of Nantucket, Massachusetts (BROWN, 1953).

Shipworm larvae of other unidentified species have been collected in surface waters south of Great Britain, west of the Bay of Biscay, throughout the Mediterranean Sea, off Senegal, in the Gulf of Guinea, in the Guiana Current off the northeast coast of Brazil, in the Antilles Current, in the Caribbean Sea, in the Gulf of Mexico, in the Gulf Stream off the northeast coast of the United States, and finally in the North Atlantic Drift (*ca.* 39°N, 49°W).

Discussion

The geographical distribution of *Teredora malleolus* demonstrates the effectiveness of ocean currents in dispersing bivalve larvae. The distance that larvae may be transported along the coasts of continents or even across ocean basins is limited by the duration of the planktonic development and the current velocity. If the pelagic life of the bivalve veliger larva is long enough, or if somehow settlement can be postponed, then it is possible that the larva may drift many thousands of kilometers (*vide*, THORSON, 1961; MILEIKOVSKY, 1966; SCHELTEMA, 1966a, 1966b; SCHELTEMA, in press, a).

It has been demonstrated experimentally that bivalve larvae, given the right kind and quantity of phytoplankton food, will grow very rapidly (DAVIS, 1953; DAVIS and GUILLARD, 1958; WALNE, 1963; DAVIS and CALABRESE, 1964; BAYNE, 1965), whereas, in the absence of such optimal food conditions, as frequently occurs in the open sea, larvae may survive over long periods yet show very little growth or development (MILLER and SCOTT, 1967). TURNER and JOHNSON (1968, p. 14) remark that "... it is quite evident that the duration of the straight-hinge stage is dependent on food and that it can be extended for a considerable period if food is scarce, a factor which may be very important in dispersal."

HARRINGTON (1921) showed in the laboratory that larvae of *Nototeredo norvagica* (= *Teredo norvegica*, TURNER, 1966, p. 113) are attracted by extracts of wood and 1% solution of malic acid, and WILSON (1952, p. 56) demonstrated that larvae of "*Teredo*" could delay settlement in the absence of wood or paper. Even in larviparous species such as *Teredo furcifera* and *Teredo clappi* in which development is completed within the mantle cavity and larvae are released at a stage ready for immediate metamorphosis, it has been found that, in the absence of wood, settlement can be delayed as much as 22 days. When presented with wood after this period of time, metamorphosis proceeds normally (TURNER and JOHNSON, 1968).

These various data suggest the ways in which planktonic life of shipworm larvae is extended and the manner in which their settlement is delayed. Actual data for the length of larval development in laboratory culture are available for only one oviparous phytoplanktotrophic species, *Nototeredo norvagica*, which was kept alive for 5 weeks after fertilization without the onset of metamorphosis (YONGE, 1924). Evidently development for this species is longer than 35 days at the laboratory conditions under which it was grown.

The velocities of the major surface ocean currents in the North Atlantic Ocean have recently been summarized (SCHELTEMA, 1971) and range from 0.5 to 3.7 km/h. At these rates, larvae can be transported between 84 and 722 km per week. The higher current velocity is that of the Gulf Stream, and shows that even with a short larval development, bivalve veligers can be carried a considerable distance northward along the coast of the North American Continent. The possibility of larval dispersal across ocean basins cannot be excluded (SCHELTEMA, 1966a); the geographical distribution of the larvae is such as to suggest that such transport must indeed occur.

Most of the larvae found in the plankton samples of the open ocean probably originate from coastal regions rather than from wood adrift at sea. Three points support this view.

Firstly, the concentration of larvae tends to decrease "downstream" along the axes of major ocean currents. Such a decrease, for example, is found along

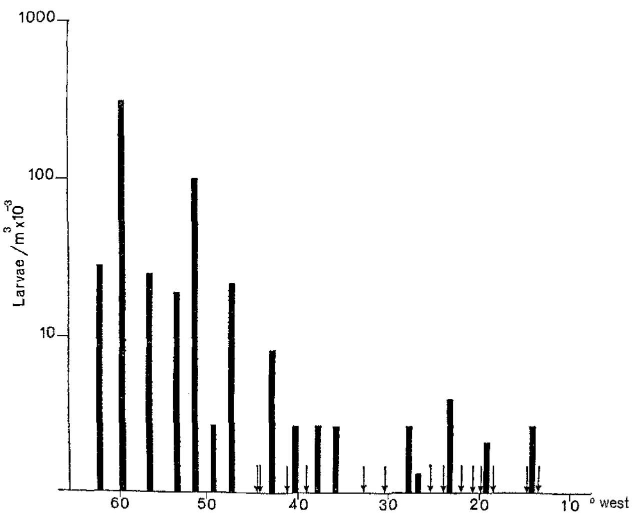

Fig. 3. Numbers of late-stage teredinid veliger larvae from transects taken along the North Atlantic Drift. Arrows: stations where no larvae were found. A few locations were omitted at points where tows were made very close together. All stations are, however, included in computations described in text. Ordinate: numbers of larvae. Abscissa: degrees West longitude

the North Atlantic Drift where the numbers of late-stage teredinid larvae decrease in an eastwardly direction across the Atlantic (Fig. 3). If the coastal region serves as a major source of larvae, then their numbers would be expected to decrease markedly with increasing distance from shore, whereas, if most larvae arose from drifting wooden objects at sea, then no such decrease need necessarily be expected. Reduction in the number of offshore larvae is a reflection of their mortality during their drift from the shore.

Secondly, the number of wooden objects encountered at sea seems to be inadequate to explain the numbers of shipworm larvae present. If the North Atlantic Drift is arbitrarily defined as that region bounded on the north and south by latitude 45° and 35°N and to the east and west by longitude 20° and

50°W, and only the upper 50 m are considered, then its total volume will be approximately 1.42×10^5 km^3. By dividing the total number of larvae captured by the total number of samples taken, the average concentration of late-stage teredinid larvae in the North Atlantic Drift is computed to be approximately 1.4×10^{-3}/m^3. The total number of larvae present in the entire "drift" region at the time of sampling must then consequently have been about 2.73×10^{11}. These larvae, however, will be numerically a very small fraction of the eggs which were spawned. If it is assumed that each adult shipworm produces 10^6 eggs[1], then the survival required to maintain a steady-state population will be 0.0001%. Deevey (1947, Fig. 1, p. 285) has shown how the expected mortality during the very early development of planktotrophic bivalve larvae is very high. If it is assumed that the number of late-stage teredinid veligers in the North Atlantic Drift represents 0.01% of the eggs which were spawned (quite likely an overestimate), then, from the data and assumptions above, 2.73×10^9 adult shipworms will have been required to produce these advanced-stage larvae (i.e., 2.73×10^{15} eggs with each adult contributing 10^6 eggs). Assuming that each drifting wooden object will contain 1,000 shipworms, then 2.73×10^6 pieces of floating wood will be required. Since the total surface area of the North Atlantic Drift, as defined above, is 2.84×10^6 km^2, the density of floating wood required would be 0.96 pieces/km^2. Of course no accurate "floating wood" counts have ever been made, but such a density implies a hazard to plankton sampling! Doubtlessly, computations of the kind just made should not be too seriously taken, but they in fact do show that if more data on the life history of teredinids were available, a better notion could be gained of the importance of larval dispersal over very long distances.

Finally, the geographical distribution of shipworm larvae is similar to that of other species of bivalve veligers whose parents could not possibly have been rafted to sea on floating objects (Scheltema, 1966b). It is, therefore, concluded that the drift of larvae is an important factor in the geographical distribution of oviparous Teridinidae species. The transport of larvae must also serve to maintain genetic continuity between populations otherwise isolated from each other (Scheltema, 1971; in press, b).

Summary

1. The pelagic phytoplanktotrophic larvae of oviparous species of Teredinidae or shipworms are widely dispersed in the temperate and tropical waters of the North Atlantic Ocean and adjacent seas.

2. The larva most commonly collected in the North Atlantic Gyre has been provisionally identified as that of the amphi-Atlantic species *Teredora malleolus* (Turton).

3. The geographical distribution of shipworm larvae suggests that they are carried great distances along the margin of continents and possibly even across ocean basins.

4. From the data it is concluded that larvae are an important factor in the geographical distribution of shipworm species, and probably also in the maintenance of genetic continuity between populations otherwise isolated from each other.

[1] The estimate of 10^8 eggs in *Teredo dilatata* made by Sigerfoos (1908) must surely be incorrect, for if each egg has a diameter of 45 μ, then their total volume would exceed 2,000 cm^3.

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