# PATTERNS OF LARVAL DEVELOPMENT IN STENOGLOSSAN GASTROPODS

GEORGE E. RADWIN AND J. LOCKWOOD CHAMBERLIN

ABSTRACT.—Studies of egg capsules and the mode of development in certain species of stenoglossan pro-sobranchs from the northeastern Gulf of Mexico revealed an apparent disproportionate number of species with non-pelagic larval development. Thorson (1950) suggested that among shallow-water marine invertebrates incidence of pelagic development increased from the arctic to the tropics and predominated in the subtropics and tropics. His conclusions were based largely on prosobranch mollusks. We suggest that the mode of early development in the Stenoglossa tends to follow phyletic lines, regardless of latitude or climatic conditions.

Many prosobranch gastropods lay their eggs in parchment-like capsules, separately or in clusters, attached to firm substrata. Unequivocal species identification is possible when the capsules are deposited in an aquarium containing individuals of a single species or when observations on ovipositing snails are made. The young of most higher prosobranchs pass the veliger stage within the capsule and may be sufficiently developed before emergence to be identifiable either by the sculpture of the early teloconch sculpture or by the radular dentition. In other groups the young are released as veligers and are carried in the plankton until they settle and metamorphose. Pearse (1969) described a third mode of development which seems to be intermediate between these two. In this type a modified veliger (called by some authors a veliconcha) emerges from the egg capsule and swims feebly for a short time in the bottom-most layer of water before settling. He has called this a demersal mode of development. The only stenoglossan species we know to exhibit this kind of development is *Olivella verreauxi* (Duclos).

Identification of capsules of marine gastropod species can contribute to distributional data which may be useful in zoogeographic studies and may serve as an ecological tool in determining the reproductive range of a species. In addition, their use as taxonomic characters at the generic level should be considered.

In this paper the spawning conditions and egg capsules of nine species of stenoglossan mollusks from the northeastern Gulf of Mexico are described. These observations were made from March 1963 to July 1964. The species treated are: *Phyllonotus pomum* (Gmelin), *Muricanthus fulvescens* (Sowerby), *Calotrophon ostrearum* (Conrad), *Urosalpinx tampaensis* (Conrad), *Urosalpinx perrugata* (Conrad), *Thais floridana* (Conrad), *Cantharus cancellarius* (Conrad), *Cantharus multangulus* (Philippi), and *Pollia tincta* (Conrad).

## SPAWNING SITES, EGG CAPSULES, AND LARVAL DEVELOPMENT

*Phyllonotus pomum* (Gmelin, 1791) (Fig. 1, 1a). Localities: St. Teresa and Bay Mouth Bar, Franklin Co., Fla., attached to large, empty bivalve shells. Period: May-July. The capsules are deposited in irregular compact masses up to 30 cm across; individual capsules are superficially similar to those of *Buccinum* and *Neptunea*. From two to five larvae develop in each.

Tryon (1880), Webb (1942), and Perry and Schwengel (1955) described and figured the capsule mass of *P. pomum*, and Webb reported communal spawning by as many as twenty-five females. This egg mass is similar to that reported for *Murex senegalensis* (see Knudsen, 1950). D'Asaro (1970b) reported non-pelagic development for *P. pomum*.

*Muricanthus fulvescens* (Sowerby, 1834) (Fig. 5). Locality: St. Andrews State Park, Bay Co., Fla., attached to rocks of the breakwater. Period: June-August. Capsules deposited in clusters with their bases fused. Each capsule is a flattened cylinder about 25 mm

high, with the top broader than the base. All were empty when collected. Identification was made on the basis of a laying female and an egg mass (catalogue no. 599643) in the collection of the Division of Mollusks, U.S. National Museum of Natural History. Moore (1961: 26) figured a similar capsule collected off Mississippi as *M. fulvescens*. He gave the height of "one typical specimen" as 14 mm which, from the examples we have seen, seems to be too small. He also reported that there are over one hundred eggs in each capsule.

*Calotrophon ostrearum* (Conrad, 1846) (Fig. 7,7a). Localities: 1) St. Teresa, Franklin Co., Fla., on the blades of turtle grass; 2) dredged in 13 m off Dog Island, Franklin Co., Fla., attached to the sides of egg capsules of *Ficus communis* (Röding); and 3) attached to the walls of aquaria in which specimens of *C. ostrearum* were isolated (see Radwin and Wells, 1968). Period: early May to mid-June. Numerous capsules are laid individually, their bases separated; they are roughly semicircular, average about 4 mm high, and when first deposited usually contain 3 to 5 large, spherical, reddish eggs. Emergence is in the crawling stage (pelagic stage absent). Egg capsules apparently of this species were attributed by Perry and Schwengel (1955) to both *Urosalpinx perrugata* and *Cantharus floridanus*.

*Urosalpinx perrugata* (Conrad, 1846) (Fig. 2). Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla., attached to empty mollusk shells; 2) attached to the sides and bottoms of aquaria in which adults were isolated (see Radwin and Wells, 1968). Period: late April to mid-June. Numerous erect capsules, with fused bases, are deposited in a mat; the capsules, about 10 mm high, are inversely pyramidal and have two lateral alae and apical protuberances. An egg mass may contain as many as 200 capsules. A large but undetermined number of eggs is initially deposited; the majority are apparently nurse-eggs, since only 5 to 15 larvae develop fully. Larvae emerge in the crawling stage (pelagic stage absent). Egg capsules of this species are misidentified in Perry and Schwengel (1955) as the product of *Nassarius vibex*.

*Urosalpinx tampaensis* (Conrad, 1846) (Fig. 3). Locality: Attached to the floor of an aquarium in which individuals of this species were isolated (see Radwin and Wells, 1968). Period: March (in aquarium). The erect egg capsules, about 8 mm high, are deposited singly. They resemble plump fingers on stalks and are more similar to those of *Eupleura sulcidentata* (see Perry and Schwengel, 1955) than to those of the other two western Atlantic species of *Urosalpinx* (*cinerea* and *perrugata*). Each capsule contains numerous eggs which, in our material, did not develop.

*Thais floridana* (Conrad, 1837) (Fig. 4,4a). (For characters distinguishing this species from *T. haemastoma*, see Radwin and Wells, 1968.) Locality: St. Andrews State Park, Bay Co., Fla., attached to empty bivalve shells and rocks of the breakwater. Period: July-August. The elongate, trough-shaped capsules are about 12 mm high, have apical escape pores, and are deposited in large masses. The capsules at the base of a mass tend to be nearly erect and are attached side by side to the substratum, with their bases fused. Other capsules are attached to those beneath in an arborescent pattern.

Burkenroad (1931) figured a capsule mass and commented on the hatching process. D'Asaro (1966), who figured the capsule and described the spawning and embryology in detail, reported communal spawning occurring from February through November at Miami, Fla. He suggested that spawning "probably occurs also in December and January when the temperature is above average." A shorter spawning season in the northeastern Gulf of Mexico is consistent with the shorter period of warm water temperature there. Large numbers of veligers emerge and have a prolonged pelagic development (D'Asaro, 1966). This mode of development (also reported by other workers for this species in North American waters) contrasts with that of most stenoglossans treated in this paper.

Thorson (1946, 1950) cited *T. floridana* as having pelagic development in some parts of its range and direct, non-pelagic development in others. This may be correct, but his evidence is apparently inferred from Lamy (1928), who referred, in turn, to Korschelt and Heider (1900), which reference we have not seen. Lamy reported only that many of the larvae die after cleavage and are then eaten by the others in the capsule. Although this "nurse-egg" type of feeding is usually associated with non-pelagic larval development, it
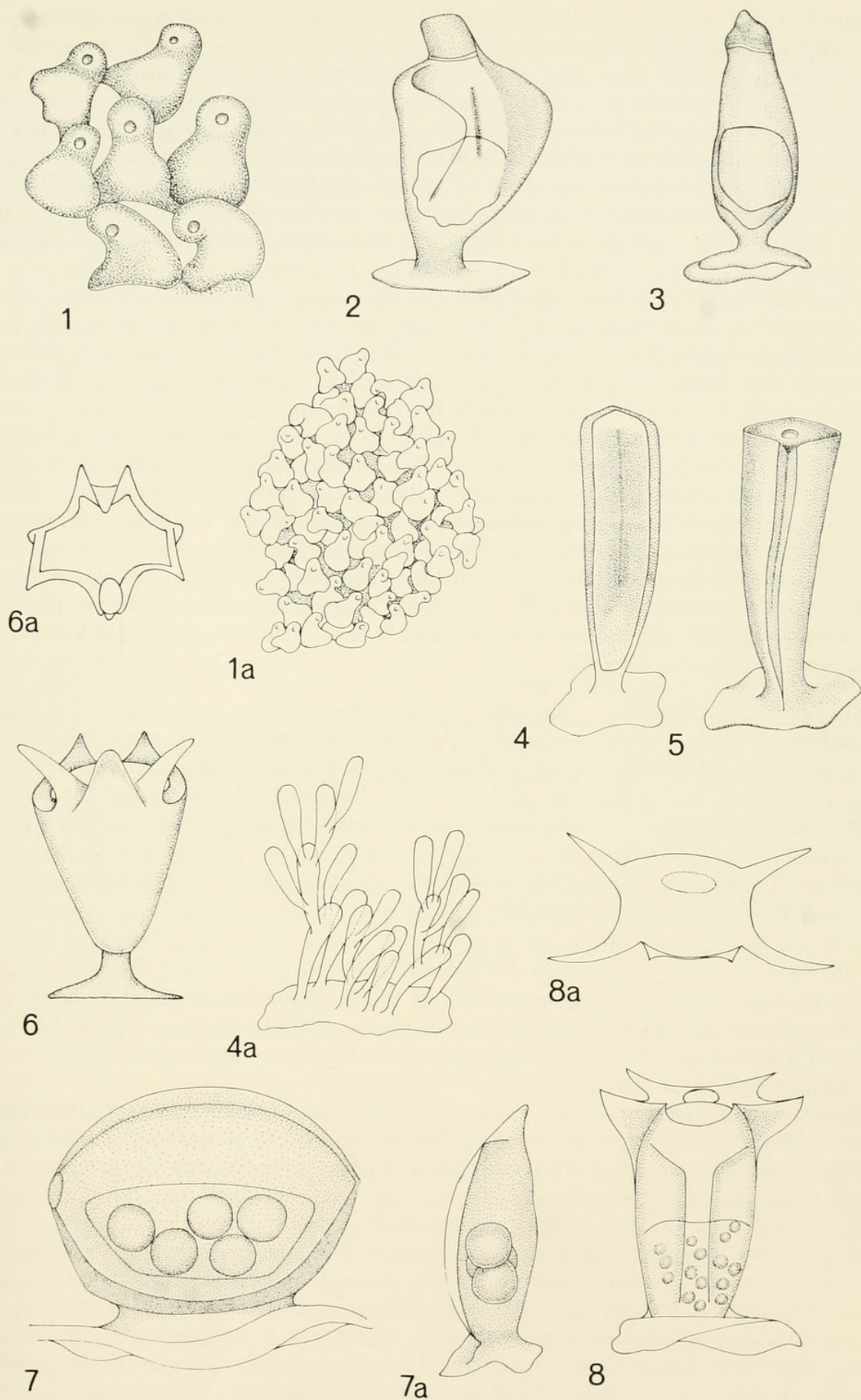
Figure 1, *Phyllonotus pomum*—seven capsules from an egg mass. 1a, *P. pomum*—small egg mass. 2, *Urosalpinx perrugata*—single egg capsule. 3, *Urosalpinx tampaensis*—single egg capsule. 4, *Thais floridana*—single egg capsule. 4a, *Thais floridana*—portion of an egg mass. 5, *Muricanthus fulvescens*—single egg capsule. 6, *Cantharus multangulus*—single egg capsule. 6a, *Cantharus multangulus*—top view of a single egg capsule. 7, *Calotrophon ostrearum*—single egg capsule. 7a, *Calotrophon ostrearum*—side view of a single egg capsule. 8, *Cantharus cancellarius*—single egg capsule. 8a, *Cantharus cancellarius*—top view of a single egg capsule.

is not proof of such development, as Thorson (1950) pointed out for *Natica catena*.

*Cantharus cancellarius* (Conrad, 1846) (Fig. 8, 8a). Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla., on empty mollusk shells; 2) Seahorse Key, Cedar Keys, Levy Co., Fla., on stones and empty mollusk shells; and 3) attached to the sides of aquaria in which adults were isolated (Radwin and Wells, 1968). Period: early May to late June. The erect capsules are deposited in a mat with their bases confluent. In nature the mats contained 15-20 capsules; the number of capsules laid in aquaria was smaller. Individual capsules are roughly rectangular, have four distinctive spinose projections at the top, and are about 4 mm high. In each capsule approximately 10-20 larvae develop to the crawling stage.

Moore (1961:26) figured a capsule of this species as *Cantharus reticulatus*. He also noted that on the Mississippi coast "these capsules are rather common objects during March, April, and May," and that from one capsule "a dozen or more eggs hatch out while still in the veliger stage." We have seen no other report of pelagic development in this species or elsewhere in the entire family Buccinidae.

*Cantharus multangulus* (Philippi, 1849) (Fig. 6, 6a). Capsules illustrated in Perry and Schwengel (1955), fig. 340. Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla.; 2) St. Teresa, Franklin Co., Fla.; and 3) deposited on the floor of aquaria. The capsules collected in the field were on shells and turtle grass. Period: May-July. Each capsule is inversely pyramidal and about 4 mm high; the top surface bears four spine-like projections. The capsule mass is a mat formed by the confluent bases of the capsules. When first deposited each capsule contains 8-20 flesh-colored eggs, a number of which apparently serve as nurse-eggs, as only a few crawling-stage larvae eventually emerge from each capsule.

*Pollia tincta* (Conrad, 1846) (see Perry and Schwengel, 1955; Lebour, 1945). Localities: St. Teresa, Franklin Co., Fla., and Seahorse Key, Cedar Keys, Levy Co., Fla., on shells and small rocks. Period: June-July. Clusters of several capsules are deposited, each about 5 mm high, broadly goblet-shaped and basally pedunculate. Each capsule contains 5 to 15 eggs, which, in our material, did not hatch. Lebour (1945) described the larval development as non-pelagic. Generic distinction of *Cantharus* and *Pollia* (as *Pisania*), based on radular dentition (see Troschel, 1866), is corroborated by differences in egg capsule morphology. *Cantharus* capsules are four-sided and rectangular or inversely pyramidal, with a flat top. *Pollia* capsules are goblet-shaped.

## DISCUSSION

The nine species studied belong in either the family Muricidae (six species) or the Buccinidae (three species), and constitute a majority of these families reported to live in the area of field work (Perry and Schwengel, 1955). The two families are both in the suborder Stenoglossa, order Neogastropoda.

Among shallow-water, benthic, marine invertebrates, Thorson (1950) found that species with pelagic larval stages were rare in polar regions but increased, and indeed predominated toward the tropics. This conclusion was based primarily on samples of prosobranch mollusks from several widely separated areas. However, our data and those of D'Asaro (1970) indicate that at least in the stenoglossans, non-pelagic forms of development may be more common in tropical waters than is generally recognized. Thorson's data demonstrate a substantial increase in the percentage of species with pelagic development from arctic to temperate waters (0% in East Greenland to 63.5% in southern England) but they show a much smaller increase in percentage from temperate to tropical waters (e.g. southern England to a) Canary Islands, 4.5%; b) Persian Gulf, 11.5%; c) Bermuda, 21.5%). These facts have led us to question whether the proportional increase implied by Thorson (1950) is demonstrable in lower latitudes.

A review of the literature on modes of larval development among marine prosobranchs shows that in the Archaeogastropoda there is no clear predominance of either pelagic or non-pelagic development. In the Mesogastropoda, however, pelagic development predominates. Within the Neogastropoda the suborder Toxoglossa exhibits pelagic larval development, whereas the suborder Stenoglossa is the only major prosobranch

group in which non-pelagic larval development seems to clearly predominate (Table 1).

The apparent predominance of non-pelagic development in the Stenoglossa, regardless of latitude, as well as the abundance of species of this suborder in lower latitudes suggests that the Stenoglossa were under-represented in at least some of the areas discussed by Thorson. The Bermudas, the Canaries, and the Persian Gulf are not typical of the main tropical and subtropical shelf regions of the world. The first two are small island groups, separated from the adjacent mainland by deep water (over 1,000 m), and the third is a hypersaline body of water with excessively high water temperatures (Mohr, 1929) and a restricted outlet to the Indian Ocean.

*Bermuda.*—Lebour's (1945) data, on which Thorson (1950) based his estimate of 85% of Bermudan species having pelagic development, are biased toward species with pelagic development, as her study was based principally on plankton samples. Only 29 of her prosobranch species were sufficiently identified to be used in a calculation. Of these, only three (10%) are stenoglossans; two have non-pelagic development. All 26 of the non-stenoglossans have pelagic development.

The actual percentage of Bermudan prosobranchs with pelagic development, though apparently less than 85% may, nevertheless, be higher than is typical of tropical and subtropical western Atlantic areas. Evidence for this supposition stems from the fact that stenoglossans make up a smaller percentage of total prosobranchs at Bermuda than is typical of other similar areas. Peile (1927) listed 215 Bermudan species of marine prosobranchs, excluding abyssal species, of which 21% are stenoglossans. In comparison, faunal lists for the adjacent mainland and Caribbean island areas give the following percentages of stenoglossans: western Florida, 28% (Perry and Schwengel, 1955); West Indies, 29-32% (Arango, 1878; Dall and Simpson, 1901; Mörch, 1878); Brazil, 32% (Lange de Morretes, 1949).

*Canary Islands.*—Thorson (1950) reported that 68% of the Canary Islands marine prosobranchs exhibit pelagic development. Faunal lists for these islands and for the adjacent coast of western Africa indicate a situation parallel to that in Bermuda, with fewer stenoglossans among marine prosobranchs at the islands than at the mainland areas: Canaries, 30% (Dautzenberg, 1890, 1891); western Africa, 37% (Nicklés, 1950). São Thomé, in a more tropical position off the western coast of Africa, has an essentially similar situation; 28% of the marine prosobranchs are stenoglossan (Tomlin and Shakleford, 1923).

Evidence of a lower percentage of prosobranchs with non-pelagic larval development at Bermuda, the Canaries, and São Thomé is, in itself, of biogeographical and ecological interest. The faunal lists cited above show that the marine mollusks of these islands include few endemics. Such low endemism is evidence of recent faunal origin by immigration. The marine molluscan fauna of Bermuda is considered a depauperate Antillean fauna (Warmke and Abbott, 1961), and the prosobranchs of the Canaries and São Thomé are just as clearly depauperate western African. The colonization of these islands largely by species with pelagic larvae could be attributed to their ability, as larvae, to traverse the geographical and bathymetric barriers isolating the islands from the mainland.

*Persian Gulf.*—Thorson (1940a, 1950) found that 75% of the prosobranch species studied from the Persian Gulf had pelagic development. His data seems moderately biased toward such species as only 24% of them (5 of 21 species) were stenoglossans. Melvill and Standen (1901) and Melvill (1928) indicate that just over 30% of the marine prosobranchs from this area are stenoglossans.

In view of Thorson's original data showing only a small increase in the percentages of prosobranch species with pelagic larval development from temperate to tropical waters the question arises whether any significant increase exists. Regardless of the answer to this question—and our evidence is not enough to resolve it—there remains the question of why a steep gradient exists in higher latitudes but only a weak one (if, indeed, any exists) in lower latitudes. Of course, data on larval ecology and distribution must include other invertebrate groups as well.

After a draft of this paper was sent to Thorson in 1968, he informed us (in litt.) that the data he had compiled on stenoglossan early development, more extensive than the data in Table I, suggest an appreciably lower percentage of species with non-pelagic de-

TABLE I
OCCURRENCE OF PELAGIC AND NON-PELAGIC LARVAL DEVELOPMENT WITHIN THE STENOGLOSSA

| Superfamily<br>Family<br>Genus | No. Species With<br>Pelagic Larvae | No. Species With<br>Non-pelagic Larvae | Reference |
|---|---|---|---|
| Muricacea | | | |
| Rapanidae | | | |
| Rapana | 3 | — | 18,37,83 |
| Muricidae | | | |
| Murex | 4 | 5 | 15,43,63,75,83 |
| Chicoreus | — | 3 | 26,62,76 |
| Phyllonotus | 3 | 1 | 26,83 |
| Boreotrophon | — | 6 | 30,50,55,85 |
| Calotrophon | — | 1 | xx |
| Bedevina | 1 | — | 61 |
| Bedeva | — | 1 | 7 |
| Favartia | — | 1 | 74 |
| Vitularia | 1 | — | 25 |
| Ceratostoma | — | 1 | 6 |
| Ocenebra | — | 1 | 30 |
| Urosalpinx | — | 3 | 11,34,xx |
| Eupleura | — | 1 | 11 |
| Thaididae | | | |
| Purpura | 1 | — | 49 |
| Neptunea | — | 4 | 6,30,40 |
| Siphonalia | — | 1 | 81 |
| Pollia | — | 1 | 48 |
| "Cantharus" | — | 2 | xx |
| Buccinum | — | 8 | 30,84 |
| Volutharpa | — | 1 | 30 |
| Macron | — | 1 | 14 |
| Chauvetia | — | 1 | 30 |
| Melongenidae | | | |
| Melongena | — | 1 | 35,45,71 |
| Syrinx | — | 1 | 36,61 |
| Busycon | — | 3 | 45,71,xx |
| Hemifusus | — | 1 | 6 |
| Fasciolariidae | | | |
| Leucozonia | — | 2 | 26,49,75 |
| Peristernia | — | 1 | x |
| Fasciolaria | — | 3 | 26,45,xx |
| Pleuroploca | — | 2 | 45,75 |
| Fusinus | — | 2 | 6,14,43 |
| Troschelia | — | 1 | 30 |
| Volutacea | | | |
| Volutidae | | | |
| Voluta | — | 2 | 45,80 |
| Thais | 9 | 1 | 6,15,24,26,43,45,49,63,83 |
| Nucella | — | 3 | 30,39,47 |
| Buccinacea | | | |
| Columbellidae | | | |
| Pyrene | — | 2 | 72 |
| Mitrella | 1 | 1 | 6,63 |
| Anachis | 5 | 1 | 6,25,54,78 |
| Zafrona | 1 | — | 4,6 |
| Astyris | — | 1 | 82,85 |
| Amphissa | 1 | — | 70 |
| Columbella | 2 | 1 | 43,72 |
| Nassariidae | | | |
| Nassarius | 11 | 3 | 3,17,30,41,42,45,63,79,83,92,93 |
| Tritia | 2 | 2 | 3,5 |
| Ilyanassa | 1 | — | 79 |
| Buccinidae | | | |
| Beringius (Jumala) | — | 4 | 21,30,50,82 |
| Volutopsius | — | 1 | 30,85 |
| Pyrulofusus | — | 2 | 22,32 |
| Colus | — | 9 | 30,82,84,xx |
| Plicifusus | — | 1 | 50 |
| Alcithoe | — | 1 | 33 |
| Melo | — | 3 | 6,20,38,88 |
| Cymba | — | 1 | 51 |
| Cymbiola | — | 2 | 9,45 |
| Marginellidae | | | |
| Persicula | — | 1 | 43 |
| Marginella | — | 7 | 43 |
| Prunum | — | 1 | 26 |
| Cancellariidae | | | |
| Cancellaria | — | 1 | 43 |
| Admete | — | 1 | 82 |
| Vasidae | | | |
| Vasum | — | 1 | 26 |
| Mitridae | | | |
| Strigatella | 3 | — | 26,66 |
| Atrimitra | 1 | — | 16 |
| Turbinellidae | | | |
| Turbinella (Xancus) | — | 1 | 26 |
| Olividae | | | |
| Ancilla | — | 1 | 63 |
| Olivella | — | 4 | 6,30,53,67 |
| Oliva | 1 | — | 65 |

x — E. Allison Kay, personal communication
xx — this paper

TABLE I

OCCURRENCE OF PELAGIC AND NON-PELAGIC LARVAL DEVELOPMENT WITHIN THE STENOGLOSSA

| Superfamily<br>Family<br>Genus | No. Species With<br>Pelagic Larvae | No. Species With<br>Non-pelagic Larvae | Reference |
|---|---|---|---|
| Muricacea | | | |
| Rapanidae | | | |
|    *Rapana* | 3 | — | 18,37,83 |
| Muricidae | | | |
|    *Murex* | 4 | 5 | 15,43,63,75,83 |
|    *Chicoreus* | — | 3 | 26,62,76 |
|    *Phyllonotus* | 3 | 1 | 26,83 |
|    *Boreotrophon* | — | 6 | 30,50,55,85 |
|    *Calotrophon* | | 1 | xx |
|    *Bedevina* | 1 | — | 61 |
|    *Bedeva* | — | 1 | 7 |
|    *Favartia* | — | 1 | 74 |
|    *Vitularia* | 1 | — | 25 |
|    *Ceratostoma* | — | 1 | 6 |
|    *Ocenebra* | | 1 | 30 |
|    *Urosalpinx* | — | 3 | 11,34,xx |
|    *Eupleura* | — | 1 | 11 |
| Thaididae | | | |
|    *Purpura* | 1 | — | 49 |
|    *Thais* | 9 | 1 | 6,15,24,26,43,45,49,63,83 |
|    *Nucella* | — | 3 | 30,39,47 |
| Buccinacea | | | |
| Columbellidae | | | |
|    *Pyrene* | — | 2 | 72 |
|    *Mitrella* | 1 | 1 | 6,63 |
|    *Anachis* | 5 | 1 | 6,25,54,78 |
|    *Zafrona* | 1 | — | 4,6 |
|    *Astyris* | — | 1 | 82,85 |
|    *Amphissa* | 1 | — | 70 |
|    *Columbella* | 2 | 1 | 43,72 |
| Nassariidae | | | |
|    *Nassarius* | 11 | 3 | 3,17,30,41,42,45,63,79,83,92,93 |
|    *Tritia* | 2 | 2 | 3,5 |
|    *Ilyanassa* | 1 | — | 79 |
| Buccinidae | | | |
|    *Beringius (Jumala)* | — | 4 | 21,30,50,82 |
|    *Volutopsius* | — | 1 | 30,85 |
|    *Pyrulofusus* | — | 2 | 22,32 |
|    *Colus* | — | 9 | 30,82,84,xx |
|    *Plicifusus* | — | 1 | 50 |
|    *Neptunea* | — | 4 | 6,30,40 |
|    *Siphonalia* | — | 1 | 81 |
|    *Pollia* | — | 1 | 48 |
|    *"Cantharus"* | — | 2 | xx |
|    *Buccinum* | — | 8 | 30,84 |
|    *Volutharpa* | — | 1 | 30 |
|    *Macron* | — | 1 | 14 |
|    *Chauvetia* | — | 1 | 30 |
| Melongenidae | | | |
|    *Melongena* | — | 1 | 35,45,71 |
|    *Syrinx* | — | 1 | 36,61 |
|    *Busycon* | — | 3 | 45,71,xx |
|    *Hemifusus* | — | 1 | 6 |
| Fasciolariidae | | | |
|    *Leucozonia* | — | 2 | 26,49,75 |
|    *Peristernia* | — | 1 | x |
|    *Fasciolaria* | — | 3 | 26,45,xx |
|    *Pleuroploca* | — | 2 | 45.75 |
|    *Fusinus* | — | 2 | 6,14,43 |
|    *Troschelia* | — | 1 | 30 |
| Volutacea | | | |
| Volutidae | | | |
|    *Voluta* | — | 2 | 45,80 |
|    *Alcithoe* | — | 1 | 33 |
|    *Melo* | — | 3 | 6,20,38,88 |
|    *Cymba* | — | 1 | 51 |
|    *Cymbiola* | — | 2 | 9,45 |
| Marginellidae | | | |
|    *Persicula* | — | 1 | 43 |
|    *Marginella* | — | 7 | 43 |
|    *Prunum* | — | 1 | 26 |
| Cancellariidae | | | |
|    *Cancellaria* | — | 1 | 43 |
|    *Admete* | — | 1 | 82 |
| Vasidae | | | |
|    *Vasum* | — | 1 | 26 |
| Mitridae | | | |
|    *Strigatella* | 3 | — | 26,66 |
|    *Atrimitra* | 1 | — | 16 |
| Turbinellidae | | | |
|    *Turbinella (Xancus)* | — | 1 | 26 |
| Olividae | | | |
|    *Ancilla* | — | 1 | 63 |
|    *Olivella* | — | 4 | 6,30,53,67 |
|    *Oliva* | 1 | — | 65 |

x — E. Allison Kay, personal communication

velopment (62% compared to our 72%). Thorson's reasons for believing "that the species with a non-pelagic development predominate more in available data than they do in nature" are 1) these species have egg capsules which are large, conspicuous, and easy to discover; 2) they tend to be discovered more often with their capsules than do species with pelagic development because they have a longer spawning season; 3) the capsules are easier to identify to species and 4) his experience at the Canary Islands and in Thailand indicates "that most species with pelagic development there will reproduce in the hottest season of the year," whereas "biologists tend to make expeditions to such places at the cooler times of the year." Correction for these biases would lower Thorson's entire gradient of pelagic vs. non-pelagic development, except for the Arctic, where we have seen no evidence to indicate the existence of pelagic development among stenoglossans; thus the slope of the gradient probably would be increased from high to mid-latitudes. We would not, however, expect the slope to be changed much from mid- to low latitudes by corrections for any of the sources of bias suggested by Thorson, except his last one, which would, in theory, result in some steepening.

## SELECTIVE ADVANTAGE OF NON-PELAGIC LARVAL DEVELOPMENT

The apparent predominance of non-pelagic development in the Stenoglossa has necessitated a more detailed review of early development in this group (Table 1). The mode of larval development in the Stenoglossa seems generally to follow phyletic lines, regardless of latitude or climatic conditions (beginning with the Buccinidae pelagic development is almost unknown). Exceptions include the Nassariidae, in which pelagic development is clearly predominant and the Mitridae, whose wide distribution in the Indo-west Pacific (Cernohorsky, 1965) suggests that the pelagic mode of development predominates. We cannot explain these apparent inconsistencies on the basis of our data.

Thorson (1950) argued that pelagic development is disadvantageous in the Arctic because the period of rich plankton production on which most pelagic larvae depend for food is too short. For the lower latitudes, where both modes of development are practical, the problem remains.

Garstang (1928) and Thorson (1950) showed that pelagic development permits rapid dispersal, repopulation of depleted areas, and establishment of dense populations when the larvae encounter optimal conditions. By contrast, non-pelagic larvae tend to remain in established optimal situations, are not as numerous as pelagic larvae, and are provided with protection and a large food supply by parental brooding. This mode inhibits rapid dispersal, repopulation of depleted areas, and short-term establishment of dense populations.

There is little information on the advantages of the various modes of larval development to marine prosobranchs and other marine invertebrates of shallow waters. Thus, the selective advantage of non-pelagic larval development in the stenoglossans is not clearly understood. However, most stenoglossans are carnivorous and, therefore, occupy relatively high trophic levels in their ecosystems. It seems reasonable to suggest that these animals are probably food-limited. Thus, it may be more advantageous for stenoglossans to use their energy in producing relatively few, non-pelagic young that can utilize "proved" local food resources, than to adopt the alternative strategy of producing vast numbers of highly vagile young that must find suitable conditions to insure survival.

### LITERATURE CITED

1. Abbott, R.T.
    1950. The Genera *Xancus* and *Vasum* in the western Atlantic. Johnsonia 2: 201-220.
2. Abbott, R.T.
    1954. American Seashells, D. Van Nostrand, New York. 555p.

3. Amio, M.
   1956a. On the egg capsules and larvae of *Tritia festivus* (Powys) and *Nassarius livescens* (Philippi). J. Shimonoseki Coll. Fish. 6: 271-280.
4. Amio, M.
   1956b. Studies on the eggs and larvae of marine gastropods—I. J. Shimonoseki Coll. Fish. 7: 107-116.
5. Amio, M.
   1959. Studies on the eggs and larvae of marine gastropods—II. J. Shimonoseki Coll. Fish. 8: 73-83.
6. Amio, M.
   1963. A comparative embryology of marine gastropods, with ecological considerations. J. Shimonoseki Univ. Fish. 12: 229-358.
7. Anderson, D.T.
   1966. Further observations on the life histories of littoral gastropods in New South Wales. Proc. Linnaean Soc. N.S.Wales 90: 242-251.
8. Arango, R.
   1878-1880. La Fauna Malacologia Cubana. G. Montiel and Co., Havana, 280p.
9. Berry A.J.
   1968. A gastropod and its spawn. Malay Nat. J. 21:223-224.
10. Burkenroad, M.D.
    1931. Notes on the Louisiana conch *Thais haemastoma* Linné in its relation to the oyster *Ostrea virginica*. Ecology 12: 656-664.
11. Carriker, M.R.
    1955. Critical review of the biology and control of the oyster drills *Urosalpinx* and *Eupleura*. Fish Wildlife Serv. Special Sci. Rep.—Fisheries 148.
12. Cernohorsky, W.O.
    1965. The Mitridae of Fiji. Veliger 8: 70-160.
13. Cernohorsky, W.O.
    1966. The radula, egg-capsules and young of *Murex torrefactus* Sowerby (Mollusca; Gastropoda). Veliger 8: 231-233.
14. Chace, E.P.
    1916. Egg cases of some local Mollusca. Lorquinia 1: 9-10.
15. Chari, V.K.
    1950. Breeding habits of *Thais bufo* Lam. J. Bombay Nat. Hist. Soc. 49: 317-318.
16. Chess, J.R., and R.J. Rosenthal
    1971. On the reproductive biology of *Mitra idae* (Gastropoda: Mitridae). Veliger 14: 172-176.
17. Christiansen, M.E.
    1964. Some observations on the larval stages of the gastropod *Nassarius pygmaeus* (Lamarck). Pubbl. Staz. Zool. Napoli 34: 1-8.
18. Chukhchin, V.D.
    1957. On the pelagic larva of *Rapana* in the Black Sea. Akademiia Nauk S.S.S.R. A translation of Doklady, Biological Sciences Sections, 117: 1082-1083. AIBS, Washington.
19. Clarke, G.L.
    1954. Elements of Ecology. John Wiley, New York and London. 548 p.
20. Cotton, B.C.
    1944. The egg capsule of the southern Australian baler shell *Melo miltonis* Gray. Rec. S. Austr. Mus. 1944: 143-144.
21. Cowan, I.M.
    1964. The egg-capsule and young of *Beringius eyerdami* Smith (Neptuneidae). Veliger 7: 43-44.
22. Cowan, I.M.
    1965. The egg-capsule and young of the gastropod *Pyrulofusus harpa* (Mörch) (Neptuneidae). Veliger 8: 1-2.
23. Dall, W.H., and C.T. Simpson
    1901. The Mollusca of Porto Rico. U.S. Fish Commission Bull. for 1900. 1: 351-524.
24. D'Asaro, C.N.
    1966. The egg-capsules, embryogenesis and early organogenesis of a common oyster predator, *Thais haemastoma floridana*. Bull. Mar. Sci. 16: 884-914.
25. D'Asaro, C.N.
    1970a. Egg-capsules of some prosobranchs from the Pacific coast of Panama. Veliger 13: 37-43.
26. D'Asaro, C.N.
    1970b. Egg capsules of prosobranch mollusks from South Florida and the Bahamas and notes on spawning in the laboratory. Bull. Mar. Sci. 20: 414-440.
27. Dautzenberg, P.
    1890. Recoltes malacologiques de M. l'Abbé Cullieret aux Îles Canaries et au Sénégal. Mem. Soc. Zool. France 3: 148-168.

28. Dautzenberg, P.
    1891. Voyage de la Goelette "*Melita*" aux Canaries et au Sénégal, 1889-1890. Mollusques Testacea. Mem. Soc. Zool. France 4: 1-50.

29. Edwards, D.C.
    1968. Reproduction in *Olivella biplicata*. Veliger 10: 297-304.

30. Fretter, V., and A. Graham
    1962. British Prosobranch Mollusca. Ray Society, London. 771p.

31. Garstang, W.
    1928. The origin and evolution of larval forms. Presidential Address, Section D., British Assoc. (Adv. Sci.) Rep., Glasgow, p. 77-98.

32. Gonor, J.J.
    1964. Egg capsules and young of *Pyrulofusus deformis* (Neptuneidae) at Barrow, Alaska. Arctic 17: 48-51.

33. Graham, D.H.
    1941. Breeding habits of 22 species of marine Mollusca. Trans. Roy. Soc. N. Z. 71: 152-159.

34. Hancock, D.
    1956. The structure of the capsules and the hatching process in *Urosalpinx cinerea* Say. Proc. Zool. Soc. London 127: 565-571.

35. Hathaway, R.R., and K.D. Woodburn
    1961. Studies on the crown conch *Melongena corona* Gmelin. Bull. Mar. Sci. Gulf Carib. 11: 45-65.

36. Hedley, C.
    1900. Studies on Australian Mollusca—pt. 2. Proc. Linn. Soc. N.S. Wales 25: 495-513.

37. Hirase, S.
    1928. Eibläge von *Rapana thomasiana* Crosse. Arch. f. Moll. 60: 173-178.

38. Hornell, J.
    1922. The common mollusks of South India. Madras Fisheries 14: 97-215.

39. Houston. R.S.
    1971. Reproductive biology of *Thais emarginata* (Deshayes, 1839) and *Thais canaliculata* (Duclos, 1832).
    Veliger 13(4): 348-357.

40. Johnson, C.W.
    1921. Egg-capsules of the ten-ribbed whelk. Occ. Papers Boston Soc. Nat. Hist. 5: 1-4.

41. Kaicher, S.D.
    1972. A second ovoviviparous *Nassarius*. Nautilus 85: 126-128.

42. Knight-Jones, E.W.
    1954. Notes on invertebrate larvae observed at Naples during May and June. Pubbl. Staz. Zool. Napoli 25: 135-144.

43. Knudsen, J.
    1950. The eggs and larvae of some marine prosobranchs from tropical West Africa. "Atlantide" Report 1: 85-130.

44. Korschelt, E. and K. Heider
    1900. [Textbook of Embryology of Invertebrates] MacMillan, London and New York. Vol. 4. (not seen; referred to by Lamy, 1928).

45. Lamy, E.
    1928. La ponte chez les gastéropodes prosobranches. J. Conchyl. 72: 25-52, 80-126, and 161-196.

46. Lange de Morretes, F.
    1949. Ensaio de catalogo dos molluscos do Brasil. Arg. Mus. Paranense 7: 1-216.

47. Leboeuf, R.
    1971. *Thais emarginata* (Deshayes): description of the veliger and egg capsules. Veliger 14: 205-211.

48. Lebour, M.V.
    1945. The eggs and larvae of some prosobranchs from Bermuda. Proc. Zool. Soc. London 114: 462-489.

49. Lewis, J.B.
    1960. The fauna of rocky shores of Barbados, West Indies. Canad. J. Zool. 38: 392-435.

50. MacGinitie, G.E.
    1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. Smithsonian Misc. Coll. 128.

51. Marche-Marchad, I.
    1968a. Un nouveau mode de developpement intracapsulaire chez les mollusques prosobranches néogastropodes: l'incubation intrapédieuse des *Cymba* (Volutidae). Compte Rendu Hebd. Séanc. Acad. Sci. Paris 266D: 706-709.

52. Marche-Marchad, I.

1968b. Remarques sur le developpement chez Fond., *Cymba* (Prosobranches, Volutidae) et l'hypothese de leur origine sud-americaine. Bull. Inst. Fond., Afr. Noire. 30A: 1028-1037.

53. Marcus, E., and E. Marcus
1959. On the reproduction of "Olivella." Bol. Fac. Fil. Cîen. Letr. Univ. São Paulo (232), Zool. 22: 189-200.

54. Marcus, E., and E. Marcus
1962. Studies on Columbellidae. Bol. Fac. Fil. Cîen. Letr. Univ. São Paulo (261), Zool. 24: 335-402.

55. Melvill, J.C.
1928. The marine Mollusca of the Persian Gulf, Gulf of Oman and North Arabian Sea . . . addenda, corrigenda, and emendanda. Proc. Malac. Soc. London 18: 93-117.

56. Melvill, J.C., and R. Standen
1898. Notes on a collection of marine shells from Lively Id., Falklands, with a list of species. J. Conch. 9: 97-105.

57. Melvill, J.C., and R. Standen
1901. The Mollusca of the Persian Gulf, Gulf of Oman and Arabian Sea . . . with descriptions of new species. Proc. Zool. Soc. London 70: 327-460.

58. Mohr, A.
1929. Den Persiske Bukt, en politisk-geografisk studie. H. Aschehoug and Co., Oslo. 173 p.

59. Moore, D.R.
1961. The marine and brackish water Mollusca of the state of Mississippi. Gulf Research Reports 1: 58.

60. Mörch, O.A.L.
1878. Catalogue of the West Indian shells in the collection of Dr. C.M. Poulsen. Bianco Luno, Copenhagen. 16p.

61. Murray, F.V.
1964. The spawn of some Australian marine prosobranch mollusks. Austr. Nat. Hist. 14: 405-408.

62. Murray, F.V., and M.H. Goldsmith
1963. Some observations on the egg capsules and embryos of *Torvamurex territus* (Reeve, 1845). J. Malac. Soc. Austr. 7: 21-25.

63. Natarajan, A.V.
1957. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and Palk Bay. Proc. Indian Acad. Sci. 46: 170-228.

64. Nicklés, M.
1950. Mollusques testaces marins de la côte occidentale d'Afrique. Manuels Ouest Africains. Vol. 2. Paul Lechevalier, Paris.

65. Olsson, A.A., and M.E. Crovo
1968. Observations on aquarium specimens of *Oliva sayana* Ravenel. Veliger 11: 31-32.

66. Ostergaard, J.M.
1950. Spawning and development of some Hawaiian marine gastropods. Pacific Sci. 4: 75-115.

67. Paine, R.T.
1962. Reproduction of *Olivella mutica*. Nautilus 75: 139-142.

68. Pearse, J.S.
1969. Slow developing demersal embryos and larvae of the antarctic sea star *Odontaster validus*. Mar. Biol. 3: 110-116.

69. Peile, A.J.
1927. The Mollusca of Bermuda. Proc. Malac. Soc. London 17: 71-98.

70. Pelseneer, P.
1906. Biscayan plankton collected during the cruise of H.M.S. "Research" 1900. VII—Mollusca. Trans. Linn. Soc. London, Zool. 10: 137-157.

71. Perry, L.M., and J.S. Schwengel
1955. Marine Shells of the Western Coast of Florida. Paleont. Res. Inst., Ithaca, N.Y. 318p.

72. Petit, G., and J. Risbec
1929. Sur la ponte de quelques gastropodes prosobranches. Bull. Soc. Zool. France 54: 564-570.

73. Radwin, G.E., and H.W. Wells
1968. Comparative radular morphology and feeding habits of muricid gastropods from the Gulf of Mexico. Bull. Mar. Sci. 18: 72-85.

74. Raeihle, D.
1966. An observation on captive *Murex cellulosus* Conrad. Amer. Malac. Union, Ann. Rept. for 1966, p. 28.

75. Risbec, J.
1931. Note sur le reproduction de quelques prosobranches néo-Calédoniens. Ann. Inst. Oceanog. 10: 23-33.

76. Risbec, J.