

FOOD AND FEEDING OF *PAEDOCLIONE DOLIIFORMIS* DANFORTH,
A NEOTENOUS GYMNOSOMATOUS PTEROPOD

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Paedoclione doliiformis, like other gymnosomes, is a shell-less, holoplanktonic, opisthobranch mollusc. The species is unusual, however, in retaining larval characteristics throughout sexual maturity.

Danforth (1907) originally described *P. doliiformis* from collections made in Casco Bay, Maine, in 1902. This gymnosome has never been reported since, either from the type locality or other areas. I first collected this species during July, 1968, in the Gulf of Maine, and it has been taken regularly since then in the Gulf and shelf waters of Nova Scotia. The collection of numerous specimens of *Paedoclione* over a four year period has afforded the opportunity to expand and correct Danforth's original description and to study the behavior and ecology of this gymnosome.

MATERIALS AND METHODS

Paedoclione doliiformis was collected from St. Margaret's Bay, Nova Scotia, and the Gulf of Maine, using conventional plankton nets towed at slow speed. Plankton tows were diluted immediately after collection in buckets of fresh sea water. Juvenile and adult specimens of *P. doliiformis* collect near the water surface where they are conspicuous by size, color, shape and swimming behavior; specimens were removed by pipette.

Specimens of *Paedoclione* were maintained in the laboratory in small containers of sea water kept at various temperatures between 2° and 20° C. Feeding experiments were carried out by placing *Paedoclione* in small glass containers together with mixed plankton or with thecosomatous pteropods of the genus *Spiratella* (*Limacina*). Feeding behavior was observed under a dissecting microscope.

Specimens used for anatomical studies were narcotized with urethane, then fixed in Bouin's fluid. Whole mounts were prepared by dehydrating specimens in an alcohol series, then clearing them in clove or wintergreen oil, and mounting them directly in Permount. For comparative purposes, larvae of *Clione limacina* (Phipps) were prepared in the same way. Whole mounts proved much more instructive for studying anatomical details than dissections. In addition, paraffin serial sections of 5 μ thickness were stained with Ehrlich's hematoxylin and eosin.

RESULTS

Sexually mature *Paedoclione doliiformis* (Fig. 1) retains the small size and three ciliary bands characteristic of gymnosome larvae; thus the species is con-

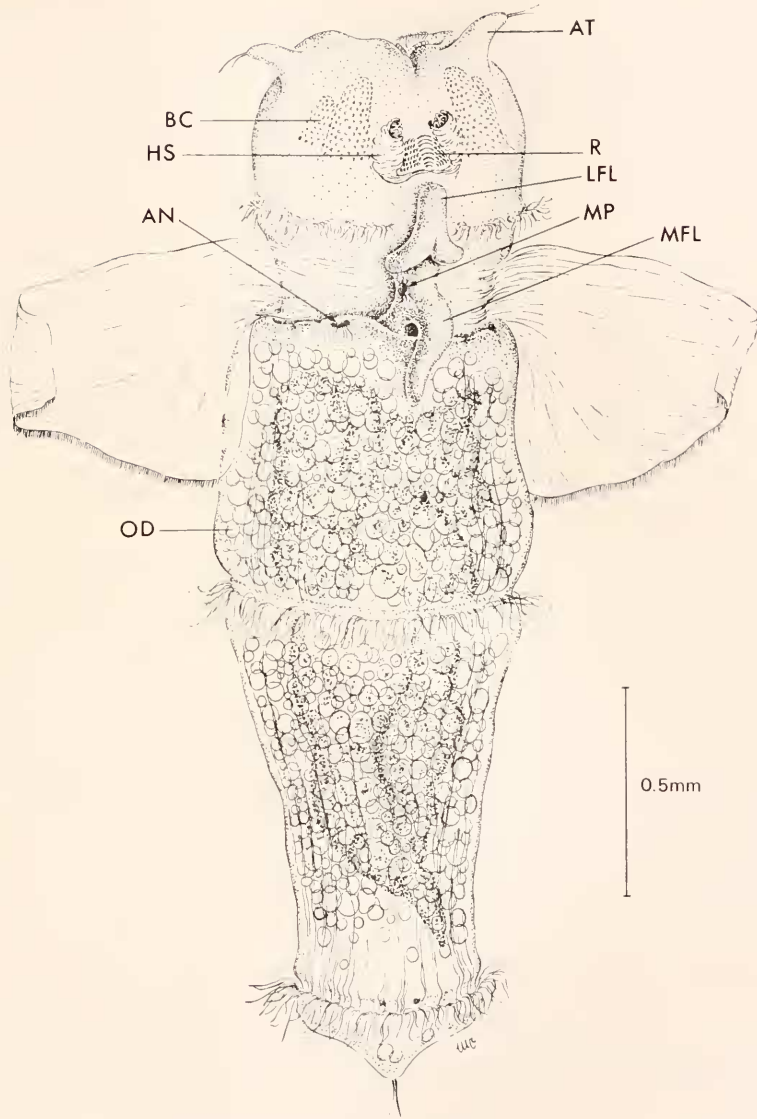


FIGURE 1. Ventral view of *Paedoclione doliiformis* with the retracted feeding structures as they appear in histologically cleared specimens; AN, anus; AT, anterior tentacle; BC, buccal cones; HS, hook sac; LFL, lateral foot lobes; MFL, median foot lobe; MP, male genital pore; OD, integumentary oil droplet; R, radula.

sidered to be neotenous. The maximum length of live, extended specimens is 2.5 mm. The three ciliary bands encircle the head, mid-body and posterior tip, with the discontinuous anterior band being interrupted ventrally by the foot. The distinct head bears a pair of retractile anterior tentacles. Very small posterior tentacles are located in depressions on the postero-dorsal surface of the head.

The foot is divided into paired lateral lobes and a narrow, pointed, median lobe. The male genital pore opens between the right, lateral foot lobe and the median foot lobe, and anteriorly to the anus. The integument of the remainder of the body contains numerous oil droplets which obscure the viscera. There are no gills. The brown or brownish-orange viscera extend almost to the posterior tip of the body. The body is highly contractile, and the head, posterior tip of the body, and wings may be completely retracted so that the animal resembles a ciliated ball.



FIGURE 2. *Paedocione doliiformis* capturing a swimming *Spiratella retroversa*. Three buccal cones are everted to capture the prey; the papillae of the cones adhere to the prey's shell. The fourth, rudimentary buccal cone (RBC) remains retracted. Scale bar equals 0.25 mm.

All of the above features frequently are obscured in rapidly preserved, contracted specimens.

The wings are well developed, with cilia on their posterior edges. They move synchronously, dorsally and ventrally, during swimming. However, in the laboratory, the wings commonly are retracted completely, and locomotion is accomplished solely by movements of the cilia of the three bands.

Feeding observations

In the laboratory, *Paedoclione doliiformis* fed only on the thecosomatous pteropods *Spiratella retroversa* (Fleming) or *S. helicina* (Phipps). However, most feeding experiments were done with *S. retroversa* as it was the more commonly available species. *Paedoclione* showed feeding responses only to live prey, ignoring dead *Spiratella* or empty *Spiratella* shells. Other plankton offered as potential food, including prosobranch and bivalve veligers, never elicited a feeding response; nor were other recognizable food remains found in the gut of sectioned *Paedoclione*.

Paedoclione employs three, prehensile buccal cones to capture active *Spiratella retroversa* (Fig. 2). The buccal cones are everted and elongated immediately upon contact with the prey, and the buccal cone papillae adhere to and hold the shell of the prey during the initial stages of feeding. Active specimens of *Spiratella* usually struggle to escape by swimming, but are seldom successful. The buccal cones maintain their hold until the prey ceases violent movement or manages to retract into its shell, or until *Paedoclione* secures a grip with other feeding structures on the soft *Spiratella* body. The buccal cones then are withdrawn immediately to their resting position (Figs. 1 and 3) and play no further role.

Employment of the buccal cones is eliminated completely, however, if the prey is initially inactive or retracted into its shell. In these circumstances, the predator swims around the *Spiratella* shell seeking the aperture if the prey is retracted, or the base of the wings if it is extended and inactive. The proboscis is often everted at this time and its tip may move over the shell. The next stage of feeding proceeds only after the aperture is directly opposite the head of *Paedoclione*. If the *Spiratella* is retracted and the shell aperture sealed by the operculum, *Paedoclione* uses its proboscis or head as a wedge to force aside the operculum and gain access to the soft body parts of the prey.

From this point on, feeding on either extended or retracted *Spiratella* is completed in the same manner (Fig. 3). *Paedoclione* everts its proboscis and buccal mass, and the radular teeth and small hooks (Fig. 3, HK) are inserted into the *Spiratella* body. The teeth and hooks secure a grip on the prey and the proboscis alternately is pulled back and thrust forward. Each time the proboscis is pulled back, the radular teeth release, the radula is thrust further out of the proboscis, and the teeth secure a new hold further up on the *Spiratella* body. In this way, the entire *Spiratella* body is gradually pulled from its shell and ingested whole. Upon completion of feeding, *Paedoclione* leaves the intact, empty *Spiratella* shell.

Paedoclione generally eats small *S. retroversa* measuring less than 1.0 mm in diameter across the largest shell whorl. The total time occupied in the capture and ingestion of one *Spiratella* varied from 2 to 40 minutes and was dependent upon the initial activity of the prey and its size relative to that of the predator.

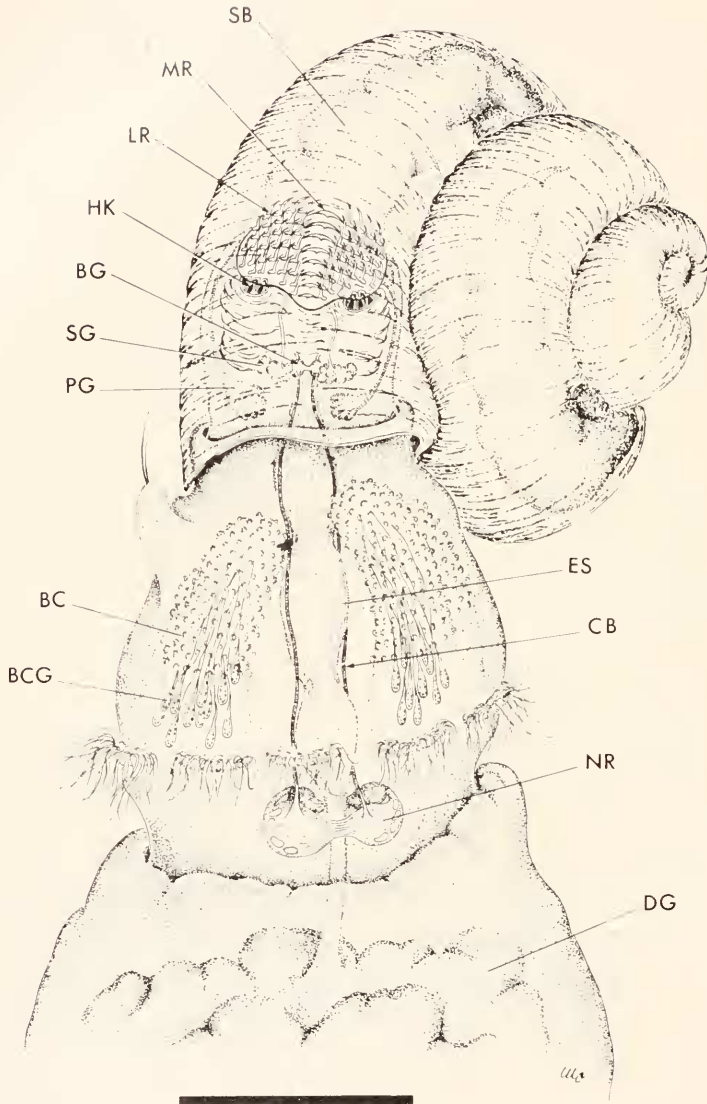


FIGURE 3. *Pacdoelione dolliformis* extracting and ingesting *Spiratella retroversa*. The proboscis is everted into the shell aperture, and the radula is protruded from the mouth. The feeding organs within the proboscis are slightly enlarged to show structural detail. The buccal cones are retracted during this stage of feeding; BC, buccal cone; BCG, buccal cone gland; BG, buccal ganglion; CB, cerebrobuccal connective; DG, digestive gland; ES, anterior area of esophagus distended with ingested food; HK, hooks; LR, lateral radular teeth; MR, median radular teeth; NR, cerebral ganglion of nerve ring; PG, labial gland; SB, body of *Spiratella*; SG, salivary gland. Scale bar equals 0.25 mm.

Paedoclione occasionally was observed feeding on *Spiratella* larger than 1.0 mm diameter. *Paedoclione* began feeding on large, extended *Spiratella* by engulfing one wing at a time. The proboscis was placed against one wing at the base closest to the prey body. The radular teeth and hooks secured a grip on the wing tissue, and the wing gradually was engulfed by the alternate movements of proboscis and radula as described above. The predator began to ingest the remainder of the *Spiratella* body only after the second wing was engulfed in a similar manner. *Paedoclione* fed on both large and small retracted *Spiratella* by thrusting the proboscis into the shell aperture. However, if the shell is relatively large, *Paedoclione* may enter the aperture and first shell whorl farther than is possible with small prey. *Paedoclione* has been observed with the entire head, back to the wing level, thrust into a large shell to effect contact and extraction of the prey. *Paedoclione* feeding on large prey frequently stopped ingestion before complete extraction, leaving a portion of the prey body within the shell. Predation on large *Spiratella* presumably occurs only in the laboratory, and even then is infrequent. It seems unlikely for several reasons that *Paedoclione* could capture and ingest large *Spiratella* under natural conditions. Large specimens of *Spiratella* are faster swimmers than *Paedoclione*, the time necessary for extraction of relatively large prey is longer than for small, and, in nature, *Paedoclione* must support the weight of its prey once the *Spiratella* can no longer swim. Under laboratory conditions, feeding on large prey is accomplished on the bottom of feeding containers; in nature, the weight of a large *Spiratella* would cause the prey and predator to sink rapidly.

Specimens of *Paedoclione* also ate small *Spiratella helicina* on the few occasions when this species was available. The general feeding method is the same, but it is unlikely that *S. helicina* constitutes a regular food item of *Paedoclione*. This thecosome species occurs only rarely in the Gulf of Maine and Nova Scotian shelf waters, and *Paedoclione* is not known to inhabit other areas.

Spiratella retroversa shows various responses to contact with *Paedoclione*. It may react by vigorous wing movements in an attempt to swim away; this maneuver is successful only if the predator does not have a secure hold with the buccal cones or radula and hooks. *Spiratella* more frequently responds by retracting into its shell, closing the aperture with the operculum. The operculum does not appear to be an effective defensive structure as it can be easily pushed aside by *Paedoclione*. At certain times, however, the prey retracted so far into its shell that it was physically impossible for the predator to enter far enough to grasp the prey body. *Paedoclione* has been observed to spend as long as 20 minutes in unsuccessful attempts to reach retracted prey. It is also of interest that initially retracted prey never attempted to expand from the shell and swim once a *Paedoclione* began to enter the shell. The effectiveness of any prey defense observed in the laboratory should not be extended to natural conditions; the small volume of experimental containers probably conferred an unnatural advantage on *Paedoclione*.

Feeding apparatus

The feeding apparatus of *Paedoclione doliiformis* consists of the buccal cones, proboscis, paired hook sacs, radula and associated glands (Fig. 3). The buccal cones are retracted into the lateral walls of the head except during prey capture.

Contrary to Danforth's original description (1907), there are four, not three, buccal cones located dorso-laterally and ventro-laterally of the buccal cavity. The two cones on the right side are equally well developed. The left, dorso-lateral, buccal cone is the largest. The fourth cone, overlooked by Danforth, is rudimentary and is located ventro-laterally on the left side. The fourth cone usually is not obvious in dissections or cleared whole mounts; it can be demonstrated in histological cross sections.

The general structure of all four buccal cones is similar to that described for *Clione limacina* (Pelseneer, 1885; Lalli, 1970a), but histological details can not be made out clearly in paraffin sectioned material. The surface of each buccal cone is papillate, caused by clusters of projecting epithelial cells which are relatively longer than those of *C. limacina*. The papillae appear to be arranged in alternating transverse rows. Glands within the hemocoelic cavity of each buccal cone connect with the epithelial cells and presumably discharge their secretion to the surface of the cones. During feeding, three of the prehensile buccal cones are everted and elongated by increased blood pressure; the hemocoelic cavities within the cones are continuous with the cephalic hemocoel and there are no protractor muscles. Retraction to the resting position is accomplished by contraction of the several retractor muscles of each buccal cone. The fourth buccal cone only once has been everted; this occurred under unnatural circumstances when a specimen became entangled in fibers being used to slow locomotion for measurement (R. J. Conover, personal communication).

The anterior part of the gut of *Paedoclione* is everted during feeding to form a proboscis. Eversion is apparently accomplished by increased fluid pressure in this region as there are no protractor muscles. Changes in blood flow to the proboscis are apparently linked with flow to the buccal cones, as the proboscis and cones are never everted at the same time. The proboscis expands upon eversion and is capable of considerable elongation. The mouth is located terminally on the proboscis tip. Retraction of the proboscis is brought about by contraction of several retractor muscles which originate on the walls of the head and insert near the tip of the proboscis. Paired, multicellular, lobed glands open near the mouth (Fig. 3, PG); their function remains unknown.

The paired hook sacs and radula are connected and form the buccal mass proper. The hook sacs lie slightly dorsally of the radula and are connected with it laterally and posteriorly by muscle and connective tissue. The very small size and structural simplicity of the hook sacs was pointed out by Danforth (1907), who preferred to call them "ankistrophores." Nevertheless, these structures are homologous with the more complex hook sacs of other gymnosomes. Each sac is composed of intermixed muscle and connective tissue. It is noteworthy that the central areas of the sacs contain glandular cells with secretory material; this has not been reported in other gymnosome species. A maximum of seven, slightly curved, chitinous hooks permanently project from the anterior end of each sac into the buccal cavity. The hooks are similar to those of other species although they measure only 0.02 mm in maximum length. The hook sacs lack the complex musculature found in *Clione limacina* (Lalli, 1970a), but limited movement of the hooks apparently is possible during feeding. The hooks are inserted into the prey body during feeding and assist in ingestion.

The radular membrane, bearing the teeth, is supported by two lateral cartilages which form part of the odontophore. Figure 4 shows the shape of the radular teeth. The median teeth are sickle-shaped and lie in the groove between the odontophore cartilages. Completely formed median teeth have a small, single, median cusp. The five lateral teeth on each side of a median tooth have long spines and are exsertile. During feeding, the radula and hook sacs are forced out of the mouth and the radula protrudes beyond the level of the hooks (Fig. 3). The two odontophore cartilages rotate laterally, exposing the median teeth, and the lateral teeth erect as the radular membrane is stretched. The teeth are inserted into the prey tissue and the prey is pulled into the gut as the cartilages rotate medially and the radula is pulled posteriorly. Successive grasping actions of the radula continue until the entire prey body has been ingested. Although blood circulation to the radula has not been studied in detail, it is reasonable to assume that movements of the radula are controlled by changes in fluid pressure as well as by muscular action.

The hook sacs and radula are innervated by nerves from the buccal ganglia which lie dorsally of the esophagus and between the salivary glands. The buccal

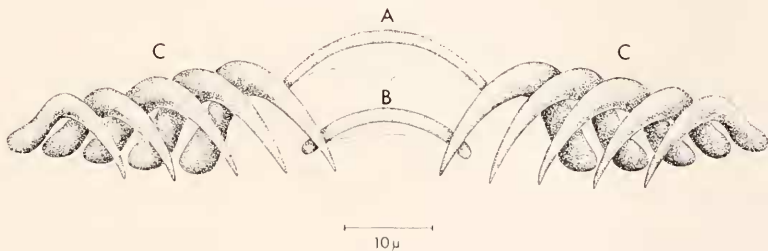


FIGURE 4. Radular teeth of *Paedoclonie doliiformis*: A, fully formed median tooth with a median cusp; B, newly formed median tooth without a distinct cusp; C, lateral teeth.

ganglia are joined with the cerebral ganglia of the nerve ring by long connectives.

Paired salivary glands are located immediately posterior to the hook sacs. The salivary ducts run anteriorly through the buccal mass and discharge separately into the buccal cavity.

The remainder of the digestive tract is structurally simple. The ciliated epithelium of the buccal cavity contains numerous unicellular glands. The extensible, ciliated esophagus passes through the nerve ring and opens directly into the lumen of the large digestive gland, where extracellular digestion takes place. The stomach is reduced to a small ciliated area on the right side of the digestive gland, as it is in other gymnosome species (see Morton, 1958; Lalli, 1970b). A narrow, ciliated intestine leads directly from the right side of the digestive gland to the anus.

DISCUSSION

Taxonomy

Paedoclonie doliiformis has so far been reported only from the Gulf of Maine and Nova Scotian shelf waters. However, it seems unlikely that the species is

endemic to these localities. Such a restricted distribution within areas where considerable water exchange takes place with the adjacent North Atlantic would be most unusual in a gymnosome species, or in other zooplankton groups. Since the species has not been familiar to many zooplanktologists, the possibility remains that *Paedoclione* has been overlooked or incorrectly identified in collections from other localities.

During the past four years, *P. doliiformis* has been a relatively common species in the collection areas. The absence of reported occurrences in the intervening 66 years between Danforth's collections and my own, in an area in which plankton collections have been numerous, has certainly been due to confusion with another gymnosome species. *P. doliiformis* frequently coexists with *Clione limacina*. Although the two gymnosomes are not anatomically similar, the differences are not always apparent between *Paedoclione* and the small polytrochous larvae of *Clione* which also have three ciliary bands. Live specimens usually can be distinguished by differences in coloration and general body form, *Paedoclione* having a darker brown or brownish-orange color and a truncated body shape compared with the conical form of *Clione* larvae. However, rapidly preserved, contracted specimens usually cannot be identified with certainty by cursory examination. The most rapid method of identification of such specimens is by the preparation and examination of cleared, whole mounts. The buccal organs stand out distinctly when these unstained preparations are examined under a compound microscope with the condensor lowered to increase contrast. The three largest, retracted, buccal cones of *Paedoclione* show clearly and extend from the anterior tip of the head to the level of the anterior ciliary band. The six, retracted, buccal cones of *Clione* larvae are shorter and concentrated only in the anterior part of the head. The hooks of *Paedoclione* number seven or less in each sac and are very short and blunt, while those of *Clione* are numerous, long and tapered, and extremely conspicuous as they extend throughout the length of the head. Radular teeth differences should not be relied upon as the preparations seldom separate the teeth sufficiently to determine structural details.

Two previously overlooked features of *Paedoclione doliiformis* are of considerable taxonomic importance. One is the rudimentary, fourth buccal cone. Following Danforth's description (1907), the major taxonomic character of *Paedoclione* has been the presumed unique asymmetry of the buccal cones. Thus *Paedoclione* was not considered to be closely allied with other gymnosome species which have one to three pairs of buccal cones, symmetrically arranged around the buccal cavity (Danforth, 1907; Tesch, 1950). Secondly, the presence of a cusp on the fully formed median radular teeth must be taken into account in taxonomic consideration.

There can be no doubt that *P. doliiformis* should be included in the family Clionidae. On the basis of similarity of buccal structure, *Paedoclione* is most closely related to the genus *Paraclione* (*Clionina*). Species of *Paraclione* also have two pairs of buccal cones, small hook sacs and unicuspid median radular teeth, but they differ from *Paedoclione* in other respects (Tesch, 1950; Pruvot-Fol, 1954). It is of interest to note that *Paraclione flavescens* (Gegenbaur) has been reported to have sexually mature larvae, although adults of 22 mm in length have also been found (Tesch, 1950).

Feeding

Paedoclione doliiformis feeds principally on *Spiratella retroversa*, although it is also capable of eating *S. helicina*. Food specialization on thecosomes also has been reported for *Pneumodermopsis paucidens* which eats *Creseis* species (Sentz-Braconnot, 1965) and for *Clione limacina* which preys exclusively on *Spiratella retroversa* or *S. helicina* (Lalli, 1970a). Although the feeding structures differ among these gymnosomes, the general method of feeding is the same. All three gymnosome species capture thecosomes by prehensile structures, either buccal cones or sucker-bearing appendages, and extract the prey body from its shell by combined actions of the hooks, radula, and proboscis if present.

A comparison of feeding between *Paedoclione doliiformis* and *Clione limacina* reveals certain differences, although both eat the same prey species. *Paedoclione* preferentially feeds on veliger or small *Spiratella retroversa* measuring 1.0 mm or less in shell diameter. Prey size preference of *Clione* changes with age; the youngest polytrochous larvae (0.3 mm in length) eat only veliger *Spiratella*, while the adults feed exclusively on large, metamorphosed prey (Conover and Lalli, in press). *Paedoclione* uses its three buccal cones to capture active *Spiratella*, but frequently eliminates this step of feeding if the prey is inactive or relatively small. Juvenile and adult *Clione* consistently use their six buccal cones to capture larger, metamorphosed *Spiratella*. Thus the number and relative importance of the buccal cones in feeding seems to be dependent upon the size and activity of the prey. In *Paedoclione*, the radula and proboscis are the most important organs used to extract the prey from its shell; the poorly developed hooks apparently play only a minor role. A true proboscis is lacking in *Clione*, although the anterior part of the gut can be everted to a limited extent; instead the well developed hooks are capable of extending far into the prey shell, and the hooks and radula are used for prey extraction and ingestion.

The frequent coexistence of *P. doliiformis* and *C. limacina* in the collection areas leads one to ask two basic questions. How can these two gymnosomes coexist when both feed exclusively on *Spiratella*, and what is the selective advantage of neoteny to *Paedoclione*? One possible explanation is that neoteny in one species limits food competition to the small-sized, more abundant prey. Competition for food thus would occur only between *Paedoclione* and larval *Clione*, with adult *Clione* feeding on the larger, less abundant *Spiratella*. My colleague, Dr. R. J. Conover, and I are presently attempting to examine this relationship between *Paedoclione* and *Clione* by laboratory studies on the size of prey eaten versus predator size, and by comparing feeding and growth rates of *Paedoclione* and *Clione* both in pure and mixed cultures. We are also attempting to gather information on the life cycles of both gymnosomes and of *Spiratella retroversa* in Nova Scotian shelf waters to determine abundance and size of the predators and their prey during times of coexistence.

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SUMMARY

The neotenous gymnosome, *Paedoclione doliiformis*, feeds exclusively on the thecosomatous pteropods, *Spiratella retroversa* or *S. helicina*. Three prehensile buccal cones are used to capture prey; the fourth buccal cone is rudimentary. *Paedoclione* employs its proboscis, radula and hooks to completely extract the prey body from its shell.

Paedoclione doliiformis frequently coexists in the collection area with another gymnosome, *Clione limacina*, which is also a feeding specialist on *Spiratella*. *Paedoclione* and polytrochous larvae of *Clione* preferentially select small-sized prey of less than 1.0 mm shell diameter and thus are potential competitors for food; adult *Clione* feed exclusively on *Spiratella* larger than 1.0 mm. It is suggested that neoteny in *Paedoclione* permits coexistence of these two gymnosome species by limiting food competition to the small-sized, more abundant prey.

LITERATURE CITED

- CONOVER, R. J., AND C. M. LALLI, 1972. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. *J. Exp. Mar. Biol. Ecol.*, in press.
- DANFORTH, C. H., 1907. A new pteropod from New England. *Proc. Boston Soc. Natur. Hist.*, **34**: 1-19.
- LALLI, C. M., 1970a. Structure and function of the buccal apparatus of *Clione limacina* (Phipps) with a review of feeding in gymnosomatous pteropods. *J. Exp. Mar. Biol. Ecol.*, **4**: 101-118.
- LALLI, C. M., 1970b. Morphology of *Crucibranchuca macrochira* (Meisenheimer), a gymnosomatous pteropod. *Proc. Malacol. Soc. London*, **39**: 1-14.
- MORTON, J. E., 1958. Observations on the gymnosomatous pteropod *Clione limacina* (Phipps). *J. Mar. Biol. Ass. U.K.*, **37**: 287-297.
- PELSENEER, P., 1885. The cephalic appendages of the Gymnosomatous Pteropoda, and especially of *Clione*. *Quart. J. Microscop. Sci.*, **25**: 491-509.
- PRUVOT-FOL, A., 1954. Mollusques opisthobranches. *Faune Fr.*, **58**: 1-460.
- SENTZ-BRACONNOT, E., 1965. Sur la capture des proies par le Ptéropode Gymnosome *Pneumodermopsis paucidens* (Boas). *Cah. Biol. Mar.*, **6**: 191-194.
- TESCH, J. J., 1950. The Gymnosomata II. *Dana Rep. Carlsberg Found.*, **36**: 1-55.