OBSERVATIONS ON THE GROWTH, REPRODUCTION AND FEEDING OF THE NUDIBRANCH *ARMINA TIGRINA*

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ABSTRACT

One specimen of the sand-burrowing nudibranch *Armina tigrina* Rafinesque was collected from South Carolina in June. The specimen deposited a single egg mass of approximately 6 500 white eggs which developed into lecithotrophic veligers in 8 days at 23°C. Of the veligers which metamorphosed, 9 lived 4-5.5 months (i.e. the life cycle was subannual). Eight individuals reached sexual maturity in about 80 days. Copulation began at a body length of 24 mm and oviposition at 28 mm. During the 1.5 month egg-laying period, each individual laid 2-4 wavy egg masses with 2 000-7 000 eggs per mass. Death followed oviposition. Average growth rate of fed and starved pre-ovipositional nudibranchs was 3.4% and 0.9% per day respectively. Growth rate of ovipositing specimens was 0.6% or less per day. Based on average feeding rates, each nudibranch consumed approximately 1.6 g damp weight of *Renilla reniformis* (one small colony) between metamorphosis and egg laying and 6.1 g damp weight (about two average colonies) from egg laying to death. Feeding efficiency is presumably increased by interlocking and abutting radular teeth. Egg diameters reported for *Armina tigrina* from South Carolina and Florida were 199 μm and 82 μm respectively. This difference suggests the existence of two species of *Armina* or one species with two geographically separated developmental types.

INTRODUCTION

Among the four nudibranch suborders, life histories have been described for the Doridacea (e.g. Thompson, 1958, 1961b; Potts, 1970; Perron & Turner, 1977; Todd, 1979a, 1979b), Dendronotacea (Ajeska & Nybakken, 1976), and Aeolidacea (e.g. Harris, 1975; Christensen, 1977; Harrigan & Alkon, 1978; Rivest, 1978). The fourth suborder, the Arminacea, is a heterogeneous group containing both doridacean-like and aeolidacean-like species. There is little known about the life histories of arminacean nudibranchs.

Specimens of the arminacean *Armina tigrina* Rafinesque have been reported from the Mediterranean Sea, the western Atlantic Ocean, the central Atlantic Ocean (Sargasso Sea), and from North Carolina southward to Texas and the Yucatan Peninsula (Marcus & Marcus, 1966; Abbott, 1954, 1974). The species lives in sandy subtidal areas and feeds on sea pansies. *A. tigrina* may be locally common (Abbott, 1954), but due to its burrowing habit specimens are rarely reported. The purpose of this paper is to describe various aspects of the growth, reproduction and feeding of *A. tigrina* specimens reared in the laboratory.

METHODS AND MATERIALS

A single *Armina tigrina* was collected June 1976 off Debidue Island in North Inlet Estuary, South Carolina (33°20'N, 79°10'W). The nudibranch was dredged from a sandy area populated with the sea pansy *Renilla reniformis* (Pallas). The specimen and one colony of *R. reniformis* were placed in filtered sea water (1 μm pore size) in an aerated aquarium. After 6 days, the nudibranch laid one egg mass (Day 0) and died (Day 6). On Day 37 nine metamorphosed *A. tigrina* juveniles including one runt were found on the sea pansy. Observations were made on these individuals at room temperature (*c.*23°C) until they died.

Throughout the study the nudibranchs were kept in aerated two gallon aquaria lined with crushed oyster shell. The filtered sea water was changed when fouled by dying sea pansies. Sea pansies were provided as food except

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during one week (Days 67-73) when none were available. Newly-hatched *Artemia* nauplii were provided as food for the sea pansies.

The 9 nudibranchs were kept together in one aquarium (Days 37-91) and then divided between two aquaria (Days 92-103) until each adult had copulated and laid 1-2 egg masses. To examine actual reproductive output per individual, 4 adults and the runt were placed singly and 4 adults were placed in pairs in separate aquaria (Days (104 to death).

Growth

The nudibranchs were measured periodically to the nearest 0.5 mm to record changes in body length in the presence and absence of food, and before and during reproduction. Only those nudibranchs which could be located without greatly disturbing the substratum were removed and measured. Measurements were made from the tip of the tail to the anterior edge of the semilunar veil in actively-crawling individuals.

Reproduction

Body length at first copulation (MCL) and first oviposition (MOL) were measured. The number of egg masses laid per nudibranch, uncleaved egg diameter and time from oviposition to hatching were recorded. The number of eggs per egg mass was estimated by multiplying the average number of eggs per mm of egg mass length by the egg mass length in mm.

Feeding

The jaws and radular teeth of dead nudibranchs were removed from adhering buccal tissues, soaked in NaOH, rinsed well with distilled water, mounted on carrying stubs, and sputter coated with gold. The structure of the jaws and teeth was examined with a Jeolco JSM-U3 scanning electron microscope.

The time it took *Armina tigrina* to eat weighed *Renilla reniformis* colonies was recorded and feeding rate per individual was calculated. The wet weight of moderately firm *R. reniformis* was measured after forcing the colony to expel water. The external surface of the colony was blotted of water and mucus before weighing. Several colonies were allowed to re-expand with water and then forced to re-expel the water as a test for reliability of the results. Remeasured wet weight values were within ±0.4 g of the initial reading, with greatest variation occurring in the largest colonies. To determine if this treatment adversely affected survival, control colonies were handled in the same way, but placed in aquaria without predators. Weight of *R. reniformis*

Fig. 1. *Armina tigrina* juveniles on *Renilla reniformis* colony with retracted feeding polyps. Scale bar is approximately 5mm.

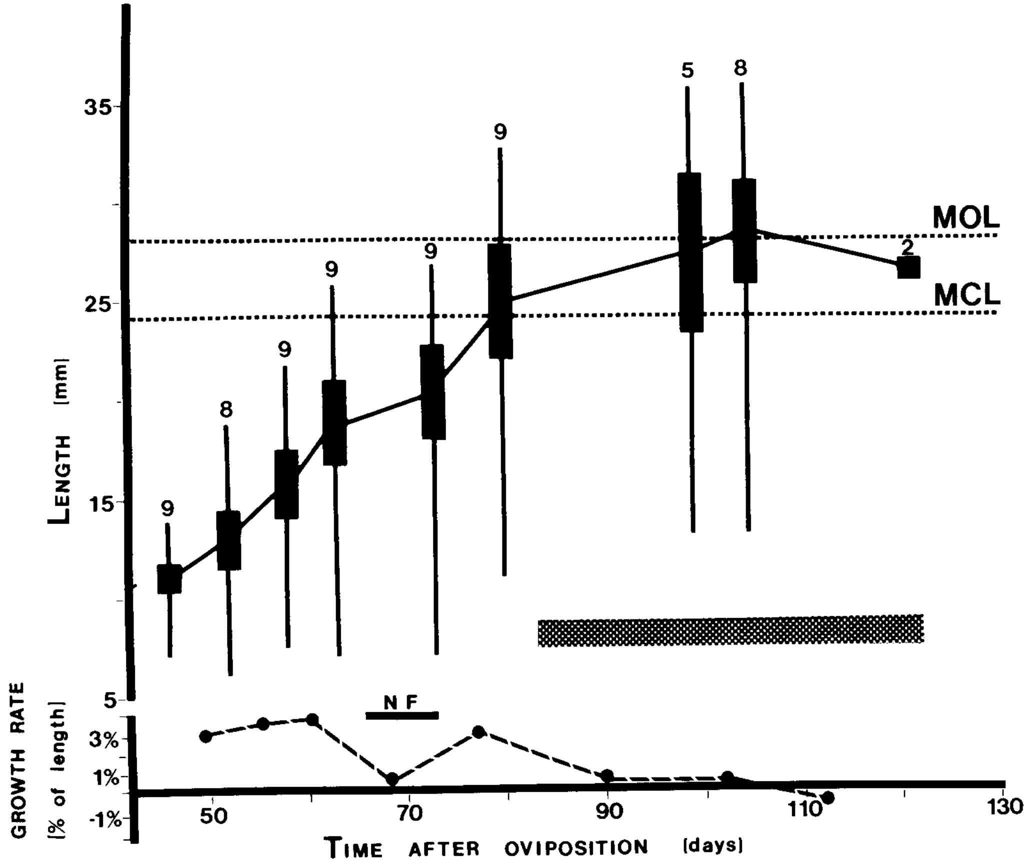

Fig. 2. *Armina tigrina* growth (top) and daily growth rate (bottom) in the laboratory, based on changes in total body length. Narrow vertical bars = range; wide vertical bars = standard error; numbers above bars = sample sizes; MOL = minimum ovipositional length; MCL = minimum copulational length; checkered horizontal bar = period of oviposition by the nudibranchs; NF = week when no food was provided.

spicules was obtained by dissolving whole colonies in NaOH and collecting, rinsing, drying, and weighing the spicules. The water content was determined from the difference between the wet weight and dry weight of whole colonies. Dry weight was determined by drying colonies to a constant weight in an oven (60°C).

RESULTS

Growth

Armina tigrina were first observed as juveniles 31 days after hatching (Fig. 1). Their mean length was 11 mm (7-14 mm). The pre-ovipositional growth rate of the nudibranchs in the presence of food ranged from 3.0% to 3.8% per day (Fig. 2). However, when no sea pansies were available for one week (Days 67-73), the growth rate dropped to 0.9% per day (Figure 2). During oviposition the growth rate decreased further, to 0.6% per day for the first half of the reproductive period and to —0.4% during the second half of the reproductive period.

Reproduction

The minimum copulational length (MCL) was 24 mm and the minimum observed ovipositional length (MOL) was 28 mm (Fig. 2). The runt never exceeded 13.0 × 5.0 mm in size, never oviposited, and was never observed copulating. The other specimens reached sexual maturity in about 2.5 months (Fig. 2) and reproduced for a 1.5 month period (Days 83-128). Each adult laid 2-4 egg masses

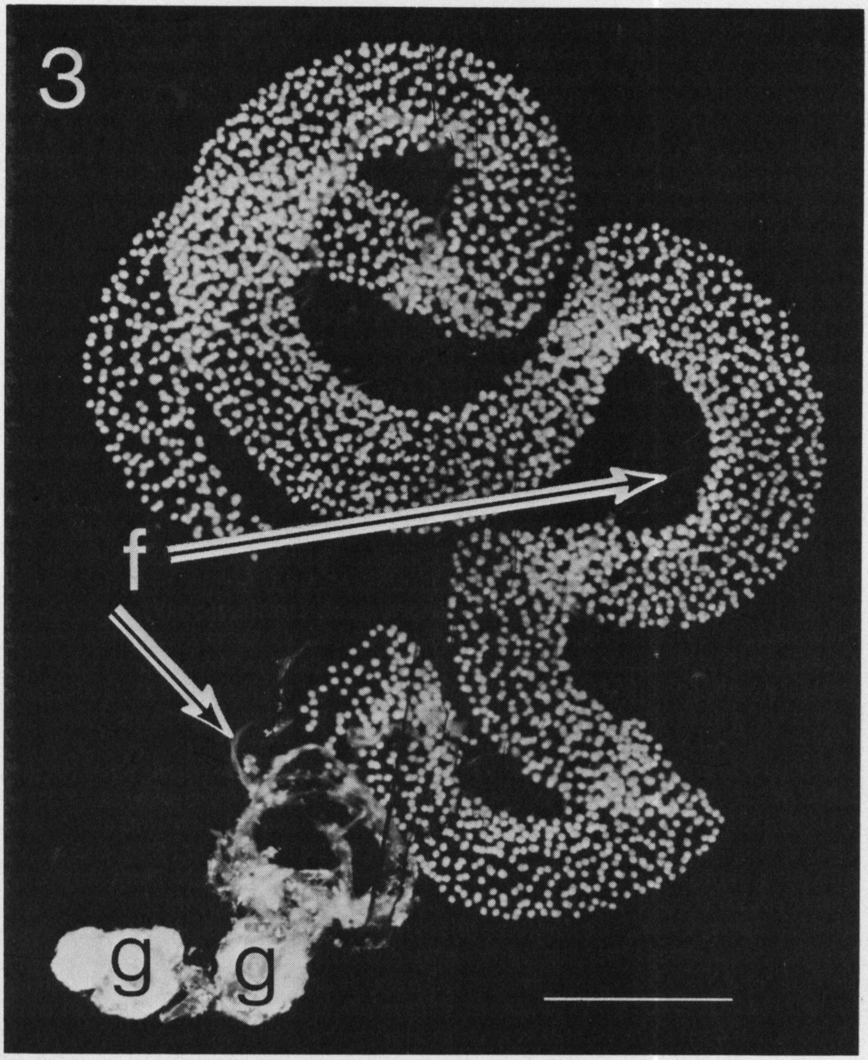

Fig. 3. *Armina tigrina* egg mass, about 95 mm in length, showing fiber (f) for attachment of egg mass to fragments of the gravel (g) substratum. Scale bar is approximately 5 mm.

with 2 000-7 000 eggs per mass. Individuals isolated on Day 104 laid fertile egg masses up to 16 days after known copulation. All nine nudibranchs lived 4-5.5 months (mean = 141 days for n = 7), and died from Days 123-170.

Copulation lasted 10-25 minutes. The nudibranchs mated on the aquaria walls with the right sides of their bodies pressed together. Prior to oviposition, *A. tigrina* burrowed into the substratum. The nudibranch then emerged in a vertical position and remained stationary while extruding the egg mass into the water column. The egg mass was attached to the substratum by a narrow, tough white fiber (Fig. 3). The fiber ran along one edge of the egg mass in a serrated manner and extended about 5 cm beyond both ends.

The egg masses averaged 130 mm long and 3 mm wide. Each mass was wavy (not secondarily twisted) and contained about 50 creamy-white eggs per mm of egg mass length. The capsules were about 290 × 310 μm, were well spaced, and contained only one egg each. The mean uncleaved egg diameter was 198.7±2.5 μm (s.e.).

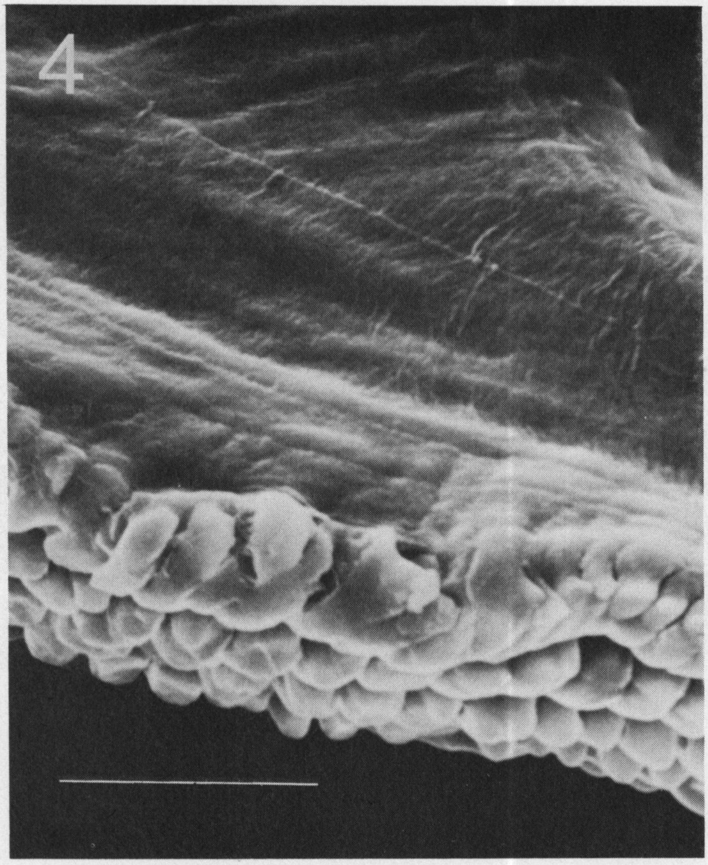

Fig. 4. Scanning electron micrograph of knob-like denticles on free process of *Armina tigrina* jaw. Scale bar = 50 μm.

The eggs developed into free-swimming lecithotrophic veligers in 8-9 days. One day after hatching each veliger had eye spots, a foot 170 μm long, and a Type 1 shell (Thompson, 1961a), which was 290 μm long.

Feeding

Armina tigrina has both jaws and radular teeth for feeding. The masticatory border of the jaw had a smooth anterior edge but its free process was lined with rows of knob-like denticles (Fig. 4). The radular formula for a 34 mm specimen was 36×45-47.1.1.1.45-47. The rachidian teeth were about 115 μm wide with 4-5 lateral cusps on each side of a mono- to tri-denticulate central cusp (Figs 5, 6). The central rachidial cusp fits into a notch in the anterior edge of the succeeding tooth (Fig. 6). Both posterior corners of the rachidian basal plate were ridged. Each lateral tooth was broadly based, with a prominent rounded notch on the inner anterior corner (Fig. 7). The lateral teeth were smooth on the inner surface of the primary cusp but variably denticulate (1-7 denticles) on the outer surface (Figs 6, 7). The basal plates of the lateral teeth abutted each other. The marginal teeth were hook-shaped with narrow basal plates. The posterior edge of the basal plate did not touch the anterior edge of the succeeding marginal tooth. The outer postero-lateral edge of the column of the marginal tooth was ridged; the inner side was grooved (Fig. 5). The marginal teeth were usually smooth, but some of the innermost ones had 1-4 rounded denticles on the outer surface (Fig. 6).

When no food was present, *A. tigrina* burrowed under the substratum for days at a time. When food was reintroduced, the nudibranchs emerged within a few hours and began feeding. During the

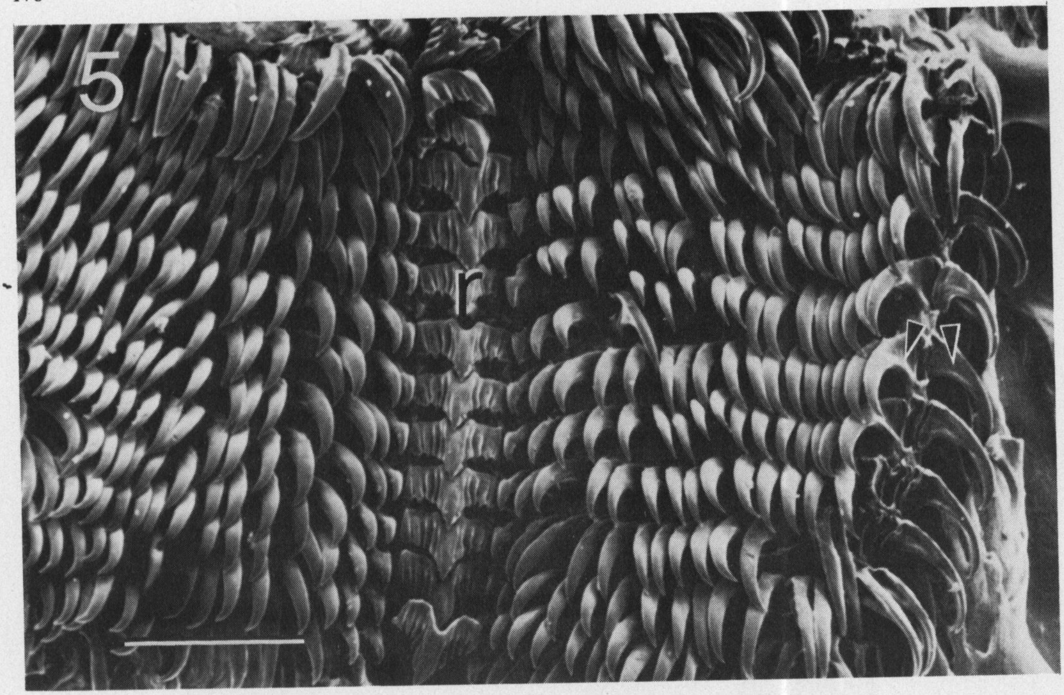

Fig. 5. Scanning electron micrograph of center of *Armina tigrina* radula, showing general shape and arrangement of teeth; r = rachidian tooth; arrows indicate ridge and groove system of marginal teeth. Scale bar = 200 μm.

Table 1. Rate of feeding of *Armina tigrina* on *Renilla reniformis* in the laboratory; nudibranchs were laid 20 June 1976 (= Day 0); consumption per nudibranch per day was calculated from the total food consumed by the total number of nudibranchs (N) in the test group; NF = not fed.

Days	Mean feeding rate (mg/indiv/day)	No. nudibranchs per test group (N)
1-52	<24	9
52-60	24	9
60-66	54	9
67-73	NF	9
73-74	160	9
75-77	170	9
77-80	180	9
80-81	83	9
81-82	96	9
		first egg mass
85-92	63	9
92-93	560	5
97-104	70	4
103-104	270	5
104-107	266	1
107-113	150	1
	275	2
	414	1
	414	1
	479	1
107-122	<110	1
$\overline{X}$ for 85-122	136	9
		last egg mass

day, young juveniles stayed on the ventral surface of the sea pansy. Adults were seen on the dorsal surface of the colony, under the substratum, and occasionally crawling around the aquarium on the glass and substratum. If disturbed when not buried, the nudibranch curled into a ball and floated above the substratum. While floating, it often remained connected to the sea pansy or the substratum by a mucous thread attached to its foot.

Some feeding polyps of *R. reniformis* retracted when *A. tigrina* crawled on the colony and most of the polyps retracted once the nudibranchs began feeding. Colonies placed with mature nudibranchs were consumed in 1-3 days while control colonies remained healthy for 7-30 days. The sea pansies were often seen in the "saddle" configuration (Kastendiek, 1976) and often moved from one end of the aquarium to the other.

Wet weight of the *R. reniformis* colonies ranged from 1.1 to 6.7 g (mean = 3.3 g). The water content of the colonies ranged from 71-77% in small colonies to 84-89% in large ones. Spicule weight was minimal. The nine *A. tigrina* consumed collectively a total of 14.0 g wet weight of *R. reniformis* (6 colonies) between metamorphosis and egg laying and a total of 55.0 g wet weight (15 colonies) from egg laying to death. Although the nine *A. tigrina* varied greatly in size and presumably in feeding rate, the average amount of *R. reniformis* used to support one *A. tigrina* to maturity was 1.6 g wet weight or one small colony. From maturity to death the average consumption per nudibranch was 6.1 g wet weight or about two average colonies. It is unknown how long before death feeding ceased.

Average feeding rate increased with increasing age and size. The feeding rate ranged from 24 mg wet weight of sea pansy per day during the first measured feeding period (Days 52-60) to several hundred mg wet weight per day in mature specimens (Table 1). Immediately after one week of

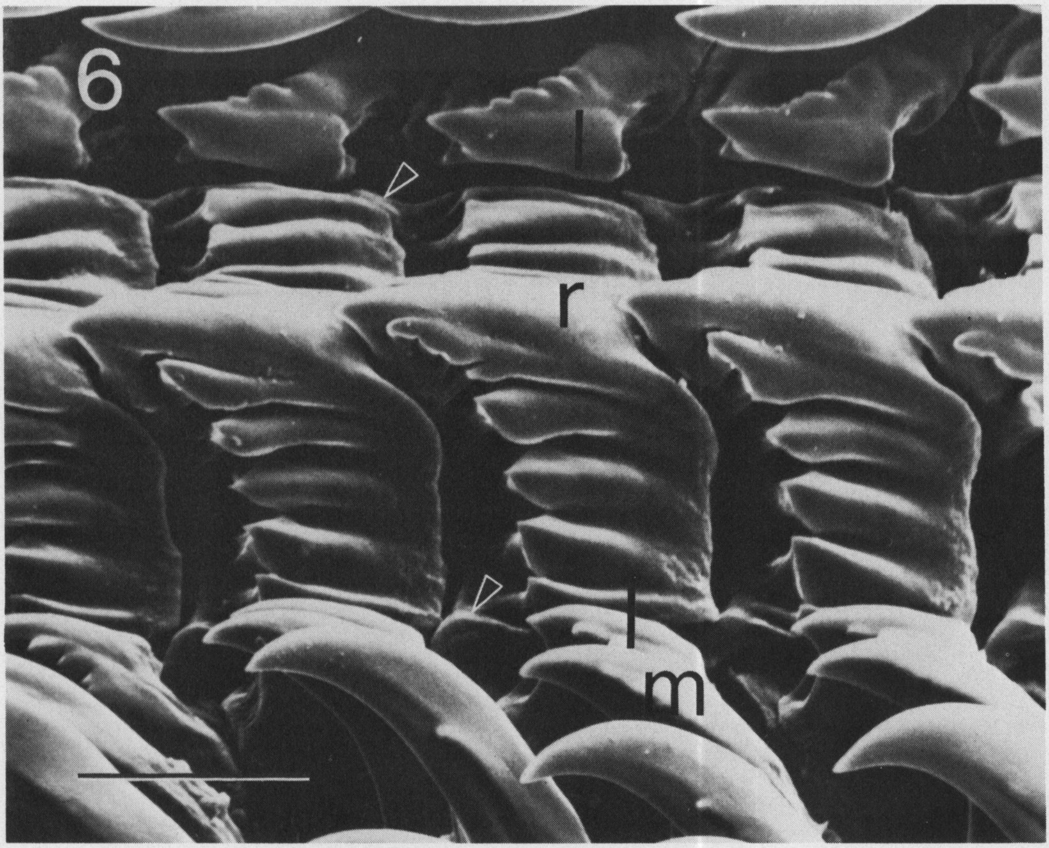

Fig. 6. Scanning electron micrograph of center of *Armina tigrina* radula, showing shape of rachidian (r), lateral (l) and marginal (m) teeth; arrows indicate ridges on rachidian basal plate. Scale bar = 50 μm.

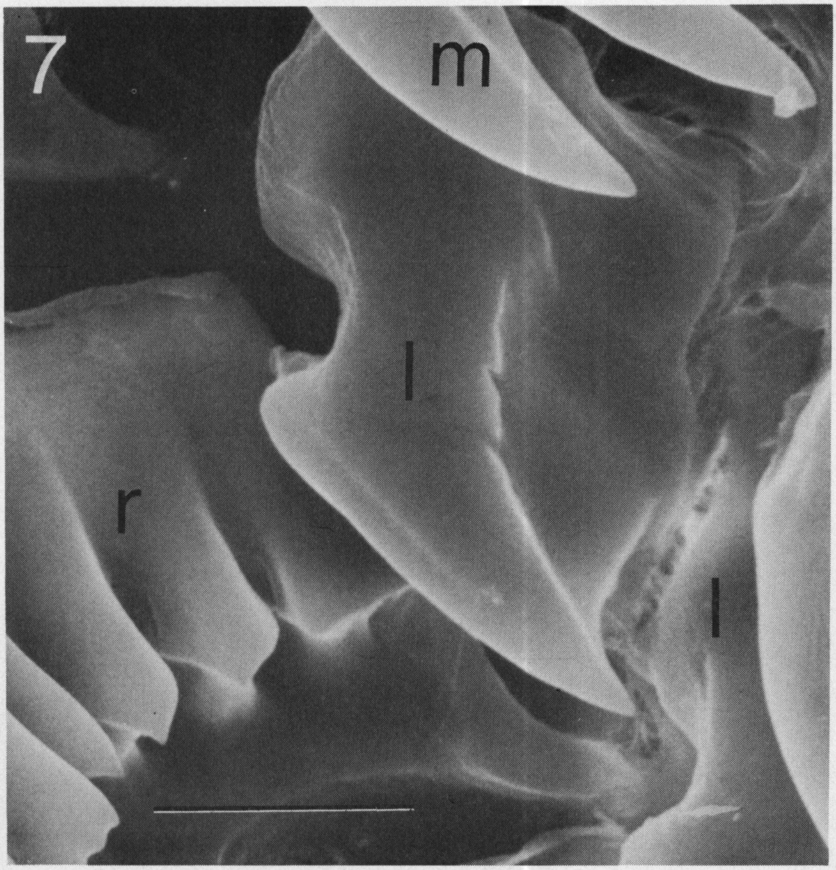

Fig. 7. Scanning electron migrograph of abutted lateral teeth (1). Scale bar = 25 μm.

starvation (Days 67-73), the feeding rate increased three-fold for one week before it dropped back to slightly above the pre-starvation rates. During reproduction, the mean feeding rate was 136 mg wet weight per day, although it varied from about 100 to 600 mg daily during this period (Table 1). Average consumption expressed as dry weight of *R. reniformis* ranged from 5-36 mg per nudibranch per day in pre-reproductive *A. tigrina* greater than 8 mm in length (Days 52-82) and averaged 31 mg per nudibranch per day between egg laying and death.

DISCUSSION

In the presence of abundant food, pre-ovipositional *Armina tigrina* grew at an average rate of 3.4% per day. This rate lies between the rates reported for two subannual aeolids and two annual dorids. The coral-feeding aeolid *Phestilla melanobranchia* Bergh had a pre-ovipositional growth rate (based on length) of 6.3-6.8% per day in Hawaii and 3.4-6.2% per day in Singapore, while the congener *P. sibogae* Bergh grew at 6.9-7.6% per day (Harris, 1975). Elvin (1976) reported a growth rate (based on wet weight) of 1.3-4.2% per day for the spongivore *Diaulula sandiegensis* (Cooper) and 1.7% per day (calculated from Carefoot, 1967) for the spongivore *Archidoris pseudoargus* Rapp. Growth rate based on length and wet weight measurements can be compared in general terms, especially in immature nudibranchs, since length, wet weight and dry weight have been shown to be highly correlated (Clark, 1975; Eyster & Stancyk, 1981).

A tigrina increased in length at only 0.6% per day during early oviposition and eventually decreased in body length. It is presumed that either relative food intake decreased or that a major portion of the food energy taken in was utilized for reproduction; or both. Decrease in size during reproduction, followed by death is common in nudibranchs (e.g. Thompson, 1958; Miller, 1962; Potts, 1970; Clark, 1975).

Thompson (1961b) noted that non-reproductive nudibranchs died at the same time as those that did reproduce. The runt in the present study also died at the same time as its reproductive siblings. It appears that lack of reproduction does not confer increased longevity and, as suggested by Thompson (1958, 1961b) and Todd (1978), timing of death is innately determined.

Reproduction in *A. tigrina* was typical of nudibranchs except for the stance assumed during oviposition and the use of fibers for securing the egg masses to the substratum. Most nudibranchs move in tight circles while attaching their egg masses but *A. tigrina* remained vertical and stationary while extruding the egg mass into the water column. Presumably *A. tigrina* must secure one end of the fiber before emerging from the substratum, insuring firm attachment of the egg mass before it is laid. After extruding the egg mass, the nudibranch must reburrow to secure the other end of the fiber. Use of similar attachment fibers has been reported in *Armina californica* (Cooper) and cephalaspidean opisthobranchs (use jelly strings; Hurst, 1967) and seems to be an effective means of anchoring egg masses in soft, mobile substrata.

Nudibranchs must reach their respective MCL's and MOL's (minimum lengths) before they can reproduce (Todd, 1978; Eyster & Stancyk, 1981). Todd (1978) also showed that a minimum age was required for gonadal development to proceed. In the present study the runt attained the minimum age required for reproduction but it never attained the MCL.

The smallest individuals observed copulating (MCL = 24 mm) were shorter than the smallest specimens observed ovipositing (MOL = 28 mm), i.e. the nudibranchs were functional males before they were fully functional females. This difference may be due to earlier maturation of sperm than ova (Todd, 1978). A similar difference between the MCL and MOL has been reported in the aeolid *Phestilla melanobranchia* (Harris, 1975) and in the dorid *Doriopsilla pharpa* (Eyster & Stancyk, 1981).

Intraspecific variability of developmental type has been reported in only a few opisthobranch species. The variation may occur within geographically separated populations (Rasmussen, 1944; Thorson, 1950), or within the same population either with the aid of extraembryonic yolk (Clark, Busacca, & Stirts, 1979) or without (Eyster, 1979). In the present study lecithotrophic veligers developed from large eggs (199 μm diameter) with up to 7 000 eggs per egg mass. In contrast, Clark & Goetzfried (1978) noted that in *Armina tigrina* from southern Florida, planktotrophic veligers developed from small eggs (82 μm diameter) with up to 10 000 eggs per egg mass. This difference in developmental type suggests the existence of either two species of *Armina* or one species with two geographically separated developmental types.

Radular teeth are usually described from a structural viewpoint without comments on possible functional aspects. Solem (1972) was the first to show the existence of functional interlocking systems between rows of pulmonate gastropod teeth and to describe how the transfer of pressure from one tooth to the next during feeding increased cutting efficiency. A similar functional arrangement of teeth was seen in *A. tigrina.* The rachidian tooth was notched on the anterior side and fitted against the preceding tooth (Fig. 6). During the feeding stroke, as the radula moves backwards into the mouth, resistance on the rachidial cusp would press that tooth against the preceding tooth, providing increased cutting capacity (Solem, 1972). The rachidian tooth also had a ridge on each outer corner of the basal plate (Fig. 6). Solem (1972) proposed that such structures provide support and prevent side to side shifting of the succeeding tooth during feeding. The opposing ridges and grooves of the marginal teeth would not only provide within-row support during feeding but also would allow the teeth to fold into a smaller space when not in use (Solem, 1972). Similar structural-functional tooth arrangements occur in *A. californica* (pers. observ.), but the ridges on the rachidian basal plates are about three-fold larger.

Feeding in *A. tigrina* was affected by many factors, including size, age, and reproductive activity. Until the nudibranchs reached a mean length of 11 mm, the effect of their feeding on the sea pansies was minimal. However, several large nudibranchs destroyed whole colonies in a day. Similarly Kastendiek (1976) reported that *Armina californica* from the western U.S. coast could completely consume *Renilla kollikeri* Pfeffer. Kastendiek (1976) also reported that adult colonies were able to escape their nudibranch predators. However, in this study the aquaria prevented escape attempts and colonies of all ages were consumed. The extreme variability in feeding rates during the reproductive period (Table 1) was probably due to feeding spurts between egg-laying periods.

Life cycles of nudibranchs are related to availability of prey and can be divided into two general categories (Miller, 1962; Clark, 1975). As shown by these and other authors, species in one category have annual life cycles with one generation per year and tend to feed on abundant, stable prey; species with subannual cycles have several generations per year and tend to feed on more seasonal prey. Consequently, most sponge- and anthozoan-feeding nudibranchs are annual and most hydrozoan-feeding nudibranchs are subannual, although there are exceptions (Harris, 1975; Christensen, 1977). Unfortunately, little is known about the life history of *Renilla reniformis*. Regardless of whether *R. reniformis* provides a stable food supply and in spite of the nudibranch's large size (which is indicative of annual species; Clark 1975), the branched gut of *Armina* (Hyman, 1967, p. 518) and the present laboratory observations suggest that *Armina tigrina* is a subannual nudibranch.

SUMMARY

1. Aspects of the growth, reproduction and feeding of the sand-burrowing nudibranch *Armina tigrina* Rafinesque are described for nine siblings.
2. Average growth rate of fed and starved pre-ovipositional specimens was 3.4% and 0.9% per day respectively. Growth rate of ovipositing specimens was 0.6% per day or less.
3. Reproduction began when the nudibranchs were about 80 days old and were at a length of 24 mm (for copulation) and 28 mm (for oviposition). Each adult laid 2-4 egg masses over a 1.5 month reproductive period.
4. The egg masses were wavy and contained 2 000-7 000 eggs. Each egg mass was attached to the substratum by a fiber which extended about 5 cm beyond both ends of the mass.
5. The eggs were white and about 199 μm in diameter. Development was lecithotrophic and took 8-9 days at 23°C. Planktotrophic development has been reported elsewhere for this species.
6. Specimens lived 4-5.5 months, i.e. were subannual.
7. The radular teeth presumably increased their cutting efficiency by abutting each other.
8. Each nudibranch consumed during its lifetime the equivalent of 2-3 colonies (6-9 g) of the sea pansy *Renilla reniformis* Pallas.

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