

PREDATOR-INDUCED POLYMORPHISM IN THE BRYOZOAN *MEMBRANIPORA MEMBRANACEA* (L.)

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Abstract: Three described species of the bryozoan genus *Membranipora*, *M. membranacea* (L.), *M. serrilamella* Osburn, and *M. villosa* Hincks, occurring together on brown macroalgae off the west coast of North America are eco-phenotypic variants. These forms should be called *M. membranacea* on the basis of priority.

The presence of spines, an important diagnostic feature separating these *Membranipora* forms, is induced by two nudibranch predators, *Corambe pacifica* MacFarland & O'Donoghue and *Doridella steinbergae* Lance. Spines protect *Membranipora* zooids against predation by these nudibranchs. The population costs of spine production include lower growth and reproductive rates.

INTRODUCTION

Membranipora colonies encrusting on the giant kelp *Macrocystis pyrifera* (L.) in southern California waters are presently ascribed to three species, *M. membranacea* (L.), *M. serrilamella* Osburn, and *M. villosa* Hincks. Characteristics used to distinguish these species are the presence of a cryptocyst (a serrated inner extension of the zooid wall) in *M. serrilamella*, a cryptocyst as well as numerous spinous processes on the frontal membrane and lateral zooid walls in *M. villosa*, or a lack of these features in *M. membranacea* (Hincks, 1882; Robertson, 1908; Osburn, 1950).

Hincks (1882) originally described *M. serrilamella* as a form of *M. membranacea* (*M. membranacea* form *serrata*). Robertson (1908) justified raising this form to the species rank on the lack of transitional forms, a contention contradicted by several workers. For instance, Seed (1976) found considerable variation in zooid structure within a colony. O'Donoghue (1926) noted that different parts of a colony may have characteristics attributable to different species. The reported lack of transitional forms may be partly due to misidentifications. For example, Osburn (1950) commented that some colonies described as *M. serrilamella* by Robertson (1908) belong to a different species *M. perfragilis* (MacGillivray) which exhibits strong development of the cryptocyst. However, Osburn (1950) maintained the specific rank of *M. serrilamella*. The development of spines characteristic of *M. villosa* is also subject to variation. Pinter (1969) observed the delicate frontal membrane spines on zooids which would otherwise be ascribed to *M. membranacea*.

This report offers several taxonomic and ecological considerations which indicate that only a single species is involved and that the three forms represent eco-phenotypic

variants partly in response to predation by the nudibranchs *Doridella* (= *Corambella*) *steinbergae* Lance and *Corambe pacifica* MacFarland & O'Donoghue. The adaptive significance of these forms in terms of trade-offs between the processes of growth and reproduction and vulnerability to predation is also investigated.

Aspects of the biology and ecology of *Doridella* and *Corambe* are discussed by Lance (1962) and MacFarland & O'Donoghue (1929). These nudibranchs are very similar in appearance and their dorsal coloration pattern closely resembles the colony structure of *Membranipora*. *Membranipora* is the only known prey of these nudibranchs (MacFarland & O'Donoghue, 1929; Lance, 1962; McBeth, 1968; Seed, 1976).

METHODS

Membranipora populations on *Macrocystis* were sampled in a kelp bed offshore of the Torrey Pines State Park ≈ 5 km north of the Scripps Institution of Oceanography at 2-wk intervals. Cyphonautes larvae of *Membranipora* were sampled at least twice weekly from the sea-water flume on the Scripps pier. A full description of procedures used to monitor abundances of colonies and larvae are presented elsewhere (Yoshioka, in press).

The relationship of the nudibranch predators *Corambe pacifica* and *Doridella steinbergae* with *Membranipora* was investigated by suspending a section of kelp frond from the Scripps pier. Individual kelp blades were removed at intervals and various population and taxonomic features of *Membranipora* and the nudibranchs were recorded. The number of colonies was counted and their diameters measured for growth rate estimates. The presence of spined zooids was noted. Total zooid density, the proportion of living and dead zooids, and the proportion of spined zooids were estimated by examining 8 to 13 randomly placed 0.32-cm^2 quadrats on the blade surface. *Corambe* and *Doridella* on kelp blades were counted, sized, and identified (except for individuals < 0.07 cm which could not be differentiated to the species level). The number of egg masses of both species was also counted.

RESULTS

Extensive development of spines on *Membranipora* colonies was first encountered at Torrey Pines on January 29, 1970 during a period of high colony density (> 1 colony per cm^2). This sample was examined for features of spine formation. Detailed attention was given to the primary zooids of newly recruited colonies since ancestrula features are often a good indicator of specific characteristics in bryozoans. Robertson (1908) gave extensive details of the ancestrula of *M. villosa*. The total number of spines on the zooid walls of ancestrulae ranged from 8 to 15 indicating considerable variation in spine formation among colonies (Fig. 1). (For the purposes of this analysis spines occurring on the medial wall separating the zooids are ignored.) The number of spines often

differed between the primary zooids of a given ancestrula. Robertson (1908) suggested the presence of forked spines on the ancestrula as a diagnostic feature of *M. villosa*. However, the number of forked spines also shows considerable variation among and within colonies. The presence of spines was also associated with the outer edge of colonies regardless of colony size in this sample suggesting an eco-phenotypic origin (Table I).

Several other considerations indicating an eco-phenotypic basis for spine formation were noted in this study. Biweekly samples from Torrey Pines show that the occurrence

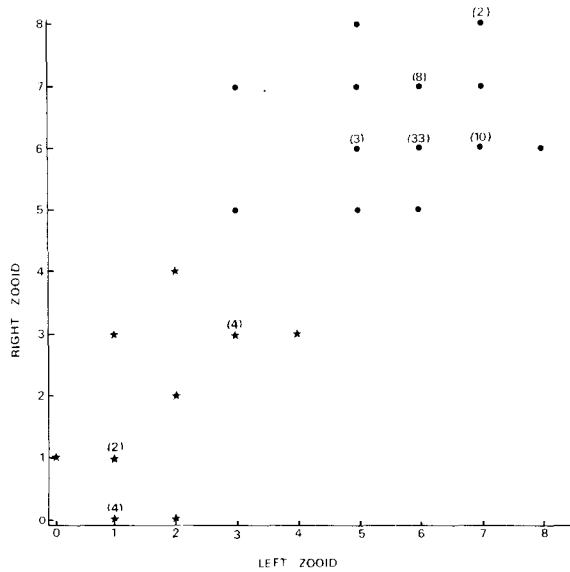


Fig. 1. Number of forked spines and total number of spines on primary zooids of the ancestrula: numbers in parentheses indicate number of colonies represented; ●, total and *, forked number of spines on right and left zooids.

TABLE I

Percent *Membranipora* with spined zooids in various colony zones: Row 1 is the primary zooids of the ancestrula; *N*, number colonies examined.

Colony size	<i>N</i>	Row						
		1	2	3	4	5	6	7
1	64	100	—	—	—	—	—	—
2	18	0	78	—	—	—	—	—
3	17	0	29	94	—	—	—	—
4	20	0	0	20	90	—	—	—
5	27	0	0	11	67	100	—	—
6	17	0	6	6	12	35	71	—
7	4	0	0	0	0	25	25	100

of spines is restricted to the late winter–early summer months in association with high colony densities (> 100 colonies per blade) with one exception, May 29, 1970 (Fig. 2).

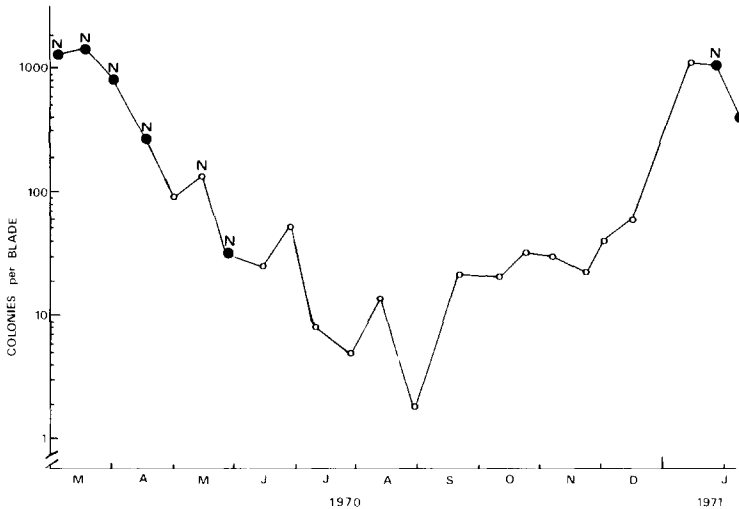


Fig. 2. *Membranipora* colony densities on kelp blades and the appearance of spined zooids and nudibranchs at Torrey Pines from March 1970 to February 1971: ●, spined zooids present; ○, only unspined zooids present; N, nudibranchs present.

Association of high colony density and spine occurrence is significant at the 0.003 level (Fisher exact probability, contingency table). The presence of two dorid nudibranch predators, *Corambe pacifica* and *Doridella steinbergae*, was also associated with high colony density and spine occurrence ($P < 0.0005$ for spine occurrence and nudibranchs, Fisher exact probability). The restriction of the nudibranchs to the former situation is attributable to a threshold settling response since recruitment of their veliger larvae was observed only during periods of high *Membranipora* populations (Yoshioka, in press). Interestingly, nudibranchs were present on the single occasion when spined zooids were observed during a period of low colony density.

A field experiment suggested that nudibranchs may actually induce spine formation, hence the relationship between the two is not merely fortuitous. On 6 November, 1970 a kelp frond was taken from Torrey Pines and hung from the Scripps pier, an area which lacks many of the kelp bed fish predators of *Membranipora*. Yoshioka (in press) has shown that fish predation has a major impact on *Membranipora* population size. As a consequence of reduced fish predator pressure, many of the colonies survived eventually growing to cover extensive areas ($> 50\%$) of the kelp blade surfaces. During this interval (≈ 12 to 18 November) zooids near the growing edges of colonies were characterized by the *M. membranacea* zooid structure. Simultaneously, nudibranch settlement was occurring in response to high prey densities. Soon thereafter younger zooids near the growing edges of colonies developed spines characteristic of *M. villosa*

(Fig. 3). The low colony density on the test blades, 80 ± 22 (95% C.I.), compared to the 100+ colonies per blade in field samples when spined zooids occurred indicates that the nudibranchs induced the formation of spines. Crowding was not a causative

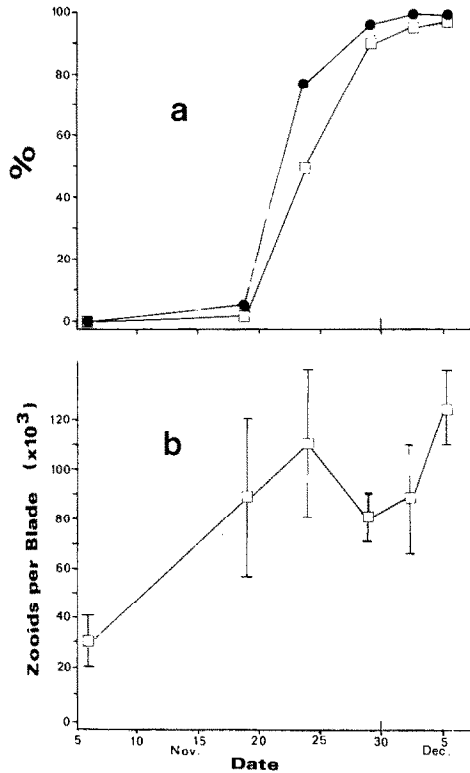


Fig. 3. a, % colonies (●) and % zooids (□) with spines on the test blades; b, zooid densities during the field experiment ($\pm 95\%$ C.I.).

factor in this case since space became limiting for many colonies prior to the appearance of the nudibranchs. Also, I never observed spine formation on large colonies without the presence of the nudibranchs irrespective of the degree of crowding. The absence of spined zooids at Torrey Pines and other local kelp beds during this period and the difference in season (fall versus late winter–early summer) negate the influence of physico-chemical oceanographic factors in spine formation. The initial sequence of colony growth, nudibranch settlement, and spine formation was also observed in two other test situations, late August 1970 and late June 1971. However, test blades in both instances were lost due to rough seas prior to the completion of the experiments.

The presence of spines may be of considerable adaptive significance for *Membranipora*. *Doridella* feeds by placing its mouth against the smooth surface of the frontal membrane of *Membranipora* zooids forming a “water tight” seal before rasping through

it and sucking out its contents (McBeth, 1968). Morphological similarities indicate that *Corambe* feeds in a similar manner. McBeth (pers. comm.) suggests that the presence of spines makes it physically difficult for these nudibranchs to place their mouths into proper feeding position. In confirmation, feeding patterns observed in the field experiment indicate that spines do indeed protect zooids from predation by these nudibranchs. Although *Corambe* usually prefers feeding on the growing edges of colonies (MacFarland & O'Donoghue, 1929), zooids consumed on the test blades were predominantly of the unspined forms occurring in the older, central part of colonies. On unspined zooids in the laboratory, *Doridella* feeds in a random manner with no preference for any particular portion of colonies (McBeth, 1968). The preference for unspined zooids is eventually manifested by the preponderance of spined zooids on the test blades (Fig. 3).

The protective function of spines is further supported by indications that the nudibranchs became food limited on the test blades despite the fact that the total abundance of potential food (intact spined and unspined zooids) showed no consistent pattern

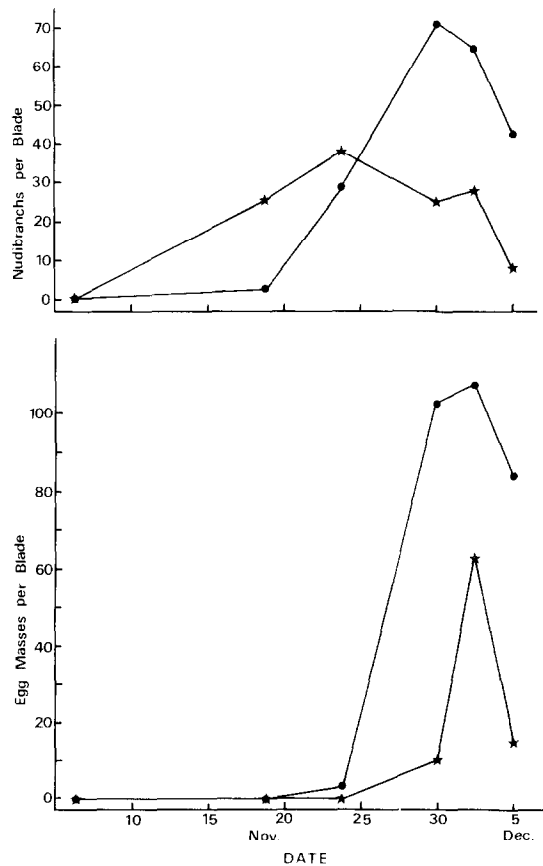


Fig. 4. Numbers of *Doridella steinbergae* (●) and *Corambe pacifica* (*) and their egg masses on test blades.

during the period when the nudibranchs were present (Fig. 3). Densities of both species and their egg masses decreased during the terminal stages of the experiment (Fig. 4). Also, individual sizes of both species decreased significantly from 30 November to 5 December ($P = 0.05$ for *Corambe* and $P = 0.01$ for *Doridella*, Mann-Whitney U -test). Under conditions of food limitation in the laboratory, individuals of both species cease growing and decrease in size before succumbing. Recruitment of veligers was quite low during this period and would not account for decreased individual sizes. Moreover, the maximum size of both species declined, *Corambe* from 0.7 to 0.61 and *Doridella* from 0.59 to 0.42 cm. Decreases in the density and size of the nudibranchs cannot be accounted for by death due to senescence since *Corambe* reaches a size of 1.3 cm (MacFarland & O'Donoghue, 1929) and has a lifespan of 6 wk while *Doridella* grows to 0.8 cm and lives for 24 days (Yoshioka, 1973).

Two possible consequences of spine production include decreased growth and reproductive rates. Estimates based on colony size show a slowing of growth rates from 0.194 to 0.095 cm per day before and after the appearance of spines (Table II). Only

TABLE II

Colony sizes and estimated growth rates before and after the appearance of *Doridella* and *Corambe* on the test blades.

Date	Colony radius (cm)	SD	Growth (cm/day)	N
19 Nov.	1.45	0.60	0.194	18
24 Nov.	2.42	0.80		11
30 Nov.	2.99	1.01	0.095	14

colonies where space was available for growth were measured. This difference cannot be attributed to size specific growth rates since linear growth of *Membranipora* increases with colony size (Yoshioka, 1973). A qualitative indication of reduced growth rates during this period was the disappearance of the "milky fringe", a translucent zone at the edge of rapidly growing colonies (Lutaud, 1961).

Field abundances of cyphonautes also suggest an association between spine production and reduced reproductive rates. The relation between larval abundance and nudibranch density is shown in Fig. 5. Details of the analytical procedure are given in Yoshioka (in press). Briefly, larval abundance was divided by zooid density to normalize for the reproductive potential of *Membranipora* populations. Larval abundance lagged nudibranch and zooid density by 4 wk, the estimated development time of the cyphonautes larva. Nudibranch abundance was divided by zooid density as an index of the relative impact of nudibranch predation. Relative larval abundances decrease by an order of magnitude following periods of high nudibranch densities indicating

decreased reproduction by *Membranipora* ($P < 0.01$, multiple regression; see Yoshioka, in press).

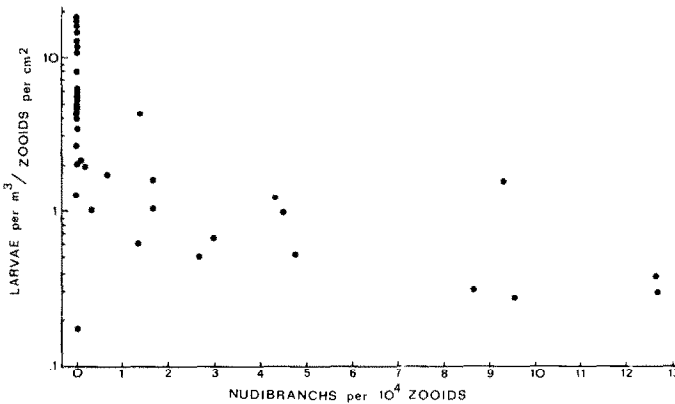


Fig. 5. Normalized larval abundance versus nudibranch density: see text for explanation of analysis.

DISCUSSION

Indications that the specific characteristics of *Membranipora* have an eco-phenotypic basis have been noted by previous authors. The small size and high densities of *M. villosa* colonies and their occurrence in spring and summer as well as the relatively large size of *M. membranacea* were reported by Robertson (1908) and Pinter (1969). Clendenning & Sargent (1958) also observed that *M. serrilamella* characteristics are most frequently encountered in medium size colonies or in the interior portions of larger colonies. This latter feature typified the *Membranipora* colonies in the field experiment prior to the appearance of the nudibranchs. Thus, characteristics of all three species can be found in different parts of a single colony. Since all zoooids are genetically identical due to asexual reproduction, the ability of single genotypes to express different species specific features should be sufficient proof that such characters are inadequate for diagnostic purposes.

The three forms represent eco-phenotypic variants and can be placed in a developmental sequence; *M. membranacea* has the simplest zooid structure, *M. villosa*, the most complex, and *M. serrilamella* is in an intermediate position. The three forms should be synonymized and called *M. membranacea* based solely on the principles of taxonomic priority. However, it must be emphasized that the relationship with *M. membranacea* described from other geographical locales is unclear. For instance, the larva of *M. membranacea* of European waters is larger and differs in ornamentation from the cyphonautes of this study (Robertson, 1908; Atkins, 1955). Only two cyphonautes are known from west coast waters, one metamorphosing into *M. tuber-*

culata (Bosc) (Hastings, 1930) and the other belonging to the three forms of this study constituting further circumstantial evidence for a single species.

Zaret (1972) explained the maintenance of predator associated polymorphism in the cladoceran *Ceriodaphnia* as a trade off of reproduction and liability to predation. A similar case can be made for *Membranipora*. Colonies possessing the simple *M. membranacea* zooid structure display high growth and reproductive rates, but are vulnerable to predation by *Corambe* and *Doridella*. Conceivably, spine production requires metabolic energy which otherwise would have been channeled into growth and reproduction. The high densities of *Doridella* and *Corambe* that may occur in kelp beds indicate that spines may be of considerable adaptive significance for *Membranipora*. For example, Lance (1962) found up to 68 individuals of *Doridella* on a single kelp blade. In this study the standing crop of zooids on one occasion, 29 June, 1971, represented only about a 10-day supply of food for the nudibranchs. Two other nudibranchs *Polycera atra* MacFarland and *Triopha grandis* MacFarland as well as fish predators consume the entire zooid structure of *Membranipora*. Thus, spines offer little protection against these feeding mechanisms. The relatively infrequent appearance of *Doridella* and *Corambe* in kelp beds and their high abundances when present confers obvious advantages of spine formation during those instances when these nudibranchs occur. The associated decrease in growth and reproduction and ineffectiveness against other predators suggests spine formation would be disadvantageous at other times.

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