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COLONIALITY AND INDUCIBLE POLYMORPHISM

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Abstract.—Although zooid polymorphism is a common phenomenon among colonial marine invertebrates, the proximate mechanisms governing transformations and coordination among the different units of a colony are largely unknown. Zooids in these often genetically homogeneous colonies may be coordinated by intrinsic, centralized, signaling mechanisms at the colony level (e.g., by giant axons in siphonophores) or by more decentralized mechanisms at the zooid level, such as environmental cues activating same-aged zooids. This second class of mechanism is responsible for coordinated defense in colonies of the marine bryozoan *Membranipora membranacea*. *Membranipora membranacea* colonies are initially populated by identical looking zooids, some of which can rapidly differentiate into an organized pattern of defensive zooids on the periphery of the colony in response to chemical cues from predators. To test the hypothesis that the age of the zooids rather than their position within the colony determines which zooids develop spines, I manipulated the normal center-to-edge age gradient. With these manipulated colonies and localized chemical cues, I established that spination is evoked independently by local action of inducers on each zooid of the appropriate age group, irrespective of its position within the colony. Thus, spines were produced in the centers of colonies as well as on the edge when the central zooids were the same age as the edge zooids. Similar age-dependent, "self-organizing" mechanisms regulate the distribution of specialized tasks within colonies of social hymenopterans. For example, honey bees form colonies of related units, and, in these, the principal basis for specialization of labor among the units is ontogeny: similarly aged individuals respond similarly to the same environmental cues. Inducible defensive polymorphisms such as those shown by bryozoans, hydrozoans, and anthozoans may be one pathway by which fixed polymorphisms in zooid form and function arise. If the transition from facultative to fixed is common, then processes such as genetic assimilation may be more important than has been thought. It seems possible that the relative ubiquity of both facultative and constitutive polymorphisms in colonial invertebrates may be a result of the compartmentalized, iterated nature of modular organisms, which allows the production of variant zooids through slight changes in developmental timing.

Polymorphism, or the division of labor among morphologically differentiated zooids within a colony, is well represented among colonial marine invertebrates in the Bryozoa and Cnidaria (Ryland 1970; Boardman and Cheatham 1973; Silen 1977). Despite its ubiquity, we know little about how polymorphic zooids are integrated into the architecture of a colonial organism. Thus even issues such as the conditions favoring the evolution of polymorphism, the developmental determinants of zooid morphology, and the mechanisms coordinating behavior or morphology among members with the same or different functions within a colony remain largely unresolved (Silen 1977). In some colonial invertebrates, polymorphism within the colony can be facultatively produced by induction of zooids with reproductive or defensive morphology. These induced zooids or

structures include spined zooids of bryozoans (Yoshioka 1982; Harvell 1984, 1986), stolons of bryozoans (Osborne 1984; Harvell and Padilla 1990) and hydrozoans (Ivker 1972; Buss et al. 1984; Buss and Grosberg 1990), nematocyst-laden tentacles and acrorhaghi of corals and anemones (Wellington 1980; Chornesky 1983; Sebens and Miles 1988), and spiral zooids and generative polyps of hydrozoans (Bravermann 1974). The polymorphs are activated by waterborne cues of predators (Harvell 1986, 1990), vibration of the substrate (Bravermann 1974), contact with competitors (Ivker 1972; Wellington 1980; Chornesky 1983; Sebens and Miles 1988; Harvell and Padilla 1990), or carbon dioxide increases mediated through high polyp density (Bravermann 1974). In some colonies such inductive events result in a transition from a nonpolymorphic to a polymorphic state.

Coordination of behavior and morphological units in colonial marine invertebrates results from an interaction of zooid-level and colony-level mechanisms (Boardman and Cheatham 1973). In most colonies, zooids retain local autonomy; interzooidal electrical pathways serve more as links between the action systems of these zooids than as integrating centers of whole colonies (Mackie 1986). However, the relative importance of these two levels of control varies with the degree of integration of zooids within a colony. For example, in siphonophores, which are highly polymorphic, motile, colonial cnidarians, slow swimming is produced by all the zooids contracting in series and is not actively integrated by a centralized control center. This zooid-level control of swimming can be overridden by escape responses generated by giant axons, which cause the sequence and frequency of zooid contractions to change. This is the only example in which the behavior of a marine colony is known to be under a higher-order colonial control and the colonial nervous system not only relays but also initiates behavior (Mackie 1986). The sophisticated interplay between zooid-level and colony-level control in siphonophores is perhaps demanded by the requirements imposed by swimming—of necessity, a highly coordinated response. The extreme opposite of this type of centralized colony-level control is decentralized, zooid-level control, regulated by extrinsic cues. Since individual colonies can often be large, with parts distributed in several separate environments, such as are created by localized competition and predation regimes, it would seem that behavioral or morphological responses should also be localized.

While neurophysiological control and coordination of simple zooid behaviors such as polyp withdrawal responses are known from several phyla of marine invertebrates (Lutaud 1977; Thorpe 1982; Mackie 1986), the mechanisms producing pattern in the more complex, slowly propagating, colonywide events such as inducible structural defenses and reproduction are poorly known (Mackie 1986). In the hydrozoan *Podocoryne*, pattern in the distribution of polymorphic polyps is produced through the action of self-organizing generative rules (Bravermann 1974). Sexual zooids are induced from nonsexual hydranths by high concentrations of carbon dioxide and appear in crowded parts of colonies where the partial pressure of carbon dioxide is presumably higher. Thus the pattern of generative polyps occurring in colony centers is produced by localized carbon dioxide buildup rather than the age of the polyps. Similarly, the allocation to the growth of stolons and hydranths appears to be a response to inhibitory substances pro-

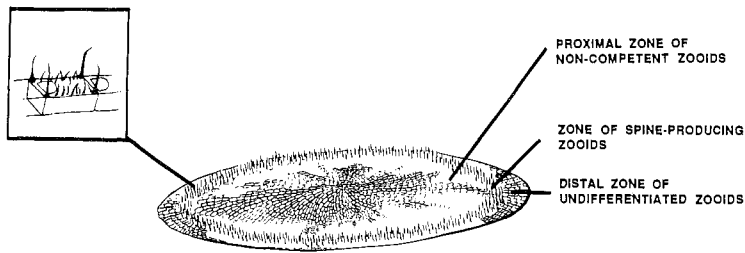


FIG. 1.—Regional production of spines by *Membranipora membranacea* colonies. The inset shows the detail of spines on a single zooid. (From Harvell 1990.)

duced by the hydranths, limiting the proximity of new hydranths to a set distance from existing ones. The distance between hydranths varies with water temperature and colony size. Similarly, defensive zooids, called spiralzooids, are induced by localized vibrations on the substrate. No particular pattern in the within-colony distribution of these defensive structures has been described. Bravermann's work shows how simple growth rules can produce pattern in the distribution of polymorphic zooids in a colony.

Another example of a patterned inducible polymorphism is the spines produced on the marine bryozoan, *Membranipora membranacea*. *Membranipora membranacea* colonies produce defensive spines within 36 h of detecting chemical cues from a trophically specialized molluscan predator (Harvell 1984, 1986). In an initial response to the waterborne nudibranch extract, permanent chitinous spines are produced, but only on zooids near the periphery of responding colonies; other, more proximal zooids do not initially produce spines (fig. 1). In laboratory experiments, all colonies that were induced with waterborne chemical cues showed a similar pattern of peripheral spination, and field-collected colonies that had been exposed to nudibranch extract usually showed a peripheral band, too. Bryozoan colonies grow by budding new zooids at the edge of the colony. The pattern of this budding is called astogeny, which is the series of age-dependent zooidal changes that determines the form of the colony. Thus the center zooids are the oldest, and more distal zooids are successively younger. The zooids on the outermost edge of the colony are usually in the process of forming and are undifferentiated buds. One goal of this investigation is to determine the processes that limit the distribution of defensive zooids to a band near the perimeter of the colony and that result in the pattern of a complete band of spined zooids.

Using the spine induction response to assess underlying mechanisms of pattern formation of zooids within colonies, I examined two hypotheses. According to the colonial coordination hypothesis, the coordinated pattern is due to intrinsic, centralized, colony-level control; that is, zooid receptors detect cues, and a colony-level mechanism transmits a signal to previously unstimulated adjacent zooids (as proposed in Harvell 1984). According to the shared environment hypothesis, the pattern is produced not by active signaling and intrinsic coordination, but by zooids of the same age responding similarly (producing spines) when activated by a common extrinsic cue.

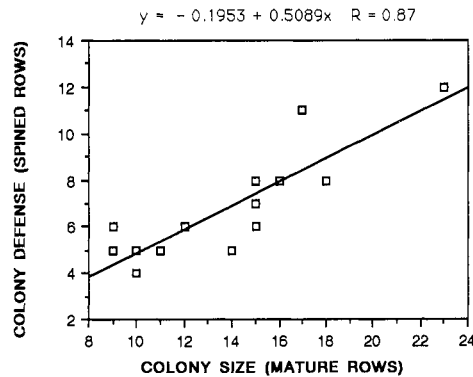


FIG. 2.—Size-specific response of colonies to a single dose of nudibranch factor. Colony size is measured as the number of mature rows in a colony. Mature rows are rows with fully developed, feeding zooids. (From Harvell 1990.)

Experiments to distinguish these hypotheses involve manipulating the normal center-to-edge ontogenetic gradient within colonies and restricting the chemical cue to particular regions of the colony. On the basis of several of these experiments, I conclude that only young zooids are competent to produce spines in response to particular chemical inducers. Thus, age-specific competence best explains differential development of spines on peripheral zooids of *M. membranacea* colonies. It remains unclear whether most functional gradients in colonial invertebrates are age based and whether morphological pattern arises naturally out of astogenetic patterns.

SIZE-SPECIFIC DEFENSIVE RESPONSE

Methods

To determine the size-specific pattern of response, colonies of a range of sizes (9–24 zooid rows in diameter, $N = 14$) were exposed to the same level of nudibranch extract. A crude extract of nudibranch factor was prepared by homogenizing (on ice) approximately 100 nudibranchs (*Doridella steinbergae*) in 15 L 10- μ m-filtered seawater. The nudibranch extract could then be added to a culture vessel (Harvell 1986). *Membranipora membranacea* colonies were grown in the field on individual Lucite panels, cultured once for 6 h in the laboratory with nudibranch extract, and returned to the field for 2 d. After 2 d, colony areas were measured and the number of rows of spined zooids was counted from photographs of the colony surface. Colony area was determined by using a video-integrated image analysis system to digitize the area inside drawn outlines of the colony.

Results

Levels of defense, measured as the number of rows of spined zooids, increased with colony size, measured as the number of mature rows in the colony (fig. 2). Mature rows are those with zooids containing feeding zooids and do not include

rows containing developing zooid buds. Since I used an extremely concentrated solution of nudibranch factor and exposed colonies for 6 h, this represents a maximal response to a single initial dose (see Harvell 1990 for dose response experiments). I calculated the proportional allocation to defense on an area basis for a 24-row colony. To do so, I independently measured the radius of a discord colony of this size as 23 mm. From this the total area can be calculated as $23^2 \times 3.14 = 1,661 \text{ mm}^2$. The area of the inner, unspined region (12 rows) of a 24-row colony is calculated as $11.5^2 \times 3.14 = 415.2 \text{ mm}^2$. The proportional allocation to spines is $(1,661 - 415.2)/1,661 = 0.75$. The proportional allocation for a small (10 rows) and large (50 rows; estimated from slope in fig. 2) colony are 0.76 and 0.75, respectively. This result suggests that colonies of different sizes apportion almost constant effort to defense.

AGE-BASED CONTROL OF SPATIAL PATTERN IN DEFENSES

Methods

The peripheral pattern of defense displayed by *Membranipora membranacea* colonies exposed to nudibranch factor could be due to age-based gradients in zooid competence or to a zooid's spatial position within the colony. It is possible to separate the effects of the two factors directly by altering the age distribution of zooids within the colony: old central zooids can be replaced with young zooids, so that younger tissue is located both on the margin and in the center of the colony. The age distribution of zooids was altered by removing a 0.6-mm-diameter circular plug of tissue (about 10 zooids) from the center of the colony with a cork borer and allowing the colony to regenerate in this area. The colonies used were approximately 2–3 cm in diameter. After 10 d the regenerated colonies had two regions of equal-aged young tissue: at the edge as in a normal colony, and in the regenerated center of the colony (fig. 3).

Manipulated colonies were cultured with and without nudibranch extract. Colonies were cultured for 6 h with extract (approximately 10 nudibranchs/L); then the water was changed, algal culture (*Dunaliella*) was added as food, and colonies were maintained in the laboratory for two additional days before monitoring (see Harvell 1986, "Culture Methods"). In addition, unmanipulated colonies of the same size were exposed to nudibranch extract, to ensure that they were capable of producing a normal response (fig. 3). Spines on the border and in the center of colonies were scored as either present or absent (methods in Harvell 1986).

Results

Control (unmanipulated) colonies exposed to nudibranch extract produced spines only near the periphery. Over half the experimentally manipulated colonies exposed to nudibranch extract produced spines on zooids both near the periphery (12 of a total of 14, summed over three trials) and at the center of a colony (eight of 14). Manipulated colonies not exposed to nudibranch extract produced no spines (of a total of 12) near the periphery and only one colony (of a total of 12) produced spines at the center. Frequencies were analyzed with a three-way

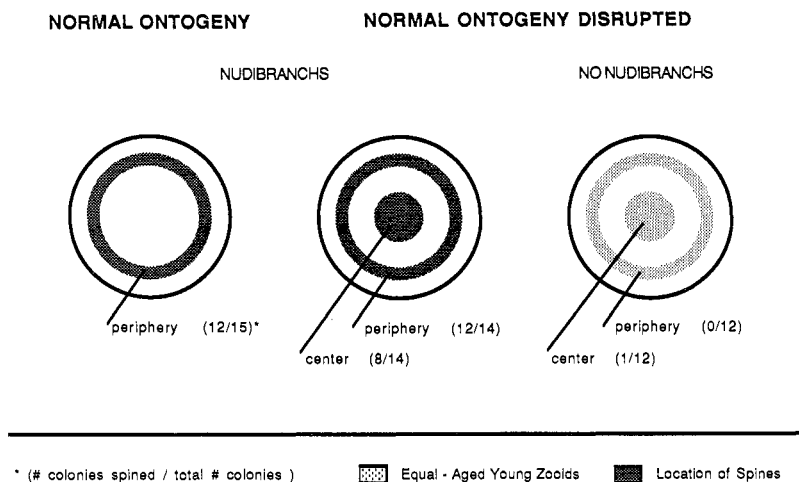
Role of Zooid Age and Position:

FIG. 3.—Experiment with *Membranipora membranacea* to separate the effects of zooid age from position in the colony. The lightly shaded zones indicate regions on manipulated colonies where zooids are of equal age.

hierarchical G -test. The three-way interaction term is not significant; nudibranch factor has a significant effect on the frequency of center and peripheral spines ($G = 31.943$, $df = 3$, $P < .001$); within-colony location has no significant effect on frequency of spination ($G = 4.328$, $df = 3$, $P > .05$). The production of spines in two spatially distinct but equal-aged parts of the manipulated colony indicates that the age of the zooid, not its position in the colony, determines the competence of a zooid to produce spines.

INDIVIDUAL ZOOID VERSUS COLONY CONTROL OF DEFENSE

Methods

What processes control the distribution of spined zooids within the colony? This experiment was designed to determine whether the response was due to (1) detection of the nudibranch factor by some colonial receptors followed by transmission of an internal signal in the colony or (2) an independent response of each competent zooid in the colony to the external nudibranch extract. Unmanipulated colonies were maintained in unidirectional flow channels, and nudibranchs were tethered to the center of each colony to determine whether all zooids would produce spines or only the zooids downstream of the nudibranch (fig. 4). Nudibranchs were tethered in place with a piece of thread through the outer edge of the dorsal mantle. The wound healed quickly and tethered nudibranchs continued to feed and even copulate with other nudibranchs when a mate was present. Because alteration of the hydrodynamic environment around a zooid

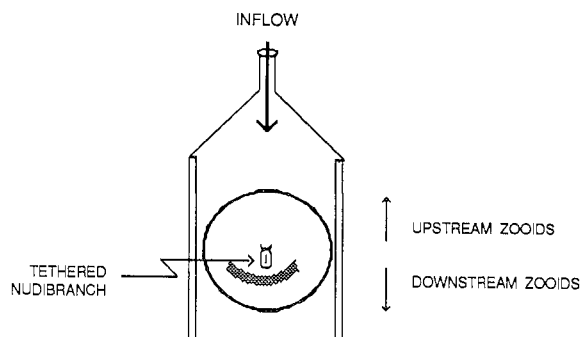


FIG. 4.—Experiment with *Membranipora membranacea* to localize application of nudibranch factor within the colony. The shaded zone indicates zooids that produced spines downstream of the tethered nudibranch.

may also induce changes in morphology (C. D. Harvell and G. Trager, unpublished data), gastropod (*Lacuna* sp.) egg masses of approximately the same shape, size, and texture as the nudibranchs were tethered to control colonies. The flow channels were shallow (1.5 cm) Plexiglas channels shaped as in figure 4, with an inflow at one end and an opened downstream side. Colonies on pieces of kelp blade were secured by slipping the edges of the kelp under narrow shelves on the sides of the channels.

Colonies were maintained in flow channels with tethered nudibranchs or egg masses for 24 h, then nudibranchs and egg masses were removed and colonies maintained in the channels for an additional 48 h. Since spines first begin to appear after 36 h, 48 h allows sufficient time for a full response. Each colony's response was scored as the number of spined zooids upstream and downstream from the tethers.

Results

In all of 15 trials with tethered nudibranchs, spines were produced on downstream zooids (frequencies were sums of three trials). In two trials of those 15, upstream zooids also produced spines; these perhaps are cases where eddies flowed backward in the channels because the water pressure dropped during the night, thus briefly exposing "upstream" zooids to nudibranch extract. Although I attempted to avoid this by testing for eddies with dye streams, variations in flow rate sometimes caused unexpected currents in the channels. In only one of 15 trials were spines produced on control colonies. This one case is likely due to inadvertent exposure of the colony to nudibranch extract before the experiment (Harvell 1986). A three-way *G*-test indicates that there is a significant three-way interaction ($G = 7.745$, $df = 1$, $P < .01$). This indicates that the production of spines, predominantly on downstream zooids in the nudibranch treatment, is significantly different from the production in the nonnudibranch treatment. The experiment indicates that only zooids exposed directly to nudibranch factor predictably produce spines. From these results, I conclude that each zooid responds independently to this chemical cue. Therefore, the production of a ring of spined

zooids in what appears as a coordinated colonial response is due to multiple independent zooid responses to a common external stimulus. The usual pattern of spined zooids in the colony is a complete band because only zooids within a certain band of a colony possess the ontogenetic competence to form spines, although the whole colony has been bathed in a chemical stimulant that elicits the morphogenetic response. I have occasionally seen larger colonies with incomplete bands of spined zooids, presumably because only some of the ontogenetically competent zooids were exposed to inducer.

DISCUSSION

What processes generate the consistent spatial pattern of inducible spines deployed as a band of zooids on the periphery of colonies of *Membranipora membranacea*? Although I suggested (Harvell 1984) that formation of the band of defensive zooids was actively coordinated by translocation of information within the colony, the experiments described here indicate that spination is evoked independently by local action on each zooid of the correct age group. Thus all zooids of the appropriate age exposed to the inducing factor produce spines, and translocation does not appear to mediate the response. The patterned morphology is thus produced by a simple self-organizing mechanism. Although zooids in an *M. membranacea* colony are joined by a nervous system (Lutaud 1977), there is no evidence for involvement of this system in the relatively slower process of spine induction. The colonial nervous system seems to function primarily to trigger rapid zooid contraction when the colony is mechanically stimulated (Lutaud 1977; Thorpe 1982; G. Mackie and C. D. Harvell, unpublished data). The colony's consistent relative allocation to defense can also be explained by this mechanism. That is, larger colonies produce more spined rows because there are more rows of approximately equal-aged zooids in a larger colony, since linear growth increment increases with increasing colony size.

Among taxa of colonial marine invertebrates, there is a continuum of integration from weakly integrated colonies using decentralized mechanisms of coordination to strongly integrated colonies using centralized signaling mechanisms. Beklemishev (1964) has suggested that the evolution of functional unity of colonies in marine invertebrates has proceeded via three trends.

1. *Weakening of zooid individuality.*—This can be seen as a decrease in the size of zooids and a simplification of zooid structure as compared with free-living individuals of related species. Such pairs are bryozoan zooids and phoronids, zoanthid zooids and anemones, and compound ascidian zooids and solitary ascidians. In all cases the component zooids lack structures that are present in the solitary form. Although some of the decreases in the function of zooids may be related to their generally decreased size rather than anything more directly linked to a colonial life-style, they do represent an increase in colony function relative to zooid function. Another example of this trend is that in some colonies the component zooids are very short-lived relative to the longer duration of the colony. In the bryozoans, thecate hydrozoans, and the botryllid ascidians, zooids undergo a cycle of degeneration so that each zooid may live for only 2 wk, after

which it regresses and is replaced by a newly budded or a regenerated zooid (Beklemishev 1964; D. P. Gordon 1977). This process may be continuously repeated throughout the often subannual lifetime of a colony.

2. *Intensification of the "individuality" of the colony.*—This is evident in the phenomenon of polymorphism and the development of "colonial organs." At its most extreme, this trend includes the loss of sexuality of some zooids in the colony, such as the modified defensive zooids in the bryozoans that form spines or avicularia. In cyclostome bryozoans all zooids can reproduce as males, but fertilized embryos are sequestered in a single colonial brood chamber. As already discussed, the giant axons of siphonophores provide a highly centralized, intrinsic control of the colony's component zooids (Mackie 1986).

3. *Development of functional regionalization via a "colony ontogeny."*—Examples of ontogenetic differences in colony function include the inducible spines and stolons (Harvell and Padilla 1990) of *M. membranacea*. Other examples are the peculiar nature of the founding zooid in many colonies; in most bryozoans the morphology of the ancestrula is distinctive, while in some ascidians it is sterile and thus functionally distinctive. The founding zooid of bryozoan colonies will often be spined even though all subsequent zooids in the colony are not. In pennatulid and siphonophore cnidarians, the primary (founding) zooid forms a stem from which the secondary zooids grow (Hyman 1940).

These trends in increased centralization resemble similar trends in the eusociality of insect colonies in showing cooperative colonial care of offspring, reproductive division of labor whereby some units of the colony remain sterile, and polymorphism. However, the situations are distinct, because the units of a marine invertebrate colony are usually all genetically homogeneous (Schopf 1973; but see Buss [1983, 1987] and Rinkevich and Weissman [1987a, 1987b] for exceptions). Thus fitness is measured for the colony as a unit, and an individual zooid will not necessarily lose fitness if its clone-mates reproduce successfully. These colonies should more properly be considered "subdivided" organisms, not "superorganisms," as colonies of social insects have been called (Wilson 1971; Seeley 1989a).

There are other examples in nature of behaviors and morphologies coordinated by a combination of ontogenetic competence and common stimulus. After all, this is the principle that governs much of metazoan development, where cell fate is determined by a combination of environmental context, ontogenetic loss of totipotency, and extrinsic inducers (Bonner 1974; Buss 1987). The production of aggressive stolons in some hydrozoan colonies also depends upon a polyp's age and the reception of an extrinsic stimulus. In some colonies of *Hydractinia symbiolongicarpus* only the tissue on the outer edges is competent to make hyperplastic stolons (Buss and Grosberg 1990).

In social hymenopterans, the principal basis for labor specialization among honey bee workers in a colony is also age (Oster and Wilson 1978; Seeley 1985). During the approximately 30-d adult life of a summer honey bee worker, each individual passes through an ontogenetically determined progression of specialized tasks including cell cleaning, food storage, and foraging (Seeley 1985). This phenomenon of behavioral change with age in social insects is called age polyeth-

ism (Oster and Wilson 1978; Seeley 1985). As with colonial marine invertebrates, a hierarchy of control at both the bee and the colony level also exists within hymenopteran colonies. Numerous complex, apparently colony-level activities are produced by the summation and integration of simple, individual-worker decision rules, and sharing an environment can align behaviors (D. M. Gordon 1987; Seeley and Levien 1987; Seeley 1989a). In discussing colonial integration, Wilson and Hölldobler (1988) suggest replacing the term hierarchy with heterarchy to emphasize that information flows among all individuals within a colony and that induced activity in lower levels of a colony hierarchy feeds back to influence higher levels. An example of heterarchy is the process that controls the foraging of a bee colony. Each bee responds independently to individual cues, both extrinsic and from her sisters; since many bees follow the same rules of response, a coordinated and highly responsive "colonial" foraging strategy emerges (Seeley 1985; Seeley 1989b).

Many polymorphs in both colonial invertebrates and social insects appear to arise through heterochronic processes (Gould 1977). The morphologies of many of the polymorphs are similar to those of the autozooids in highly polymorphic colonial taxa, such as the Bryozoa and Cnidaria, and, where investigated in hydrozoans, involve only changes in the rate of growth of some zooidal structures relative to others. Berrill (1949) describes how differences in sites and rates of cell propagation in hydrozoan colonies can produce a range of forms from stolons to polyps to medusoid gonophores. Wilson (1953) also suggested heterochronic processes such as the differential growth of head width relative to the body in soldier ants to explain morphological variation among castes in ant colonies. In bryozoans, a proposed evolutionary sequence (modified from Banta 1973) to produce composite spined zooids such as seen in *M. membranacea* involves a reduction and dorsal migration of an interzooid and elongation of its operculum (or frontal membrane) into a spine (fig. 5). Thus each spined zooid in this bryozoan is actually a composite comprising an autozooid and four reduced interzooids. The change from five ancestral to one compound, spined zooid probably involves (1) reduction in the size of the four interzooids through progenesis, (2) loss of sexuality and organs in the interzooids, because of truncation through progenesis, and (3) hypermorphosis (Alberch et al. 1979) of either the operculum or frontal membrane to produce a spine, perhaps through an acceleration in the rate of spine growth. All the zooids in a *M. membranacea* colony are of this compound form, and all have spine buds at their corners. When the stimulus for induction occurs, the spine grows at the corners of the appropriate-aged zooids.

Polymorphisms involving fixed spines are common in bryozoans, especially on the initial zooid of the colony, the ancestrula. When spined, the initial zooid is called a tata ancestrula. In *M. membranacea* colonies, several conditions can occur: (1) no spines on any zooid, (2) spines on the ancestrula only, (3) spines on a row of later zooids, but not the ancestrula, and (4) spines on both the ancestrula and later zooids. The presence of a threshold in competence to respond ensures that only younger, edge zooids in older colonies will produce spines. When the appearance of a heterochronic change in a colony is controlled by the order in which zooids are budded it is called astogenetic heterochrony (Pandolfi

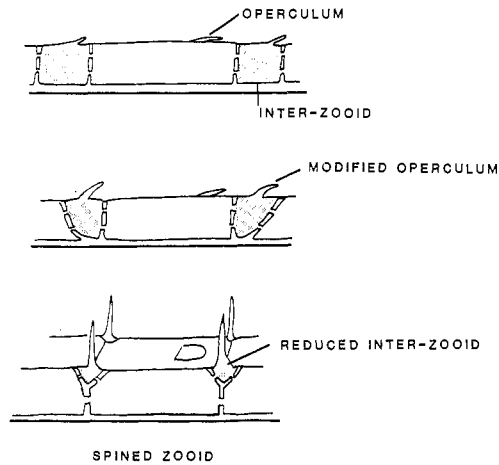


FIG. 5.—Diagrammatic longitudinal section through zooids showing a proposed evolutionary sequence of spined zooids from interzooids to adventitious spines (Modified from the description of the evolution of avicularia in Banta [1973].)

1988). Astogeny is the series of age-dependent zooidal changes that determine the form of zooids in the colony. Thus two scales of heterochrony can be distinguished in colonial invertebrates (Pandolfi 1988): zooidal heterochrony (also called ontogenetic heterochrony)—changes in the allometry or shape of a zooid—and astogenetic or colony-level heterochrony—changes in the allometry or shape of a colony due to the restriction of heterochrony to specific locations in the colony or to specific periods in astogeny.

One mechanism by which fixed polymorphs may evolve is through initially inductive events. These heterochronic structures, initially induced facultatively, may eventually persist as constitutive defenses or polymorphic zooids in the absence of inducing factors as a response to strong directional selection for a low threshold of response (Harvell 1990). This is a restatement of Waddington's (1959) theory of genetic assimilation: the genetic fixation of a threshold character that originally could only be obtained by exposure to an environmental factor. This process of reducing the threshold of an induced character has been demonstrated in selection for salt tolerance in *Drosophila* (Scharloo 1989). It is therefore plausible that a transition state to the fixed polymorphic phenotypes we commonly observe in marine colonies may be through morphs with an induced facultative polymorphism. To test this hypothesis, we need more careful studies of within-species variability in inducible and constitutive polymorphisms.

There is the potential for similar processes to affect development in any modular organism (in the sense of Harper and Bell 1979). A possible example of an induced heteroblasty in plants is the spines and trichomes that can be induced in older tissue by herbivore attacks (Bryant 1981; Myers and Bazely, in press). Spines in plants have been interpreted as a juvenile character that is usually lost in mature tissue (Schaffalitzky de Muckadell 1954; Kozłowski 1971; Bryant 1981), except when mature tissue is damaged and regenerates juvenile tissue (Bryant

1981). This regenerated juvenile tissue can be spined. It seems likely that the compartmentalized, iterated nature of modular organisms such as bryozoans and plants may favor the production of variant zooids through slight changes in developmental timing (Anstey 1987; Harvell and Padilla 1990).

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