

# KEYNOTE ADDRESS

## Life in the Colonies: Learning the Alien Ways of Colonial Organisms\*

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**Synopsis** Who needs to go to outer space to study alien beings when the oceans of our own planet abound with bizarre and unknown creatures? Many of them belong to sessile clonal and colonial groups, including sponges, hydroids, corals, octocorals, ascidians, bryozoans, and some polychaetes. Their life histories, in many ways unlike our own, are a challenge for biologists. Studying their ecology, behavior, and taxonomy means trying to “think like a colony” to understand the factors important in their lives. Until the 1980s, most marine ecologists ignored these difficult modular organisms. Plant ecologists showed them ways to deal with the two levels of asexually produced modules and genetic individuals, leading to a surge in research on the ecology of clonal and colonial marine invertebrates. Bryozoans make excellent model colonial animals. Their life histories range from ephemeral to perennial. Aspects of their lives such as growth, reproduction, partial mortality due to predation or fouling, and the behavior of both autozooids and polymorphs can be studied at the level of the colony, as well as that of the individual module, in living colonies and over time.

### Introduction

It is traditional in this lecture series to present a talk that is, among other things, a career retrospective. Strangely enough for a marine biologist I blame my career path on the planet Mars. In third grade we were asked to write a paragraph on what we would like to be doing in the year 2000, a time so still far ahead that it seemed mythical. My goal was to visit Mars. I was pretty sure we would have space travel by then, but I was a bit concerned about whether or not, at the

immense age of 55 years, I would be too feeble to make the trip.

I was a compulsive reader and as I grew up, science fiction was one of my favorite kinds of reading. I particularly liked books by authors who dealt in biological possibilities and alien life forms. For example, “Memoirs of a Space Woman”, about communication with beings from other planets by Naomi Mitchison, a biologist and a member of the scientifically famed British Huxley clan, “The Left Hand of Darkness”, about humans dealing with alien sentient

creatures with a very different kind of reproductive biology from our own, by Ursula Le Guin, and “Pilgrimage” by Zenna Henderson, about aliens with abilities we would call super powers, marooned on Earth and struggling to pass for humans to avoid extermination.

Disappointingly, we have not yet traveled to Mars. However, when I began to study marine biology in high school and college, I realized that I did not have to go to another planet to study science-fiction-like

organisms. Right here on Planet Ocean were creatures as bizarre in structure and unique in life-history patterns as any I had read about in science fiction. Many of them were marine invertebrates with clonal or colonial life histories, including bryozoans, the group on which I eventually focused my research.

### Life history studies

In the early 1970s marine ecology was thriving. Studies of reproduction, development, and life histories of marine organisms were popular topics of research. However, despite the large amount of knowledge of marine animals' life histories that had developed, most research was still being carried out on organisms, which although quite different from us morphologically, were still rather similar in terms of their life-history patterns; in other words, they were also solitary animals.

The life history of most solitary animals, whether human beings or barnacles, begins with sexual reproduction and progresses through a juvenile period, a period of reproductive maturity, then senescence and death. Solitary marine animal life histories may be complicated by such factors as free-swimming, pelagic larval stages, one or more metamorphoses during juvenile life stages, and mature sexually reproductive periods of varying duration, and even by sessile, rather than by mobile lifestyles. However, their lives are still similar, overall, to our own life histories and thus more intuitively understandable.

In spite of pioneering work on coelenterates, such as hydroids and corals, most biologists, if they considered clonal and colonial organisms at all, thought of

them as “difficult”, not amenable to the methods they used to study population biology and life-history parameters. For most marine biologists, as for non-biologists, these organisms were mainly background—habitat for the organisms on which marine research focused. Sessile clonal and colonial animals such as sponges, corals, gorgonians, hydroids, bryozoans, and ascidians might play important roles in, or even dominate, marine communities, but their life histories did not receive the same kind of study because of the perceived difficulties of working with them.

In the mid 1970s and early 1980s, marine ecologists who wanted to learn more about these groups finally discovered parallels and methodologies they could use. They came from the world of plant ecology (Harper 1977, Harper and Bell 1979, White 1979, Harper 1980). The problems that had confounded the marine ecologists, questions such as “what is the individual, the colony or the asexually budded individual of the colony?”, had been answered by plant ecologists in ways that provided new insights for marine invertebrate biologists and paved the way for a wave of new research on ecology, population biology and life histories of colonial organisms (e.g., Jackson and Buss 1975, Larwood and Rosen 1979, Hughes 1989, McKinney and Jackson 1989).

### Life histories of modular organisms

In modular organisms each genetic individual (genet) is composed of many asexually produced units (ramets, or modules), genetically identical and produced by budding from the initial sexually produced zygote. The modules may

be unconnected during most of their lives (clonal) or joined in colonies. The gift of the plant biologists was in realizing that there were two levels of population structure (genets and modular units or ramets) and in working out ways to deal with population changes at more than one level. Later, it was realized that genet-level populations were often better considered as meta-populations divided into habitat patches connected by dispersal (Okamura et al. 2002).

Some of the distinctive characteristics of modular organisms include the following.

#### The ability to reproduce both sexually and asexually

In most modular marine organisms sexually produced embryos develop into feeding or non-feeding larvae that provide a long or a short water-borne dispersal period. Once a larva settles or metamorphoses, growth of the colony proceeds by asexual budding or by fission. If colonies are able to fragment or divide asexually into separate viable colony clones, populations of those clones might represent only one or a few genets, making a third level—that of the individual colonies, regardless of their genetic identity (Karlson 2002).

#### The potential for inheritance of somatic mutation

In addition, since development in a number of groups is not constrained early, and each module may contain germ cells, somatic mutation may play a role in inheritance, as it does in many plants (Buss 1987, Gill et al. 1995, Hughes 2002a, b). We know little about the role such chimerism may play in populations of colonial marine invertebrates.

### Indefinite growth and delay of senescence

The avoidance or postponement of senescence by repair and replacement of modules can lead to genets surviving to great ages, for decades or centuries (e.g., Antarctic sponges Dayton et al. 1974), or even millennia, e.g., Caribbean brain coral, Hawaiian deep sea Gold and Black coral 2000–4200 years (Roark et al. 2009) and plants, with two genets of Norway spruce clones, Old Tjikko and Old Rasmus, approaching 10,000 years (Kullman and Öberg 2010) and a large aspen clone known as Pando reckoned to be between 80,000 and 1 million-years old (Mitton and Grant 1996). Despite these records it is doubtful that any can achieve true immortality (Martínez 2002), but life spans can be very long and senescence much delayed.

### Resistance to partial mortality

Predation, disease, and environmental disturbance all cause damage to organisms. In solitary organisms loss of a significant part of the body creates a severe handicap at best and usually leads to death. In colonial organisms damage to part of the colony can often be repaired. This resilience leads to discrepancies between the size of a genetic individual and its age, a caveat to those attempting to study growth. Fission, accidental or programmed breakage of a genet into several parts, may lead to underestimating age based on size. Fusion of previously separate parts of a genet can also complicate studies of growth and population structure (Hughes 1984, Hughes and Jackson 1985, Karlson 2002).

### Oldest may rule

In contrast to the situation in most solitary organisms, large, old genetic individuals of colonial organisms such as corals may dominate their community in terms of space occupied, control of resources, sexual reproduction, and successful recruitment of new genets (Williams, 1975).

### Asexual reproduction may extend distributions

Fission by fragmentation or formation of subcolonies may occur due to damage from storms or predators or as an integral part of a species' life history. When the asexually produced fragments are able to keep on growing after being scattered by storms or carried to a new area, the results can extend a species geographic distribution, as well as increasing a genet's population size. Other processes of asexual recruitment, such as gemmulation and encapsulation, may also play a significant role in enhancing the potential for recruitment in clonal and colonial marine organisms above that of solitary organisms limited to recruitment through sexual reproduction alone (Karlson 2002).

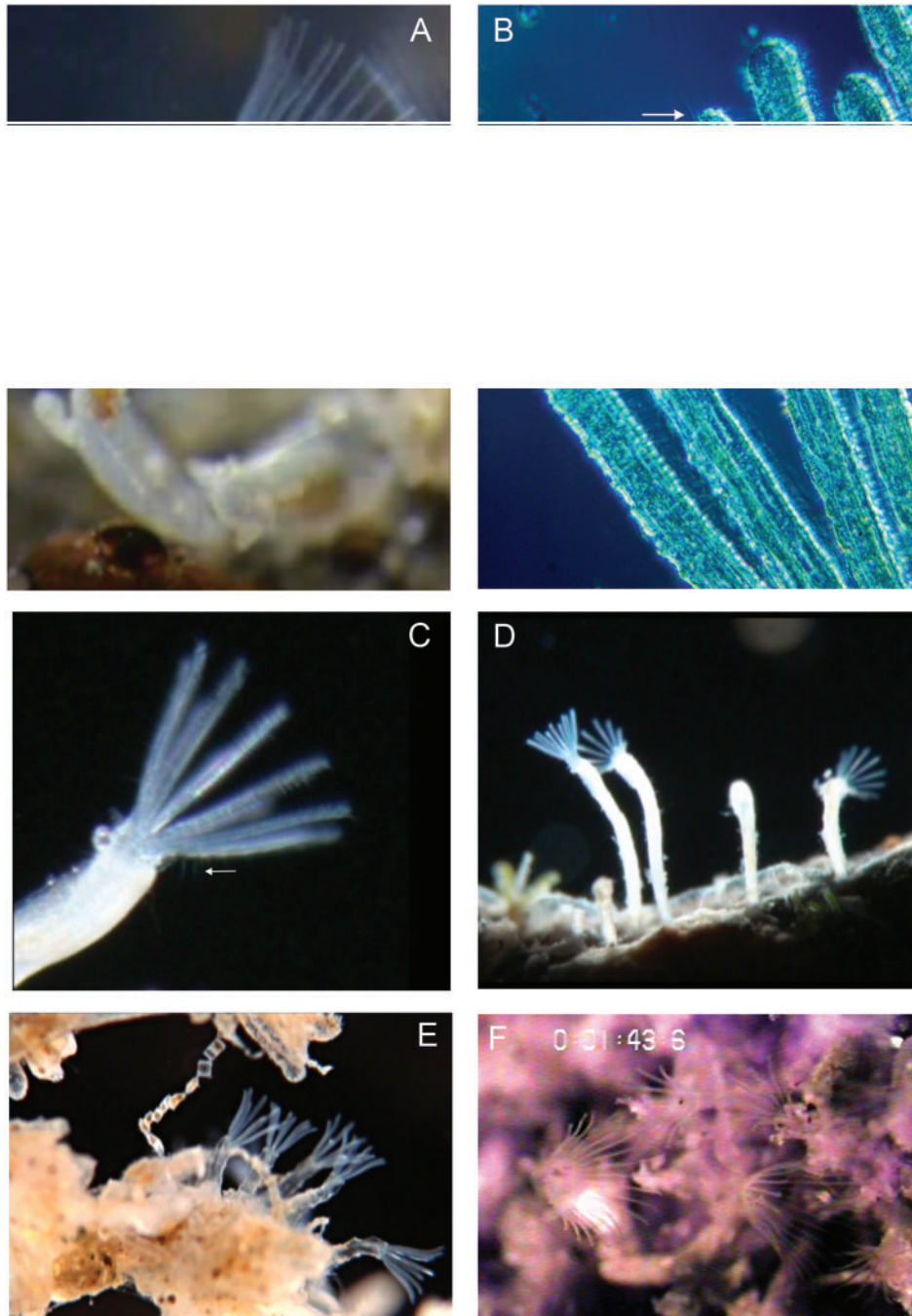
### Bryozoans as model modular animals

There are many good reasons to study bryozoans including their diversity, long fossil record, and presence in almost every benthic habitat from the intertidal zone to the abyss. They also make excellent model colonial organisms. Many species have life spans that are short enough to complete a research project over the time-frame of a PhD program or the tenure of a grant. The individuals of the colony, the modules, have discrete, easily observable

boundaries. Sexual reproduction and other functions can be observed *in vivo*. Much can be learned without needing to kill, dissect or section zooids or colonies, and living colonies can be maintained in the ocean or wet laboratory and studied periodically for weeks, months, or years.

The basic module of the bryozoan colony is the individual zooid, or autozooid (Fig. 1A). Each individual consists of a tubular or box-like body wall containing internal organs and coelomic fluid and a partly extensible polypide portion. The polypide, tentacle sheath introvert, lophophore, and gut are attached by muscles and operated by a hydrostatic system. Muscular action on flexible portions of the body wall or on a membranous sac attached to it, increases hydrostatic pressure within the body cavity, forcing protrusion of the polypide. The opening of the orifice and the extension of the lophophore by eversion of the tentacle sheath are rather slow processes, during which the still-bunched tentacles may pause for “testing” for seconds or minutes, before extending all the way and unfurling the lophophore into its expanded funnel shape (Fig. 1A). In most species movements of tentacles when feeding are rapid (0.1–1.0 s). Retraction of the lophophore may be extremely rapid (60–80 ms), although slower retractions, on the order of 0.5 s, and partial retractions, can also occur.

The entire polypide can be completely withdrawn within the zooid, which is closed by a muscular constriction (ctenostomes), a diaphragm (cyclostomes), or a trap-door like operculum (cheilostomes). Many bryozoans are polymorphic, with some zooids modified as attachment structures, stolons, or brood chambers



**Fig. 1** (A) Zooid and polypide of *Beania klugei*, showing a lophophore with one tentacle in the process of flicking inwards. The extended polypide has its mouth at the base of the lophophore and a U-shaped digestive tract (pharynx, cardia, caecum, and rectum containing a brown fecal pellet). (B) Light micrograph of a cheilostome tentacle, showing lateral cilia and sensory tufts (arrows). (C) Zooid of *Aetea*, on the lower surface of the lowest tentacle long, laterofrontal cilia can be seen faintly (arrow). (D) Zooids of an *Aetea* colony feed in an individualized manner. (E) *Amathia* zooids form temporary feeding clusters. (F) Three small (*Bowerbankia*) and two large (*Celleporaria*) lophophores form temporary interspecific clusters to feed. (Still photograph A from a video by Dr Carlos Rocha; photographs C–E from videos by Dr Alvaro E. Migotto; F. from a video by the author).

for embryos. Cheilostomes, the dominant marine bryozoans today, may also have modified zooids called avicularia and

vibracula, in which feeding organs are usually lacking, and the operculum is hypertrophied into a mandible or bristle (Fig. 3).

### **Bryozoan life histories**

Despite the potential for coloniality to provide a partial escape from limitations of growth and

mortality, not every colonial species is long-lived. Experimental work has shown that bryozoans employ a variety of life-history strategies from ephemeral to perennial, as could be expected in any invertebrate phylum. Some examples of different kinds of bryozoan life histories are given below.

### Encrusting interstitial species

Encrusting interstitial bryozoans have the most ephemeral life histories. Their colonies encrust single grains of mineral sand and particles of shell in high-energy shoal environments on subtropical continental shelves (Winston and Håkansson 1986, Winston and Migotto 2005). Their colonies are characterized by very small size, simplified zooid structure, very small zooids, and precocious sexual reproduction. Some species can produce a brood chamber and embryo within three zooids from the ancestrular zooid which metamorphosed from the settled larva. Colonies of these tiny interstitial species lack the avicularian polymorphs of their congeners from larger substrata, but do produce skeletons with an array of calcified spines, knobs, and bumps that may protect them from abrasion due to the movement of sediments and the burrowing and feeding activities of macrofauna. Dead colonies are much more abundant than are living colonies in samples of sand, indicating the lifespan for any colony is very short. However, studies in Florida showed that there could be up to 7500 living colonies in just the top-cm layer of a square meter of sediment, and living colonies were found to a depth of 16 cm in cores taken at the study site, indicating that populations

can be very large (Winston and Håkansson 1986).

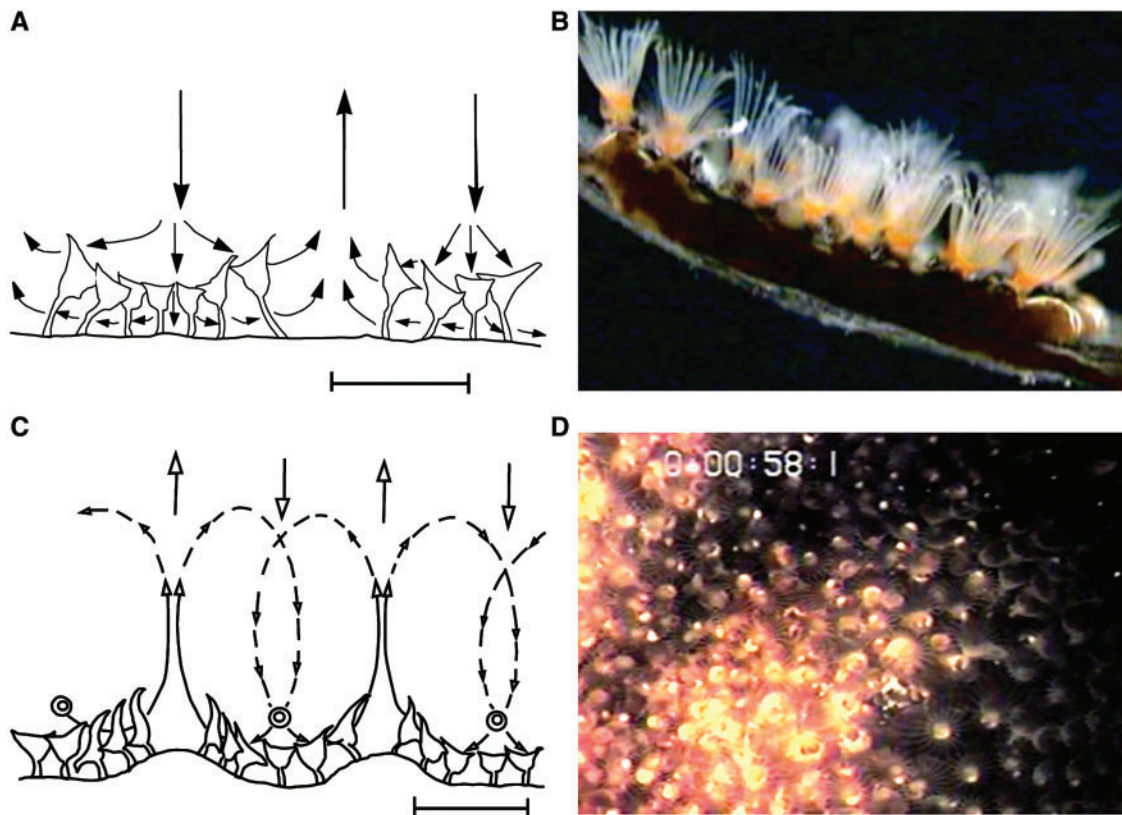
### An estuarine weed: *Conopeum tenuissimum*

*Conopeum tenuissimum* is a short-lived encrusting cheilostome bryozoan from a seasonal estuarine environment (Chesapeake Bay). Early growth is exponential. Later growth of colonies when cultured on suitable phytoplankton and protected from predation produces sigmoid growth curves much like those found in many groups of organisms. *Conopeum tenuissimum* also displays characteristics common to many organisms living in unstable estuarine environments. Zooids and colonies are small, but population size is large. Recruitment takes place from April to November, but the life of an individual colony lasts only a few weeks. Sexual development is rapid; sperm appear in colonies at about 2.5 weeks and small eggs appear in colonies between 2.5- and 3.5-weeks old. Eggs are spawned and in the water column embryos develop into modified cyphonautes larvae, which settle rapidly compared to the large, long-lived cyphonautes of marine species of the superfamily. Hard substrata are scarce in the Bay, and in summer at least, colonies settling on wood or on oyster shell can be overgrown by other organisms within a month, while those settling on a blade of eel grass have only the time until the blade is shed sometime during the summer months (Dudley, 1973).

### Free-living adults, determinate growth, and fragmentation: cupuladriids

Populations of two species of this family at Capron Shoal in Florida

were studied over a 2-year period (Winston and Håkansson 1986, Winston 1988). Juvenile cupuladriid bryozoans are part of the encrusting interstitial fauna. The larva settles on a sand grain. As the colony grows it completely encircles the grain on which the larva settled, eventually producing a conical or inverted saucer-shaped colony that uses coordinated movements of its long vibracular bristles to move through the sand, unbury itself when covered by sand grains (as shown in sequence in Fig. 3A1–3) and to raise the colony upon the sediment's surface to feed. A heavy basal layer, along with the embedded grain, provides a "weight belt". In contrast to most bryozoans, the growth of a conical colony of *Cupuladria doma* was determinate. Beginning at a size of ~3–4 mm in diameter, a colony stops producing new marginal buds and the outer edge of the colony's base is completed by a double row of vibracula and a smooth, rounded margin. In Florida, *C. doma* reproduced sexually at a low level year-round. The species was also able to repair damage and survive fragmentation, but only 3.6% of the colonies showed evidence of major damage and regeneration. The flatter colonies of *Discoporella depressa* relied much more heavily on asexual reproduction. Sexually produced recruits were found only in the spring, and 48.0% of colonies showed evidence of fragmentation with major damage and regeneration. Unlike colonies of *C. doma* the largest *Discoporella* colonies found were still producing marginal buds (Winston 1988). A mostly asexual propagation mode is carried even further in a Brazilian species of the group, *D. umbellata*, in which parent colonies bud regularly shaped



**Fig. 2** (A and B) Diagram and photograph of a colony of a flat, encrusting species with lophophores forming fixed incurrent cells. (C and D) Diagram and photograph of a colony of *Celleporaria* in which the lophophores show excurrent and incurrent patterning that reflects the underlying mound-and-channel topography of the colony's skeleton. Diagrams redrawn from Winston (1979). Scale bar of A = 2 mm; of C = 4 mm. Photograph top right is of *Watersipora subtorquata*, from a video by Carlos Rocha. (B) is a *Celleporaria* colony from a video by the author.

sub-colonies which then detach and grow separately (Marcus and Marcus 1962).

#### Cryptic Caribbean reef species: encrusting perennials

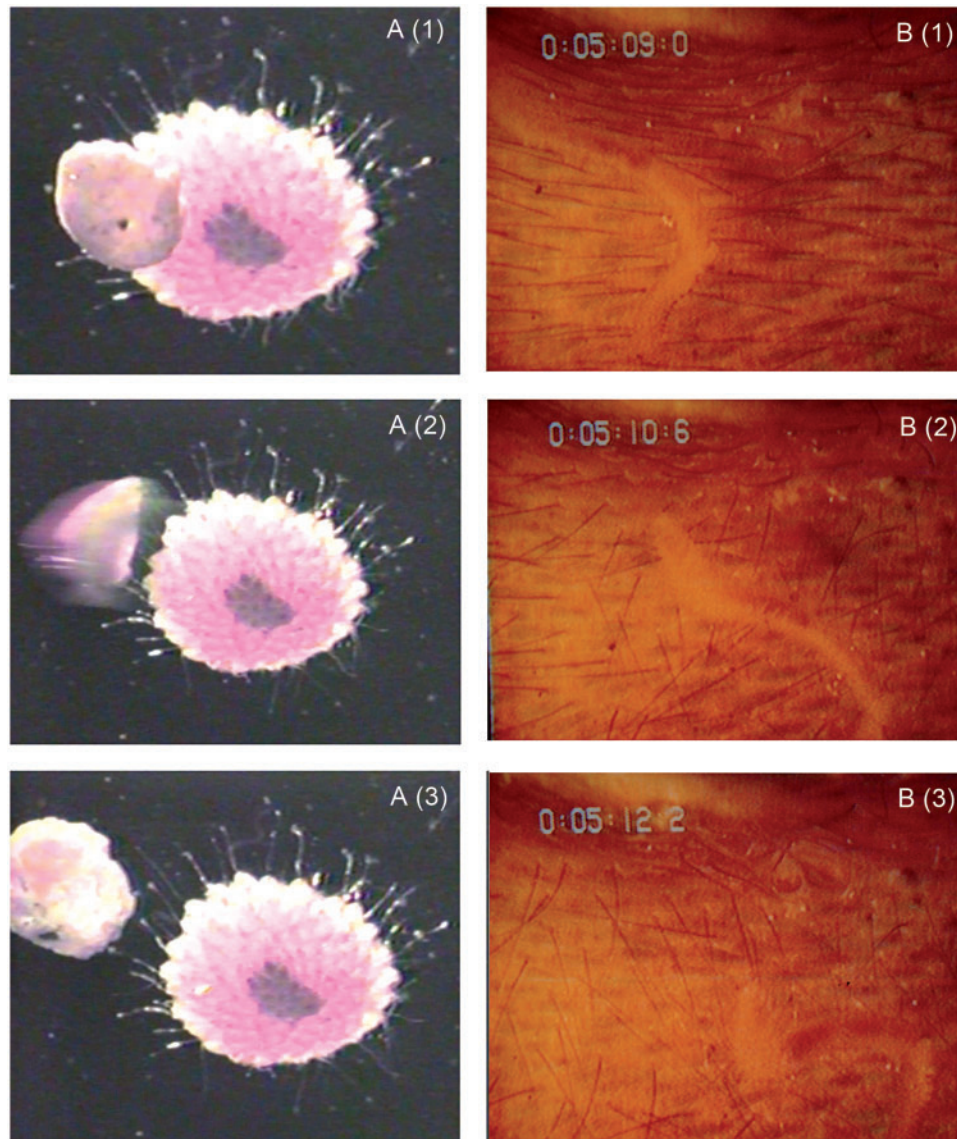
Encrusting cheilostome bryozoans are among the dominant organisms in the cryptic community on coral undersurfaces in Jamaica (Jackson 1984). On these limited surfaces competition for space is intense. The two dominant cheilostomes have differing modes of acquiring territory. *Steginoporella* genets compete by a mobile strategy, relatively rapid growth (up to 11 cm/year) and abandonment of older fouled regions of their colonies (partial mortality) while overgrowing

new areas, including old parts of themselves.

*Reptadeonella* genets grow more slowly (3–4 cm/year), but maintained an intact surface over all portions of the colony, slowly but steadily increasing their share of space. Growth rates of both are slow compared to encrusting bryozoans in temperate environments. Rates of sexual reproduction are low, but spread out over the year, and sexual maturity in these two species does not occur in less than a year and a half from recruitment. Large, established colonies of these and other encrusting reef species may live for many years (Jackson and Winston 1982, Winston and Jackson 1984, McKinney and Jackson 1989).

#### Antarctica: erect annuals and perennials

Many continental shelf environments in the Antarctic are dominated by communities made up largely of sessile suspension feeders like sponges, bryozoans, hydroids, octocorals, and tunicates, whose colonies may form dense thicket-like growths spreading over large areas of the bottom of the sea. Study of the bryozoan community in 80–100 m off Low Island in the Antarctic Peninsula included determination of growth rates of the dominant species (Winston and Heimburg 1988, Winston 2009). The most abundant bryozoan species in the Low Island community was *Carbasa ovoides*. The delicate, tan, unilaminar fronds of



**Fig. 3** Sequences showing motion of vibracula (captured from video). In the left sequence (A1–3) a *Cupuladria doma* colony removes a particle of shell from its upper surface. In the right sequence (B1–3), *Nematoflustra flagellata* vibracula sweep a polychaete worm along the colony's branch. Photographs in both sequences from videos by the author.

*Carbasa* colonies showed no growth checks, indicating that all the growth of a particular frond took place during one season, although basal rhizoids and stolons might be perennial, producing new fronds yearly. The mean increase in height for *Carbasa* fronds was 8.6 cm per year.

In the other dominant Low Island species, colonies and fronds both were perennial, and growth could be determined by back-measurement of yearly growth bands. Fronds of the

flustrid anascan, *Nematoflustra flagellata*, showed a mean increase in height of 0.92 cm per year, and those of *Austroflustra vulgaris* fronds increased 1.2 cm per year. The ascophoran cheilostome, *Kymella polaris*, is not closely related to the other two species, but its colonies grew at a similar rate, fronds increasing on average 1.3 cm in height per year. Growth rates of all three were remarkably similar to the mean increase in height of 1.5–4.0 cm measured in the related temperate

species *Flustra foliacea* by Stebbing (1971).

Seasonality of reproduction was studied in Low Island colonies by counting the numbers of embryos found in colonies at three censuses from austral summer to early autumn. The reproductive pattern of *Carbasa* contrasted with that of the other abundant species. *Carbasa* broods in external ovisacs in which several embryos may be developing at a time. Reproductive effort in *Carbasa* was very high (averaging

2953 embryos per colony) in austral summer, but had ceased entirely by early austral autumn. Mean number of embryos per colony was much lower in the other species studied, averaging a few hundred per colony per census, but sexual reproduction was still occurring on the last date that sampling occurred. However, for two species in which embryos were brooded in ovicells, *Kymella* and *Himantozoum*, the percentage of empty ovicells increased until by the last date of censusing, April 20th, 72% of *Kymella* ovicells and 95% of *Himantozoum* ovicells were empty, indicating that the end of the reproductive season was approaching (Winston 2009).

Like most colonial organisms, bryozoans have extensive powers of regeneration and can tolerate a high degree of partial mortality. A few animals, e.g., pycnogonids and nudibranchs, are specialized as single zooid predators of bryozoans, piercing zooids, one at a time and sucking out body fluids and tissues. Damage to parts of colonies can be caused by physical disturbance of their environment or by predators or grazers. Grazing and browsing activities of fish, echinoids, and mollusks leave larger scrapes, rips, and bites on colony fronds. All Low Island species studied sustained a considerable amount of damage. *Carbasa* colonies showed the least amount of injury to the most delicate and accessible portion of fronds, the growing tips, most likely due to their much higher growth rate, although, as this species also shows moderate antibiotic activity (Colon-Urban et al. 1985), production of distasteful chemicals also might be involved.

Another source of damage is caused by fouling of colonies by other organisms. Some epizoans,

such as the stalked barnacles found in branch bifurcations of erect species, or the loosely attached colonies of the bryozoan *Beania erecta*, may benefit the host, augmenting water currents to the host colony by their own feeding activities. Others, such as encrusting epizoic bryozoans like *Ellisina* and *Harpecia* kill or disable the zooids they overgrow. The overall number of taxa and number of epizoans per colony was lower for all the Low Island species studied than for the Northeastern Atlantic *Flustra foliacea* studied by Stebbing (1971). However, two species, *Austroflustra* (1.10) and *Kymella* (1.2) were in the same range as *Flustra foliacea* (1.0) in terms of number of epizoans per cm<sup>2</sup> of frond (Winston 2009).

### **Behavior and polymorphism: bryozoans as examples**

Behavioral studies of colonial animals have, like studies of their ecology, lagged far behind those of solitary organisms. This may in part be due to their modular construction, the necessity of dealing with both individuals (modules) and colony-level behavioral patterns. For many colonial marine invertebrates it may also be a matter of scale. While the same observational techniques used on birds or mammals apply to studies of sessile invertebrates, studies must be carried out through the stereomicroscope rather than through binoculars or telescope, due to the small size of the modules. The magnification necessary (50–100×) limits depth of field, and although video recordings can show behavioral actions as they occur, still photographs and frame-capture from video will only have part of the image in focus. Colonies of some

bryozoan species can cover many square cm but individual zooids, for example, seldom reach more than a mm in length. The components for which behavior is being recorded may be <100 μm long. Most studies of bryozoan behavior must take place in the laboratory rather than in the field, although with advances in video technology this is beginning to change.

Components of bryozoan behavior include the activities of autozooids and their polypides: feeding, elimination of waste and debris, ejection of larvae, competition for space, growth, and reproduction. Zooid polymorphs, such as stolons, kenozooids, gonozooids, avicularia, and vibracula function in attachment, space-filling, reproduction, competition for space, the mobility of the colony, and cleaning and defense of zooids and colonies.

Convincing biologists who work on motile animals, whether they be amphipods or zebras, that sessile colonial invertebrates can have behavior worth studying, let alone behavior with individual, colony-wide, and species-specific patterns, is difficult. However, observational studies using microphotographic and video techniques have clearly documented behavior originally discovered in the days when the animal nature of “zoophytes” had only recently been confirmed. For example, Grant (1827, p. 114) “The tentacula are exquisitely sensible, and we frequently observe them either singly or all at once, striking in their extremities to the centre of the bell-shaped cavity, when any minute floating body comes in contact with them”.

Charles Darwin was an early observer of avicularian polymorph behavior, including the bird’s head type, “. . . all that were one side of the branch moved,



sometimes instantaneously, some times in regular order one after the other; at other times the organs on both sides [of] the branch moved together; but generally all were independent of each other, and entirely so of the polypi." (Darwin 1839, p. 192)

### Polypide morphology and feeding behavior

Feeding behavior and polypide morphology have both module-level and colony-level components. Individual feeding behavior is species specific, as is polypide morphology, including morphology of the lophophore, the food-collecting funnel of tentacles. Studies of polypide morphology have found more variability than expected for such size-constrained animals. Lophophore size varies from <0.2 mm to >1 mm and tentacle number from 8 to more than 30; tentacle length and angle may also vary, both between species and, in some species, within colonies. Size and shape of the mouth is closely linked to lophophore size. The extent to which the introvert can be protruded from the zooid also varies and is a factor in both individual- and colony-level activities (Winston 1977, 1978, 1981).

In all species the basic feeding mechanism relies on currents created by waves of lateral cilia. The ciliary currents drive the water above the lophophore into the funnel, where particles may be captured by localized reversals of lateral cilia, transported on the bands of frontal cilia on each tentacle and/or by tentacular action, and swallowed into the mouth at the base of the lophophore. Most species also have well-developed rejection mechanisms. Unwanted or excess particles pass out between the tentacles or by individual or group widening or

retraction of lophophores (Strathmann 1973, 1982, Cook 1977, Winston 1978).

Ciliary currents alone carry some particles to the mouth, but tentacles also rapidly flick or slowly roll suitable particles toward the base of the funnel and may even push them into the pharynx, making tentacular movements one of the most important components of individual behavior. Flicking of tentacles varies from species to species in duration and speed and in the length of the tentacle involved. Other more complex actions involve integrated movements of several tentacles or of the entire lophophore.

Basic tentacular ultrastructure is the same throughout the group, but species differ in the numbers and kinds of sensory structures found on tentacles. These include tufts of cilia at the ends of tentacles (Fig. 1B) and motile or non-motile latero-frontal cilia, often longer than the lateral cilia (Fig. 1C).

Size is an important determinant of feeding. Species with small lophophores and mouths are limited to particles in the nanoplanktonic range, (2–20  $\mu\text{m}$ ), including small diatoms and flagellates. Large-bodied species may collect a ball of small particles in the area of the mouth, then swallow them with a gulping movement of the pharynx. They may also capture larger phytoplankton and even small zooplankton by a caging action of the tentacles. For example, small ciliates are very common among the bushy colonies of the common fouling species *Bugula neritina*. When ciliary currents carry them into the lophophore of a polypide, its tentacles rapidly twist together at the tips, forming a cage around the ciliate. The ciliate bounces around,

attempting to escape, but is often ingested.

Species that are similar in size, however, may differ in feeding behavior. For example, polypides of the cyclostome *Crisia elongata* are chiefly passive filterers, only occasionally using the tip of a tentacle to direct a particle toward the mouth. Their eight short tentacles are widely spaced, but well-equipped for filtering as their long stiff lateral-frontal cilia form a latticework between the tentacles. Polypides of the cheilostome, *Pasythea tulipifera*, although similar in size and found in the same microhabitat as *C. elongata*, feed much more actively. Ciliary currents alone carry some particles to the mouth, but tentacles also rapidly flick or slowly roll suitable particles down the funnel and may even push them into the pharynx (Winston 1978).

The two levels, individual and colony, can be seen in feeding behavior.

Some species, especially those with vine-like or delicately branching colonies with zooids spaced out along a stolon or branch, have an individualized pattern of behavior. Expanded polypides turn introverts and lophophores in a scanning motion like a radar antenna (Fig. 1D). The same pattern can sometimes be seen in erect or encrusting colonies when only a few polypides are expanded. There is little interaction between neighboring polypides except the occasional formation of temporary clusters of two or three lophophores, enhancing current flow (Fig. 1E and F).

Bryozoans have also evolved integrated colony-wide patterns that increase and channel feeding currents. In erect colonies, the orientation of expanded lophophores is controlled by the skeletal

structure of the colony. Adjacent lophophores are oriented away from each other and toward inter-branch spaces, creating a strong unidirectional current that impinges on polypide-covered surfaces, then passes through the spaces among branches. Group retractions of lophophores help clear the spaces between branches of large particles.

In encrusting colonies several patterns of structuring feeding currents have evolved. In some species polypides form temporary clusters of lophophores that increase and channel feeding currents. In other encrusting species orientation of the lophophore is fixed. In the simplest type, the colony's surface is flat, but emerging polypides are arranged into incurrent cells and excurrent chimneys (Fig. 2A and B). In a large number of encrusting, mound-like, or massively branching colonies, there is a rather regular patterning of feeding currents, based on skeletal morphology as well as on polypide morphology. Incurrent cells or incurrent channels are located in hollows of the colony's skeleton, while excurrent areas occur along ridges or on mounds (Fig. 2C and D). Increased integration of feeding behavior is part of the trend in increased integration of zooids and colonies in cheilostome bryozoans that has occurred over their Cretaceous-to-Recent existence (Winston 1978, McKinney and Jackson 1989).

### Other polypide functions

The feeding activities of polypides can be important in mediating spatial competition between bryozoan colonies. For example, Buss (1981) found that if colonies of two intertidal species, *Onychozella alula* and *Antropora tinctoria* approached each other

frontally, the species with the larger lophophores, *Onychozella*, was able to monopolize incoming feeding currents, so that *Antropora* received only water already filtered by *Onychozella*. By this means colonies of *Onychozella* could often overgrow the faster-growing *Antropora*.

Polypide actions may help keep colonies' surfaces free of debris and potential foulers. Dick (1984) described autocleaning behavior in the cheilostome *C. brunnea*, a complex series of actions in which polypides partially retract and tentacles lash outward until their abfrontal surface touches the colony's surface. When this happens thickened spine-like non-motile cilia on the abfrontal sides of the tentacles scrape the colony's surface, loosening particles to be carried away from the colony in excurrent flow.

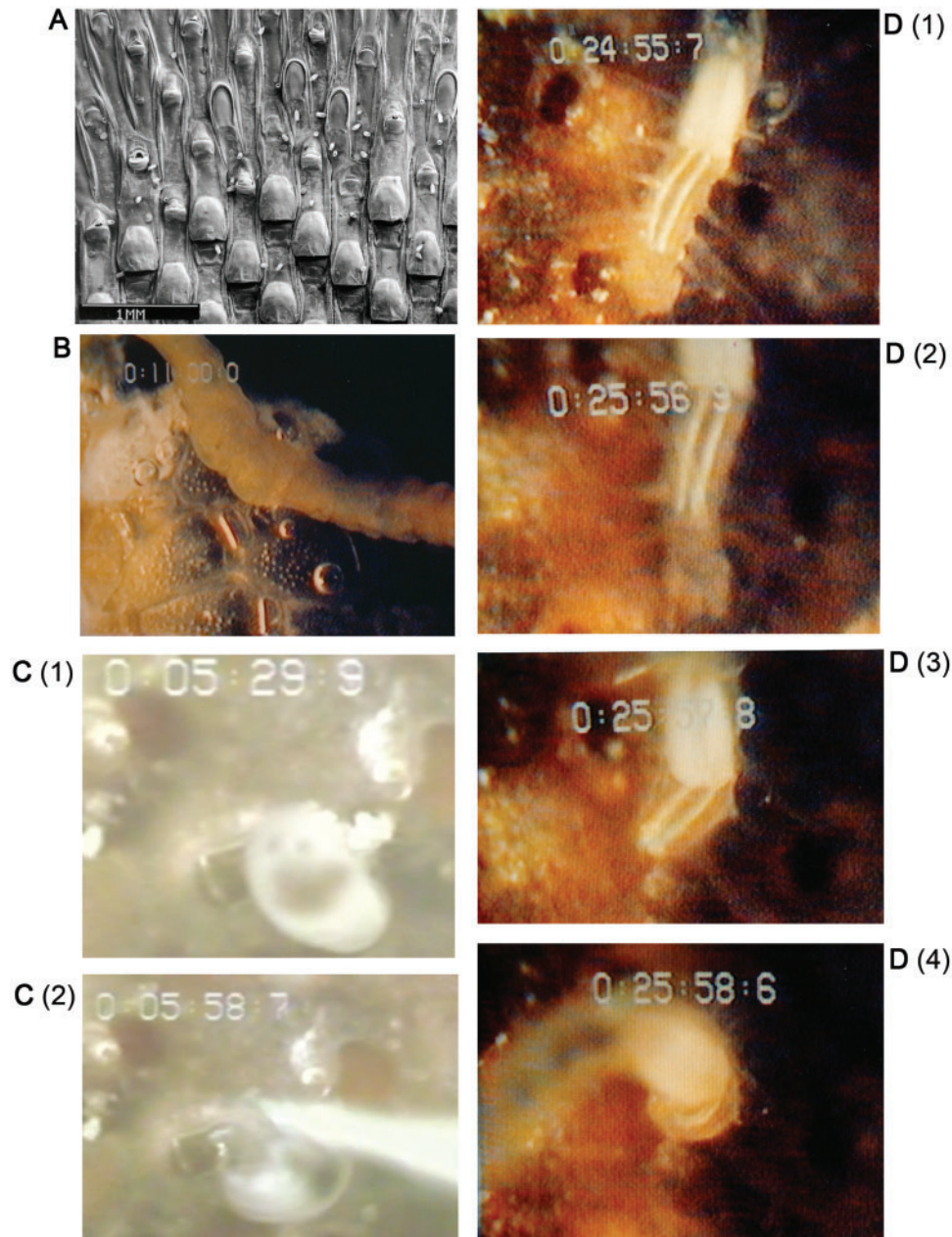
Polypides may also assist in the release of larvae by colonies, indulging in a kind of basketball with their offspring. Hall (1982) found that maternal zooids of *C. apiculata* aided larval release through a series of movements of the tentacles and lophophore. A larva emerging from an ovicell becomes entangled in the partly retracted tentacles of the maternal zooid. The lophophore is then extended, expanded, and an ejection action, consisting of a rapid widening and contraction of the funnel, expels the larva into the water column above the maternal colony's lophophores. Some larvae are immediately photopositive and swim away toward the light. Others fall downward and are drawn into the lophophores of other feeding zooids. They are passed to the edge of colony by a sequence of capture and ejection by adjacent lophophores.

### Behavior of avicularia and vibracula

The movements of avicularian mandibles (like the closure of opercula) are very rapid, in the 0.1–10 s range, and may occur only infrequently. They can be studied using a video camera attached to a macro lens or stereomicroscope. A great deal of patience is required as the movements are both infrequent in the absence of stimuli and extremely rapid when they do occur.

Sessile avicularia may be vicarious, about the same size as autozooids and spaced between them (Fig. 4A), interzooidal, located between autozooids, but smaller in size, or frontally budded on an autozooid, usually small in size. The avicularian body or cystid may contain a polypide rudiment; it also has very developed muscles used in operating the mandible, the structurally reinforced homologue of the autozooid operculum. In bird's head avicularia, found in the Buguloidea, the cystid portion is attached to the autozooid on a short or a long peduncle. Vibracula, in which the mandible is developed into a long bristle, may also differ in closing with a circumlocutory, rather than with only a unidirectional movement (examples of vibracula in action are shown in Fig. 3).

Morphological studies of avicularia and vibracula (Winston 1984) and behavioral studies carried out with living colonies (Winston 1986, 1991, 2009) have shown how different polymorphs function within colonies. These functions include sweeping debris from zooids and colonies, protecting from trespassers, and capturing motile organisms and possible predators.



**Fig. 4** (A) Polymorphism in an Antarctic cheilostome. Autozooids with opercula (small flaps), Avicularia (larger fingernail-shaped flaps), and ovicells (helmet-shaped structures at the base of the photograph). (B) *Micropora brevisisima* with a worm impaled on a spear-shaped avicularium mandible. (C1–2). Sequence showing that a needle probe does not remove a flatworm speared on an avicularium mandible of *Celleporaria*. (D1–4). Sequence showing capture of a syllid polypide by the spatulate avicularium of a *Stylopoma* colony. (A) SEM image. (B–D) photographs from videos by the author.

#### Fixed avicularia: *Micropora* and *Cellarinella*

*Micropora brevisisima* has sessile avicularia with sharp-pointed mandibles. In avicularia of this type, the avicularium body has a fixed position between the autozooids of the colony. Avicularian

mandibles close rarely, often remaining open even when autozooid opercula are shut, but the mandible shuts in response to physical stimuli such as probing, jarring, or vibration of the palate or mandible. Despite their small size, such avicularia are able to

capture and hold relative large trespassers by their appendages, e.g., cirri of polychaetes, legs of amphipods or pycnogonids. During observations of living colonies of this species, carried out at Palmer Station, avicularia of *Micropora* captured several

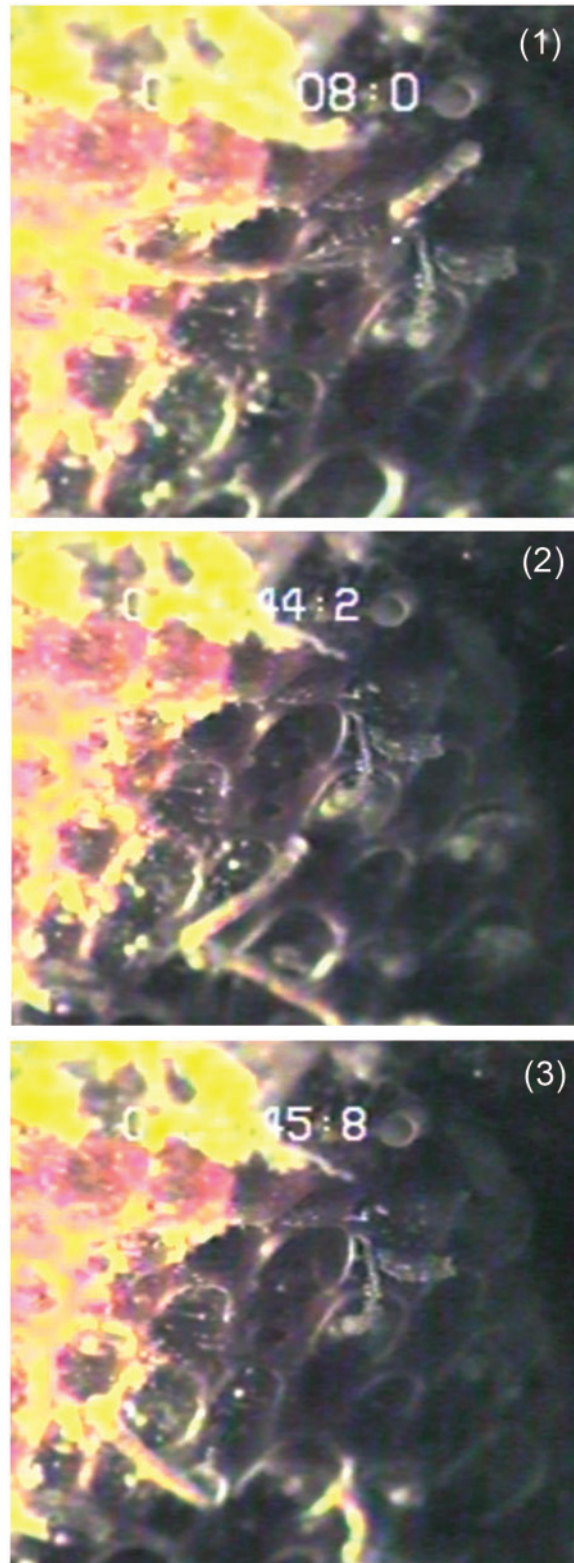
annelids and held them despite their much greater size (Fig. 4B). The heavily chitinized triangular mandibles of *Cellarinella* were also capable of detaining large polychaetes by their appendages (Winston 1991, 2009), while spatulate avicularia (Fig. 4 sequences C 1-2 and D 1-4) can capture trespassers, both large and small.

#### **B zooids: *Steginoporella***

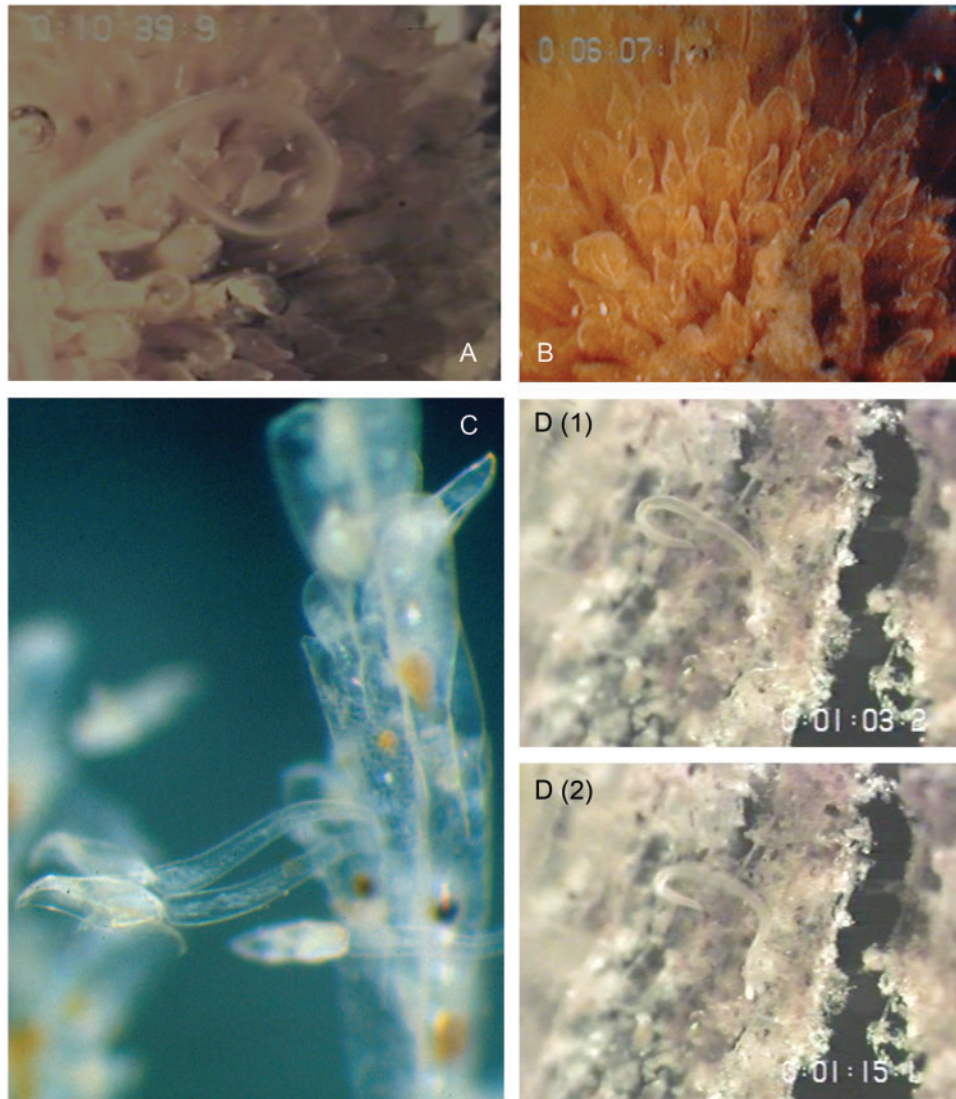
Colonies of species of *Steginoporella*, as well as those of a few other genera, have two kinds of zooids A zooids (auto-zooids) and B zooids; the latter are larger, with more reinforced opercula, but which, unlike avicularia, retain feeding polypides. Because of their enlarged, more mandible-like opercular structure they have been considered “incipient” avicularia. Some aspects of their behavior do differ from that of surrounding A zooids. B zooids open their opercula and remain open without expanding lophophores, well before A zooids open and expand to feed, suggesting they B zooids have an ear-like sensory role in colony function (Winston 2004). B zooids also capture potential predators, although A-zooids may do this as well, as shown in the sequence in Fig. 5 in which a syllid polychaete is chopped in half by their actions.

#### **Bird’s head avicularia: *Beania***

Unlike sessile avicularia, the pedunculate bird’s head avicularia found in the cellularine group of bryozoans close and open mandibles frequently even when undisturbed, showing a species-specific pattern of ongoing activity. For example, in *Beania erecta* (Fig. 6A and B) the avicularium bends forward on its peduncle, then snaps back into an upright position, while the mandible



**Fig. 5** (1–3). Video sequence showing the capture and bisection of a syllid polychaete by the heavily chitinized and toothed A- and B zooid opercula of *Steginoporella*. Photographs from a video by the author.



**Fig. 6** (A) Nematode hooked by an avicularium of *Beania erecta*. (B) Birds' head avicularia of *Beania erecta*, showing open mandibles. (C) The long, flexible stalked birds' head avicularia of an Antarctic species of *Camptoplites*. (D1–2). Sequence of a nematode being moved across the branches of *Camptoplites* by the movements of avicularia. Photographs from videos by the author.

closes. Once the avicularium is upright, the mandible slowly re-opens. Although the avicularian movements did not increase in the presence of trespassers, their activity was still effective as organisms caught by one avicularium were usually captured by the mandibles of several more in their struggles to free themselves (Fig. 6A). Some were eventually able to pull free, detaching the avicularia from their peduncles in the process (Winston 1991, 2009).

#### Long-stalked bird's head avicularia: *Camptoplites*

The long-stalked avicularia of *Camptoplites* species (Fig. 6C) showed an even more complex pattern. The long slender peduncles of these avicularia sway slowly back and forth across the frontal surface of the colony's branches. As they sway the mandibles of the avicularia snap open and shut. They show no increase in activity when a trespassing organism touches the branches, but when a mandible intercepts an

object soft and narrow enough to grasp (such as a polychaete seta or arthropod appendage), it snaps shut upon it. The swaying activity then carries the organism toward the edge of the colony, as shown in the sequence in Fig. 6D (1–2) (Winston 1991, 2009).

#### Vibracula: *Nematoflustra*

Distal to each autozooid of *Nematoflustra flagellata* is a vibraculum zooid with a long curved, bristle-like mandible. Mechanical stimulation or the vibration of a

small organism such as a pycnogonid or polychaete triggers a wave of vibracular movement over a part, or all, of the colony's surface. The circumrotary reversal of the vibracula mandibles is sequentially synchronized at first, traveling proximally from the branch tip, but later waves become less synchronous. The waves of moving setae effectively carry organisms or debris from the branches as shown in the sequence in Fig. 3B1–3 (Winston 1991, 2009).

## Conclusions

Life in the colonies has been most satisfying, providing the opportunity to understand very different kinds of lives—without leaving the planet. Like space travel, the study of clonal and colonial marine animals is just beginning. From a purely theoretical point of view we need to learn more about these organisms in order to understand the structure and dynamics of their populations (Hughes 2005). How do metapopulations of such species exist—what is the tradeoff between extinction and colonization, or re-colonization, of new patches of habitat? How do size and age affect survival of partial mortality, reproduction, and genetic structure of their populations? How do competition and cooperation operate in colonial animals? These and many other questions must be answered before we can have a complete and robust ecological theory.

From a practical point of view we need to understand these kinds of organisms so as to protect and maintain marine biodiversity. Coral reefs are the most urgent example, but many other communities dominated by colonial organisms, such as the epifaunal communities of the

Antarctic shelf and the hard grounds of the Gulf of Mexico, come to mind immediately.

From a more selfish human point of view, animals able to generate totipotent cells, to form entire new units, even containing cells and organs for sexual reproduction, throughout their lives would seem to have much to offer medically. The phenomena of rejuvenation and long-term escape from senescence, if not actual immortality, should also be worth pursuing.

What of genetics? Does somatic mutation play a significant role in ecological adaptation or in speciation in any of these species? Are there really “hopeful monsters” and fortunate founders among them? There is still not enough research on these topics, but new methods, combining ecological study with molecular genetics, are already producing some exciting new work.

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