0014-4754/95/050510-16$1.50 + 0.20 © Birkhäuser Verlag Basel, 1995

Population biology of bryozoans: correlates of sessile, colonial life histories in freshwater habitats

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Abstract. Bryozoans are common, often abundant, sessile, colonial invertebrates of freshwaters. By reviewing what is known of their general ecology and considering in further detail the population biology of specific groups, we provide evidence that 1) populations are locally ephemeral and regional persistence is attained via a dynamic equilibrium between dispersal and colonization, and 2) sex may often be infrequent and a high degree of clonality obtains at both local and regional scales. On the basis of these characteristics we discuss how the group offers exceptional opportunities for investigating a number of fundamentally important ecological and evolutionary questions.

Key words. Freshwater bryozoans; coloniality; sexuality; clonality; habitat subdivision; population structure; dispersal; molecular studies.

> *"The highly curious modification of the Molluscan type which the Polyzoa [= Bryozoa] present ... the great beauty of their forms, and the facility with which they can in general be observed in a living state, cannot but render them special favorites for every lover of Nature; and for the more profound student must confer on them a peculiar significance, and invest their study with a scientific interest which is scarcely surpassed by that of any other group of animals...."*
>
> (Allman 1856)[1]

Introduction

Despite the early enthusiasm of Allman and other Victorian naturalists, bryozoans are often overlooked inhabitants of freshwater environments. This must in part reflect their small size and sessile nature which mean they can be easily missed, while repent and gelatinous colonies may be mistaken for mosslike growths or egg cases by untrained eyes in the field. Furthermore, their details can only be appreciated fully by viewing with a dissection microscope. Yet, as is true of their marine counterparts, these colonial invertebrates are commonly found attached to submerged surfaces, often in great numbers. In temperate regions, colonies grow rapidly during the warm months of the year and can form dense mats on submerged branches, roots, aquatic plants, stones and other solid surfaces in both lakes and streams[61,117,146]. Before sand filtration was adopted in water treatment practices, growth of freshwater bryozoans commonly led to blockage problems in water supply[46].

Bryozoans are sessile, colonial invertebrates that feed on suspended particulate material using a ciliated crown of tentacles, the lophophore. In freshwater forms the lophophore is typically deflected into a U-shape with the mouth lying between the double row of tentacles at the base of the bend. Colonies are formed of a number of genetically identical, physiologically interconnected modules called zooids that are produced through asexual budding. Variation in modes of budding produces species that vary greatly in form allowing exploitation of horizontal and vertical space as encrusting and erect growths.

There are three extant classes of bryozoans: the Gymnolaemata, the Stenolaemata, and the Phylactolaemata. The Stenolaemata is entirely marine with only one small order surviving to the present although it underwent great proliferation in Palaeozoic oceans. The Gymnolaemata is the largest class and is mainly marine, but a few species (in the subclass Ctenostomata) occur in fresh or brackish waters. The Phylactolaemata contains about 50 species and is exclusive to freshwater habitats. Lacourt[77] and Bushnell[20] summarize the occurrence and distribution of freshwater bryozoans within major faunal areas. Many species are broadly distributed (four are completely cosmopolitan), and tropical regions contain the greater number of species and of endemics. This paper will be devoted primarily to the discussion of phylactolaemate bryozoans. Although entroprocts have often been included in discussion of freshwater bryozoans, similarities between the two groups likely reflect convergence to a sessile, colonial, suspension-feeding lifestyle (but see Nielsen[95] for dissenting view). Little ecological work has been conducted on entoprocts, and they will not be discussed further.

Life history of freshwater bryozoans

The life history of freshwater bryozoans is grounded in a high degree of clonal reproduction that serves to spread the genotype through local habitats and is

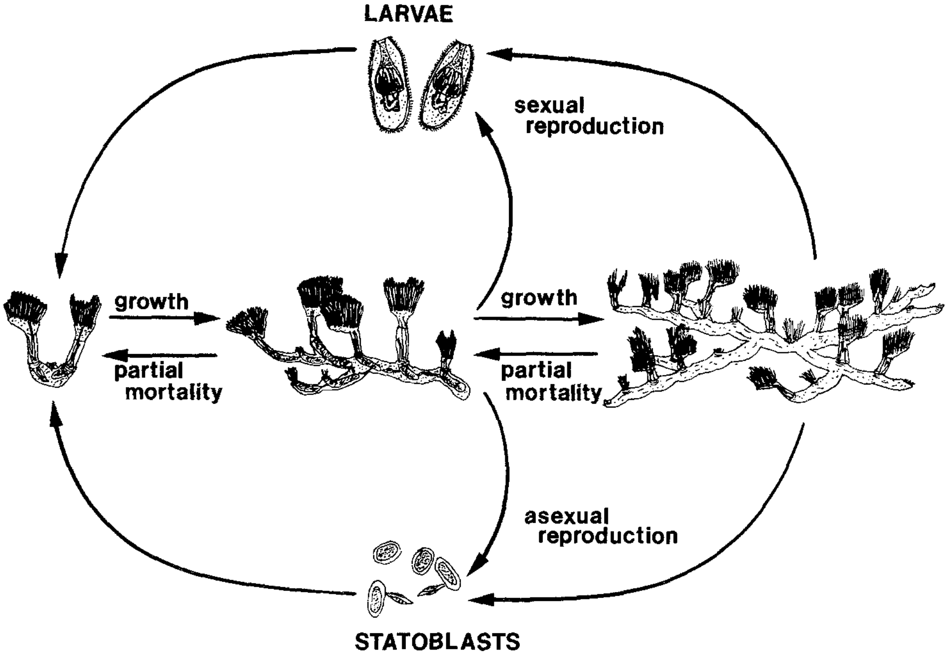

Figure. Generalized life cycle of phylactolaemates in temperate freshwaters. Colonies hatch from overwintering statoblasts in late spring/early summer and may soon enter a bout of sexual reproduction to release free-swimming larvae. Growth during the summer results in an increase in colony size. The asexual production of statoblasts may commence by mid-summer. At any time colonies may sustain partial mortality and a consequent reduction in size. A plumatellid-type bryozoan is depicted. See text for further details.

achieved through colony growth, fission or fragmentation (in some species), and the production of large numbers of statoblasts. The latter are small (generally < 1 mm in diameter), asexually-produced, encapsulated structures composed of two chitinous valves enclosing undifferentiated primordial tissue and associated nutritive yolk. As statoblasts are highly resistant to adverse physical conditions, they provide both a means of persistence during harsh conditions and of dispersal within and between habitats (see below). Fission of colonies and subsequent movement apart occurs in the gelatinous species *Cristatella mucedo* and *Lophopus crystallinus*. Fragmentation is effected through breakage and re-establishment in the erect species, *Fredericella sultana* and *Plumatella fruticosa*[143,145]. Colony subdivision may also occur through partial mortality (e.g. by predation).

The general life cycle of phylactolaemates in temperate regions is illustrated in the figure and can be summarized as follows. In the late spring, when temperatures have reached appropriate levels, the valves of statoblasts dehisce and small colonies develop from the enclosed germinal tissues. After a short growth phase, colonies may enter a period of sexual reproduction and produce larvae. Larvae effect limited dispersal within habitats as they swim for a short period of time before settling to metamorphose into a small colony. Numerous observations suggest that sexual reproduction is, however, often foregone in local populations as will be discussed later. After the brief sexual phase that generally occurs early in the season (but gametes and larvae have been observed in some species as late as August: T. Wood, personal communication) colonies invest exclusively in clonal growth. Statoblast production may begin by mid-summer and colonies can both grow in size and produce statoblasts simultaneously. However at some point, usually in the late summer/early autumn, colony growth ceases and relative investment in statoblast production is maximal. Colonies generally disintegrate in the late autumn to release overwintering statoblasts, although some species release mature statoblasts through specialized pores[61,90]. Variations from this generalized scheme will become apparent in subsequent discussion.

It is notable that overwintering in freshwater bryozoans is achieved via an asexual phase. This pattern contrasts with the life histories of many unitary, cyclically clonal forms in temperate regions in which cloning occurs throughout the growing season by apomictic (= ameiotic) parthenogenesis (e.g. cladocerans and rotifers) or by budding or fission (e.g. naidid oligochaetes) and a late bout of sexual reproduction produces overwintering fertilized eggs. The standard explanation for the latter pattern incorporates three interpretations: 1) sexuality at the end of the season confers genetic variation that is adaptive when faced with incipient unfavourable or unpredictable conditions; 2) exclusive parthenogenesis early in the growing

Table. Dormant structures in cyclically clonal invertebrates in freshwater habitats.

Animal Group	Dormant Structure
Phylactolaemate bryozoans (C)	Asexual statoblasts
Ctenostome bryozoans (C)	Asexual hibernacula
Sponges (C)	Asexual gemmules
Cordylophora (a hydrozoan) (C)	Asexual metanonts
Entoprocts (C)	Regressed basal stolon (asexual)
Hydra (U)	Fertilized resting eggs
Gastrotrichs (U)	Parthenogenetic resting eggs
Monogonont rotifers (U + C)	Fertilized resting eggs
Naidid oligochaetes (U)	Fertilized resting eggs
Aeolosomatid oligochaetes (U)	Fertilized resting eggs
Some ostracods (U)	Possibly both fertilized and parthenogenetic resting eggs
Cladocera (U)	Fertilized resting eggs; resting eggs via apomictic parthenogenesis in some *Daphnia*
Some phyllopods (U) (Eubranchiopods)	Possibly both fertilized and parthenogenetic resting eggs
Some nematodes (U)	Possibly both fertilized and parthenogenetic resting eggs
Some turbellarians (U)	Fertilized resting eggs

C = colonial; U = unitary freshwater invertebrate groups. Fertilized eggs are assumed to be the result of outcrossing although many of the animals are hermaphroditic, hence selfing may occur. Information obtained from relevant chapters in Pennak[109], Thorp and Covich[131], and from Innes and Hebert[63] for cladocerans.

season allows rapid exploitation of locally favourable conditions; and 3) dormant, sexual propagules are widely dispersed in space and/or time[140]. It is perhaps significant that all sessile colonial forms in freshwaters contrast with the standard paradigm (see table) in their timing of reproductive modes and in effecting wide dispersal via resistant asexual stages, although the low incidence of both colonial forms and other cyclically clonal groups in freshwater environments makes the robustness of this relationship questionable. A comment on dispersal via sexual and asexual progeny is also warranted. In colonial groups, larvae provide a means of dispersal within habitats and asexual dormant stages effect temporal and longer-distance dispersal between habitats. The great potential for long-distance dispersal provided by both sexual and asexual dormant stages may be a by-product of the requirement for resistant stages that allow persistence in environments subject to cyclical deterioration. Such stages will thus effect significant temporal dispersal, especially if breakage of dormancy is variable amongst propagules.

Notwithstanding the above points, if genetic variation is important for persistence through winter and/or success in the subsequent growing season, this suggests that some animals (especially sessile, modular, colonial forms) are constrained from producing overwintering, resistant sexual phases. Yet, if the timing of sex in modular colonial forms is a by-product that reflects a functional constraint in producing resistant eggs, this begs the question of why colonial forms should be so constrained when animals of unitary modular construction (e.g. *Hydra*, fissiparous flatworms, naidid oligochaetes, etc.) are not. The production of dormant, parthenogenetic eggs in obligately asexual populations of cladocerans[52] and brine shrimp[17] indicates that at least some groups of unitary animals are not constrained in producing dormant stages exclusively sexually.

Another explanation for the timing of sex in modular, colonial forms may be that the costs of sexual reproduction can only be met by food levels available early in the growing season. However, variation in the timing of gonad development throughout the year in freshwater invertebrates suggests this is an unlikely explanation. Alternatively, mixing of resistant stages (e.g. floating statoblasts) during the winter and escalation in biotic interactions during the growing season may maximize the probability of effecting outcrossing early in the growing season. Recent research suggests that benthic marine invertebrates may achieve low rates of fertilization due to sperm dilution effects[6,37,79,110]. For freshwater bryozoans, increased abundances of predators and proliferation of successful clonal types may reduce the likelihood of fertilization via allospermy or reduce the genetic variability of offspring as the season progresses. (Mobile, unitary forms generally copulate and so avoid problems of sperm dilution that sessile, free-spawners may experience.) On the other hand, for some organisms variation generated by outcrossing may be particularly adaptive during relatively early phases of the growing season. For mobile, unitary forms sex early in the season may be precluded if locating a mate is difficult when population levels are low.

The problem of why larvae are produced early in the season may of course also be unrelated to their sexual origin (as discussed later, evidence to date indicates that little variation may be generated by sex in phylactolaemates anyway). Larvae, unlike statoblasts, are capable of site selection within habitats[57,70], so production of larvae early in the season may be an adaptation to enable sessile organisms to colonize the new growth of plants in early summer.

An overview of ecological research

The first major review of the biology of freshwater bryozoans was published in 1856 by Allman[1], and his lovely illustrations continue to be used widely. Hyman[61] and Brien[14] summarize subsequent research much of which concentrated on basic histology, embryology, and development. Here we describe what, in general, is known about the ecology of freshwater bryozoans and how this may relate to broader issues. Detailed discussion of clonality, dispersal, recruitment, and population persistence will be taken up in the subsequent sections which present case studies of two groups that have been the focus of recent investigations.

Habitat characteristics

Freshwater bryozoans occur in both lotic and lentic habitats. Most species are found in relatively still waters in ponds, backwaters, bays and slow streams. They are largely restricted to growing in relatively warm (15–28 °C) water, and although a wide range of pH is tolerated, more alkaline waters tend to be favoured[61,145]. However, a few species are occasionally found in acidic habitats[38], and colonies of some species may survive at lower temperatures[145]. Most species are found only in shallower regions along the shores of lakes and ponds[36,38,61,109], which may reflect low oxygen levels that develop during the summer with depth[36] or availability of food. Although species have different ranges in tolerance[21], a few occur in fairly eutrophic water bodies[21,142] and in waters with high concentrations of heavy metals and PCB's[54]. However, in general, freshwater bryozoans are not found in highly polluted conditions[21]. As most bryozoans will not grow on soft, muddy surfaces[145], availability of appropriate substrata for attachment is of primary importance[36,38,130,145] as is also true for sponges[43], the other major group of sessile, colonial suspension feeders in freshwater habitats. Despite the general association of bryozoans with aquatic plants, bryozoans appear to colonize and/or grow better on particular plant species[19,70].

Feeding

Phylactolaemates have high rates of suspension feeding[61,114] and possibly for this reason have been difficult to culture. Observations of gut contents reveal they ingest diatoms, desmids, *Oscillatoria*, ciliates, flagellates, and small rotifers[61,69,112,114,130]. By sampling both ambient food availability and gut contents, Kaminski[69] determined that food particles ranging from 5 to 17 μm in diameter were generally preferred by three phylactolaemates and that small nannoplankton algae were the main food component.

Research on marine bryozoans has revealed that flow regime can have important effects on patterns of feeding[101–103]. Recent experiments on the freshwater bryozoan *Plumatella repens*[105] indicate that flow velocity also influences feeding, but in contrast to marine bryozoans, per zooid feeding rates increase with an increase in ambient flow velocity. In phylactolaemates, feeding may be less constrained by flow because their relatively large, U-shaped lophophores create powerful feeding currents (marine forms have smaller, circular lophophores)[105]. Powerful feeding currents may be particularly important for feeding in lentic and lotic habitats. In standing waters diversion of fluid from great distances will be beneficial because lack of flow precludes resource renewal and food depletion will result near surfaces. In lotic habitats diversion of fluid by powerful feeding currents will be less constrained by the friction drag imposed by flow. The complex hydrodynamics of marine habitats may ensure delivery of food to the level of small, circular lophophores, thus marine forms may benefit from the larger energy surplus associated with small size[118,122].

There is conflicting evidence for the influence of colony size on feeding rates. Bishop and Bahr[11] found that feeding decreased in larger colonies of *Lophopodella carteri* and thereby inferred that fission in this species functions to reduce feeding interference amongst zooids. Conversely, Okamura and Doolan[105] found an increase in per zooid feeding associated with larger colonies of *Plumatella repens* as has been found for an encrusting marine bryozoan[102]. These conflicting results probably reflect an experimental artefact as Bishop and Bahrs' studies were conducted in very small volumes of suspension and did not incorporate any water movement. Thus food depletion by large colonies feeding from small volumes of water should be reflected in reduced feeding rates, and these would have been exacerbated by the lack of flow to carry away processed water. Okamura and Doolans' study did not suffer from these problems, and they suggest that the increased feeding by larger colonies of *P. repens* may reflect a greater propensity to feed due to higher metabolic demands or production of stronger feeding currents due to the concerted pumping activity of the greater number of lophophores.

Growth, fission, and fusion

Few studies of growth in the field have been conducted. Field studies indicate that colonies grow exponentially[19,143] but at extremely variable rates[68]. In general, there is great variation in growth and abundance at both spatial and temporal scales[19,66,71,104,142,143]. A link between high levels of phytoplankton and growth suggests that the availability of food can determine abundance levels[66,68,112].

Limited data on fission rates in the field are available. Mukai, Karasawa and Matsumoto[89] found that a single colony of *Pectinatella gelatinosa* proliferated via fission to 398 colonies within two months, and Okamura (unpublished data) found that growth and fission produced as many as 374 colonies from six initial colonies of *Cristatella mucedo* within the same period of time.

The potential for fusion amongst small colonies has been investigated by Mukai and coworkers[87,88,90,91] who demonstrated that small colonies of *Plumatella* spp. and of *Hyalinella punctata* hatched from statoblasts will fuse to produce larger colonies. As is true for marine colonial invertebrates, fusion is likely to be adaptive as larger colonies are generally more competitive and less susceptible to a variety of mortality sources such as predation, physical damage, and overgrowth[25,49,65,116,141], and reproductive output increases with colony size[51,85]. However, in some cases, intracolonial interference may reduce feeding[84] and growth[127] rates beyond particular size thresholds.

Research has shown that fusion in the marine ascidian *Botryllus schlosseri* is mediated by a single histocompatibility locus[121] and that extremely high levels of polymorphism at this locus confer a high probability that fusion will only occur between clonemates or closely related colonies[44]. Thus it is suggested that the evolution of self/non-self recognition was driven by the advantages of fusing with self or closely related kin and the disadvantage of fusing with unlike individuals due to the subsequent danger that one genotype may functionally parasitize the other(s) and thereby contribute disproportionately to gamete production (= somatic cell parasitism)[26,28,39].

In phylactolaemates, fusion of small colonies derived from sessoblasts will likely entail fusion of genetically identical material as sessoblasts in close proximity will probably have been laid down by the same parental colony. However, fusion occurs amongst small colonies derived from floatoblasts and from statoblasts collected from different ponds[87,88,90]. This suggests that genetically distinct colonies may fuse and so may be subject to somatic cell parasitism, although the genetic relatedness of fused colonies has not been determined.

For phylactolaemates, both a high degree of clonality within habitats (see later) and the likelihood of fusion of clonemates via a common sessoblast origin may generally preclude high levels of selection for a histocompatibility recognition system. Alternatively, there may be a size-related advantage to fusion regardless of relatedness and despite the risk of somatic cell parasitism if mortality is very high at early stages. In some ant species, cooperative nest founding by unrelated queens effects larger initial nests and so reduces the vulnerability of small colonies to takeover by slave-making ants. When the nest attains a certain size, the queens will then fight for control or some may be evicted by workers (reviewed by Seger[123]). The system is stable because the per-foundress chance of success is maximized. In phylactolaemates the risk of somatic cell parasitism must be much lower than the equivalent danger for ants of losing control of nests because of the high probability of fusing with clonemates. Another alternative is that fusion with unlike genotypes provides phenotypic plasticity via a more complex set of physiological properties[44]. Finally, since sexual reproduction may be relatively unimportant, the appropriate currency for assessing the costs and benefits of somatic cell parasitism could be relative rates of genetic representation in chimeric and non-chimeric colonies, not in the relative representation in germ cells. In summary, although the payoff for fusion is not clear, it may be related to greater efficiency in feeding (see above), decreased susceptibility to mortality, increased reproductive output, an increased chance of outcrossing, and/or attainment of greater physiological capacities.

Sexual reproduction

Sexual reproduction results in the release of larvae that swim for a short period of time (generally minutes to several hours[86,98]) before settling and metamorphosing into a small colony. Larval dispersal and site selection[57,70] may be particularly significant for colonies that recruited from sessoblasts laid down at the end of the previous growing season, as these colonies may be bound up with vegetation from the previous year that is decomposing on the bottom. However, in general, most dispersal within habitats is probably achieved by floatoblasts and not larvae (but see Kaminski[70]). Larvae are short-lived and produced singly in only some zooids of colonies[144] while most zooids generally produce multiple floatoblasts[90]. Furthermore, sexual reproduction is apparently uncommon in many habitats.

Sexual reproduction is relatively rare in at least some populations of phylactolaemates. Larvae are often not observed in local habitats[100], although this is perhaps not surprising, given the brief period of sexual activity and the short larval life. In addition, researchers have noted a lack of gametogenesis or that testes may develop initially but are resorbed and that subsequently no ovaries (or only rudimentary ones), embryos, or larvae are seen[15,89,134,138,143]. Genetic studies provide evidence that in some populations sexual reproduction is inviable. Backus and Mukai[7] found chromosomal abnormalities indicative of meiotic non-disjunction in some populations of *Asajirella (= Pectinatella) gelatinosa*. Finally, recent genetic work on *Fredericella sultana*[147] and *Cristatella mucedo*[106] indicates that populations are largely clonal. Wesenberg-Lund[138] suggested that sexual reproduction generally declines or ceases in more northerly habitats.

Whether fertilization occurs via selfing or outcrossing has received little study until recently. The apparent lack of a route for sperm release and the hermaphroditic nature of colonies led early workers to suggest that outcrossing was inviable and so self-fertilization must occur. Subsequently it has been observed that sperm can be released through pores at the tips of lophophoral tentacles, but how free-swimming sperm locate and penetrate other colonies remains unknown[86]. The documentation of heterozygosity suggests that self-fertilization does not occur exclusively[62,93,94,104]. However, by comparing genetic fingerprints of parental colonies of *Cristatella mucedo* and their larvae, Jones et al.[67] provide the first direct evidence that sperm can locate other colonies and effect outcrossing. Their results indicate that at least some larvae are the result of outcrossing, but could not distinguish whether other larvae were produced by selfing. The general feasibility of self-fertilization is unknown, although resorption of the testes suggests a mechanism of avoidance. However, Oka and Oda (1948, cited in Mukai[86]) reared colonies of *Lophopodella carteri* derived from a single statoblast and obtained larvae.

Statoblast production and function

A variety of statoblast types are produced which have been designated specific names that infer function. Some species produce only one type. 'Sessoblasts' are statoblasts that adhere to the substratum; 'floatoblasts' contain gas-filled cells that provide them with buoyancy in the water column. 'Spinoblasts' are similar to floatoblasts but in addition have spines around the margin that may represent a means of attachment to fur and/or feathers. 'Leptoblasts' are thin-walled statoblasts that lack an obligate dormant period and thus produce young colonies rapidly. 'Piptoblasts' are unspecialized statoblasts that do not remain attached to the substratum. We concur with may others[60,77,92,117] that this current terminology is unfortunate because it is confusing, it may be unreflective of true function, and it propounds scientific terms of mixed etymological derivation. Nonetheless, the terms are relatively entrenched and we use them to distinguish between different statoblast types.

Statoblasts are produced in varying numbers per zooid both within and amongst species[90,143]. There is somewhat conflicting evidence as to the order within individual zooids in which different statoblast types develop[90]. When conditions are favourable, huge numbers of statoblasts can accumulate within a given water body. Brown[16] reported that drifts of floatoblasts exceeding one metre in width extended along half a mile of the shoreline of Douglas Lake in Michigan and estimated that colonies of *Plumatella* in a 1 m^2 area could release 800,000 floatoblasts in the autumn.

A great deal of research has been conducted on the environmental physiology of statoblasts. Various researchers, most notably Oda[97], have determined patterns of dormancy and hatching of statoblasts when exposed to variation in factors such as light, temperature, desiccation, and water chemistry (see reviews in Bushnell and Rao[22], Hutchinson[60], and Mukai[86]). In general, research demonstrates that statoblasts are highly resistant structures, but results are often conflicting and the relative importance of various factors appears to vary for different species[22,60]. Under ordinary circumstances dried statoblasts are capable of remaining dormant for at least 2 years, but Rogick[115] reported a maximum longevity of 4 years. Oda[97] succeeded in germinating some statoblasts by soaking in 15% HCl for a few minutes. Oda[97] found that *Lophopodella carteri* produces two types of statoblasts. Those produced early in the season would germinate rapidly, in some cases before being released from the parent colony. In contrast, those produced later required exposure to adverse conditions before germination. If this is true for many species, it might well explain the many conflicting results obtained by different workers.

In temperate regions, many species may release statoblasts that germinate in the same season, and several statoblast-derived generations can be observed[16,20,86,142]. Most statoblasts require at least a short dormant phase and distinct pulses in colony abundance result[142]. However, specialized, thin-walled leptoblasts require no dormant phase, and in *Plumatella casmiana* the continuous production of leptoblasts provides a means of rapid proliferation of colonies[143] which, in some sites, may account for its dominance[142,143]. Statoblasts liberated in the autumn generally overwinter[86].

As discussed earlier, the highly resistant nature of statoblasts means they are effective in dispersal, and indeed probably provide the only reliable means of colonizing new water bodies. Bushnell[20] has suggested that small statoblasts may be wind-dispersed while larger statoblasts with hooks and spines for attachment may be primarily dispersed via animal vectors. However, small, smooth statoblasts are also highly adherent (possibly via surface tension), suggesting that they may also be dispersed by animals. In addition, statoblasts may be bound up in mud adhering to animals. Statoblasts remain viable after having passed through the digestive tracts of salamanders, frogs, turtles, and ducks, although many are damaged in the process[16], and statoblasts have been observed in the stomachs of a variety of fishes[20,36,108]. Such evidence suggests dispersal via animal vectors is likely. However, wind dispersal is likely to be comparatively unimportant given that huge losses should result due to unsuitable patterns of deposition (inland waters comprise $<2\%$ of the earth's surface: Wetzel[139]). Getting statoblasts windborne initially would also require overcoming the relatively large surface tension forces exerted on such small, floating objects. Many statoblasts are stranded on the shore as water levels recede (Okamura, personal observation). The dispersal potential of these is unknown.

Annandale[2] found that in India most freshwater bryozoans produce statoblasts at the approach of hot weather (colonies flourishing during the mild winter), although some species grow throughout the year or even primarily during the hot, rainy season. In addition, he noted that some produced 'oversummering' statoblasts in ponds that dried up[2]. Other researchers have noted that statoblasts can be produced year-round in the tropics (Marcus 1925, cited in Bushnell and Rao[22]; Vorstman 1928, cited in Hyman[61]). These observations illustrate that statoblasts play a role in both dispersal and in resisting adverse conditions (i.e. they effect both spatial and temporal dispersal). However, patterns of statoblast production and other aspects of the life history of tropical freshwater bryozoans remain largely unknown.

Predators

Freshwater bryozoans are preyed upon by a variety of invertebrates. These include trichopteran larvae, snails, chironomid larvae, oribatid mites, flatworms, and spongefly larvae[19,23,113] (Okamura, pers. observ.). The sudden, complete disappearance of dense growths of colonies has been noted to be associated with the occurrence of these invertebrates predators, especially trichopteran larvae and snails[19] (Okamura, pers. observ.). Bushnell[19] observed that colonies relatively free of predation were growing on substrata with reduced accessibility to crawling predators.

The presence of statoblasts in the guts of various fishes and ducks[16,20,36,77,108] indicates some level of predation by vertebrates; however, Wood[146] suggests that predation by fish is never extensive. Dendy[36] found that bluegills ingest *Plumatella* and noted that colonies protected from bluegills were highly branched, but were unbranched and closely adherent to surfaces when bluegill abundance was high. In general, consumption by vertebrates may occur incidentally during general foraging activities[36]. However, ingestion of some species may be avoided. Tenney and Woolcott[129] found that filtered extracts of frozen colonies of *Lophopodella carteri* are specifically toxic to fish although the causative agent is not known (no ill effects were observed for tadpoles of *Rana pipiens* or a variety of aquatic invertebrate species). Wood[146] suggests that gelatinous forms such as *L. carteri* are generally immune to fish predation.

Parasites

Phylactolaemates are hosts to several endoparasites. These include the enigmatic, nematode-like *Buddenbrockia plumatellae* that, when mature, occurs in the body coelom[61]. Korotneff[75] described the myxosporean, *Myxosporidium byrozoides*, which develops into large, spore-producing plasmodia in the body cavity of *Plumatella (Alcyonella) fungosa*. Unfortunately, Kudo[76] later synonymized this parasite with the microsporidian *Nosema (Glugea) bryozoides* described by other authors[13,120]. More recently, an undescribed myxosporean has been found in populations of *Cristatella mucedo* (Canning, Okamura, and Curry, in prep.), and infected colonies generally degenerate. An unidentified microsporidian has also been observed in the epidermis of *C. mucedo* (Canning, Okamura, and Curry, unpublished data). The role of parasites in influencing patterns of distribution and abundance is not known, although a precipitous decline in abundance of a population of *C. mucedo* followed high levels of infection by myxosporeans during the previous year (Okamura, pers. observ.).

Competition

The modular nature of colonial invertebrates entails asexual spread which commonly leads to competitive interactions. These have been studied extensively in marine forms, and the documentation of spatial limitation (see review by Buss[27]) and competition for food[24,103] amongst colonies of e.g. bryozoans, sponges, ascidians, and cnidarians in encrusting marine assemblages has provided significant and unambiguous demonstration of the importance of competition in community structure. Freshwater bryozoans co-occur and often grow entangled with a variety of sessile invertebrates[19,43,113], and although spreading growth by both bryozoans and sponges may lead to competitive interactions, the role of competition for space/food amongst modular freshwater colonial forms has received no specific investigation[43].

Spatial and temporal variation in distribution and abundance

Freshwater bryozoans show great temporal variation in abundance: they can be common in one year and apparently absent or attain only low levels of abundance in others[19,66,68,145] (Okamura, pers. observ.). Within growing seasons abundances can also vary substantially[142]. In addition, at any one time there can be great variation in distribution and abundance amongst as well as within sites[19,36,38,66,68,70,71,130,142]. As noted above, dramatic declines in abundance may reflect high levels of predation by benthic invertebrates and infection by parasites. Kaminski's[70] survey of *Plumatella fungosa* revealed that: 1) greatest biomass occurred at intermediate depths in the littoral region of lakes; 2) colonies were more abundant and larger on leaf petioles than leaf blades of *Nuphar* sp.; and 3) colonies were most abundant on substrata adjacent to the open water zone. The latter distribution could be due to a number of factors such as: a high degree of water/food exchange relative to that within plant beds; preferential larval settlement; a relative refuge from fish predation within plant beds for invertebrate predators of bryozoans.

The distribution of freshwater bryozoans may often be limited by dispersal. Species are apparently absent from sites that appear suitable in terms of physicochemical factors, the availability of appropriate substrata, and presence of other bryozoan species with which they often co-occur[19,38] (Okamura, unpubl. data). In addition, growth and statoblast production of transplanted colonies of *Cristatella mucedo* suggest that previous absence from the transplant site was not due to habitat quality at least in that year[104]. Finally, both local and regional genetic divergence may reflect limited dispersal (see below and later discussion of *C. mucedo*).

Population genetics and local adaptation

Recent investigations indicate that the subdivision of freshwater bodies is reflected in the population genetic structure of bryozoans. Genetic differentiation between geographically isolated populations has been documented in *Fredericella sultana*[147] and *Cristatella mucedo*[104,106]. Isolation of subdivided populations may lead to local adaptation, and morphological variation amongst local populations is notable[96,104,132,133]. Such variation could reflect phenotypic plasticity in response to local conditions. However, rearing experiments[134] indicate that morphological variation is not entirely environmentally influenced, and transplant experiments[104] suggest that differential selective regimes amongst habitats may lead to local adaptation. Although the genetic background of the transplanted populations was not well established, preliminary electrophoretic work on allozymes revealed genetic differentiation amongst populations[104].

Given the life history of freshwater bryozoans, a high degree of clonality within local populations is expected. This issue and its implications will be explored further in later sections.

Ecological importance

Vigorous growth of bryozoans in freshwaters can result in large masses of colonies that dominate the biomass of littoral invertebrates (Glowacka et al. 1976, cited in Sørensen et al.[126]) and that can develop on fish nets[66] and in pipes in water supplies[46]. Substantial populations are also reflected in the huge nearshore accumulations of statoblasts[16]. Thus, given their high feeding rates and potentially great biomass, bryozoans may play important roles in coupling production in the water column with benthic processes as has been shown for benthic suspension feeders in marine environments[34,41,42,56].

Sørensen et al.[126] provided evidence that bryozoans contribute significantly to nutrient cycling in small, phosphorus-limited lakes by assessing the release of soluble reactive phosphorus from colonies of *Plumatella fungosa*. They found that: 1) the amount of phosphorus released by *P. fungosa* was an order of magnitude greater than that released by associated periphyton; and 2) phosphorus exchange was several times higher in the bryozoan community than typical values for other periphyton communities in the same lake.

Bryozoan colonies provide a habitat for a variety of associates and thus may play an important role in food webs in freshwater communities. Bushnell and Rao[23] note that: 1) bryozoan-associated communities have 10 to >50 times the number of organisms that are found in intervening areas of substratum that lack bryozoan growth; 2) decomposing colonies provide a rich flora of bacteria for scavengers and detritivores and are also used as a refuge by chironomid larvae; 3) oribatid mites lay their eggs and overwinter as quiescent stages inside the tubular remains of bryozoan colonies; 4) sinking particles collect among colony masses and provide a source of food for a variety of deposit feeders; and 5) feeding currents generated by lophophores may be utilized beneficially by suspension feeders such as peritrich ciliates. Joo et al.[68] found that gelatinous colonies of *Pectinatella magnifica* influence the composition of the attached algal assemblage that develops directly beneath them by reducing attached algal species diversity, effecting dominance by cyanobacteria rather than diatoms, and increasing algal biomass. Thus by providing complex three-dimensional habitats through modular growth and enhancing local productivity levels, bryozoans may be the closest equivalent in freshwater systems to coral colonies in acting as sites of local species richness and/or high productivity, albeit at much smaller scales.

Case studies

Dispersal, recruitment, and population persistence in *Plumatella*

Karlson's recent studies of plumatellid bryozoans growing on rocks in stream riffles in eastern North America demonstrate how the production of dimorphic statoblasts may be crucial in effecting both the local persistence and regional spread of clonal genotypes[71-74]. Both *Plumatella emarginata* and *P. repens* show distinctly patchy distributions in streams[71,72]. For *P. emarginata*, abundance patterns are variable amongst different sites in streams but generally decline with greater discharge rates suggesting an effect of increased levels of disturbance[71]. Within sites colonies are restricted to growing on rocks that are separated by areas of substrata which are unsuitable for attachment and growth[71]. In general, available substrata are plentiful (colonies occupied only 0.4–6.3% of the total available rock surfaces; Karlson[71]), and colonies are more abundant on larger rocks. Observations of movements of rocks over time suggest that abundance is determined by unpredictable catastrophic events and that greater colony abundances on larger rocks reflect the greater stability of these substrata.

High availability of substrata could, however, be explained by factors other than catastrophic mortality. For instance, predation could inhibit saturation of resources. However, low mortality rates per rock suggest that predation is unimportant[73], although there is no information on the relationship between mortality rates and rock size/age. Somewhat surprisingly, there is some evidence for resource limitation on older rocks. Karlson[73] found that relative variation in abundance (measured in terms of production of sessoblasts) decreased with increased age of the substratum, a trend that could reflect convergence to local carrying capacity. However, the decrease in variation may simply reflect a statistical artefact of sampling older rocks with more even distributions of bryozoans (younger substrata should have more highly skewed distributions due to variation in initial colonization events). Thus, the large amount of available free space indicates that resources are unlikely to be limiting in most cases, but resource limitation may ensue on older rocks producing local density-dependent effects.

Alternatively, or in addition, abundance patterns could be determined by recruitment limitation as has been shown for a variety of sessile marine invertebrates (see review by Underwood and Fairweather[136]). However, for stream-dwelling plumatellids, once a rock is colonized by floatoblasts, the production of sessoblasts by established colonies results in subsequent local recruitment. In general, Karlson[71,73] found that recruitment from both locally-produced sessoblasts and exogenously-produced floatoblasts increased with time so that over the long term (after 12–19 months; Karlson[73]), these processes obscured any short-term differences in recruitment history.

Karlson[72] found a shift in reproductive strategy with increasing colony size in *Plumatella repens*. Sessoblast production increases linearly whilst floatoblast production increases exponentially, indicating an increased investment in dispersal as colonies grow. Since competition can probably be excluded as a general explanation for investment in greater dispersal (see above), local catastrophic mortality must be more important as a selective force[72]. Karlson and Taylor[74] present a model of dimorphic dispersal and growth of clonal lineages in a subdivided population. The model predicts the optimal proportion of dispersed offspring assuming that: extinction probabilities are minimized, survival probabilities amongst dispersed offspring are independent, and successful dispersal is a stochastic event. One of the model predictions is that clonal populations should disperse a higher proportion of offspring as the total number produced increases, thus spreading risk and escaping local patch extinction. *P. repens* provides support for this prediction, since it follows exactly this strategy, but the model also applies to a range of other organisms such as insects with dispersal dimorphisms and plants with dimorphic fruits[74].

The evidence outlined above indicates that the mixed dispersal strategy employed by stream-dwelling plumatellids promotes the overall persistence of populations and spreads clonal genotypes by effecting: 1) the colonization of new substrata through the size-dependent increase in floatoblast production; and 2) the short-term exploitation of substrata colonized by floatoblasts through colony growth and local recruitment of sessoblasts. This work (and also that of Wöss[142]) provides support for impressions of earlier investigators that many phylactolaemates are opportunists, and that dispersal and unpredictable events are the most important factors in their population dynamics.

Clonal population structure in *Cristatella mucedo*

Recent investigations based on the amplification of polymorphic DNA using primers of arbitrary sequences (variously referred to as the RAPD assay or AP-PCR) have revealed that populations of *Cristatella mucedo* in southern England are highly clonal[106]. Clonal population structure was evident at each of three sites as illustrated by high pairwise similarity coefficients amongst putative clones, and although sample sizes were relatively small, all three populations were dominated by a particular clonal type (dominance ranged from 43% to 71% of the colonies sampled). Such clonal dominance appears to occur broadly, having been demonstrated in organisms as diverse as corals[5] and trees[18].

Cluster analysis grouped populations of *Cristatella mucedo* from more distant localities separately (Thames Valley and Norfolk), but even at the regional scale a high degree of relatedness amongst populations pertained. Thus similarity coefficients were very high both within and between the three *C. mucedo* populations. (The range in mean similarity coefficients for the three populations was: 0.9908–0.9936, and the overall mean similarity was 0.9819.) It is notable that similarity coefficients for aclonal, outcrossing taxa similarly characterized by the RAPD assay are substantially lower (e.g. similarity coefficients obtained for populations of two different species of grasshoppers ranged from 0.417–0.473 and 0.213 to 0.687: Chapco et al.[33]).

As the high similarity coefficients indicate, clonality within and amongst populations of *Cristatella mucedo* in southern England is not characterized by the presence of distinctly heterogeneous clonal types, but rather by the presence of closely related clonal replicates. Replication of clonal types occurs via colony fission and the production of statoblasts while the generation of very similar clonal types suggests that populations of *C. mucedo* in southern England may be virtually panmictic. Alternatively, similar selection pressures combined with considerable inbreeding and high clonality may mean that the rate of divergence between populations is extremely low, compared to the dispersal rate and/or that populations in southern England derive from a common source population which is itself highly clonal. Given the large population fluctuations observed it is possible that populations are repeatedly going extinct in many sites and are then recolonized from a source population.

Habitat subdivision and the associated potential for inbreeding will enhance clonality of local populations, and evidence for inbreeding in *Cristatella mucedo* has recently been obtained[67]. Comparison of RAPD fingerprints of parental colonies and their larvae provided evidence for the occurrence of outcrossing in five out of ten families analysed. However, even when outcrossing occurred, little genetic variation was generated. Genetic profiles of outcrossed larvae were very similar to those of their parent colony, and, with one exception, were represented by profiles of colonies previously characterized in the population[67, 106].

Evidence to date thus indicates that in southern England, *Cristatella mucedo* persists as a series of subdivided but closely related, clonal populations that engage in bouts of sexual reproduction that generate little genetic variation. These results indicate that dispersal is relatively widespread. On the other hand, as described earlier, there is limited evidence for local divergence and adaptation in *C. mucedo* populations[104]. These apparently contradictory observations may simply reflect insufficient genetic characterization of populations. Alternatively, or in addition, they may reflect a complex pattern in the history of dispersal and local adaptation. Dispersal to new habitats is most likely effected by waterfowl (statoblasts of *C. mucedo* are commonly attached via their hooked spines to feathers moulted in lakes: Okamura, pers. observ.) with highly resistant statoblasts conferring the potential for dispersal over great distances. Thus a pattern of both widespread geographic relatedness and local adaptation and divergence may reflect the propensity of waterfowl to visit particular sites. In this respect, phylactolaemates may be partially dispersal limited even on relatively local scales simply because waterfowl visit some sites regularly and others infrequently. Such dispersal limitation may be common in situations where organisms rely on animal vectors (e.g. seeds dispersed by fruit-eaters, insect pollination, and a variety of freshwater organisms). By contrast, dispersal effected in a more random fashion may result in a more straightforward negative relationship between genetic relatedness and geographic distance.

Future avenues of investigation

Despite the relative dearth of research on freshwater Bryozoa, we believe that this group offers unique and/or exceptional opportunities to investigate a number of fundamentally important ecological and evolutionary questions as discussed below. Subject areas are considered separately for convenience, but some degree of overlap is inevitable.

General ecological issues

Although a wide range of ecological issues have received some investigation, our basic knowledge of the ecology of phylactolaemates remains rudimentary and well behind that of comparable freshwater invertebrate taxa. Little is known about feeding or food supply, reproduction, the importance of predators and parasites in regulating population size, and the general significance of bryozoans in freshwater ecosystems. Almost nothing is known about the ecology and variation in life history of tropical forms. To date there are no detailed studies of competition in phylactolaemates, which is rather surprising given the long tradition of such studies on sessile marine invertebrates. Even less is known about entoprocts and freshwater gymnolaemates. Ecological investigations of phylactolaemates, gymnolaemates, entoprocts, sponges, and even sessile, colonial peritrichs and rotifers will provide a clearer picture of the ecology of sessile colonies in freshwater systems, which can be compared with the insights gained through the more extensive study of such forms in marine habitats (e.g. see review by Buss[27]). Only through such a comparative approach will we know the degree to which common vs unique ecological pressures confront organisms with similar life histories in diverse aquatic habitats.

Dispersal, local non-equilibrium, persistence and regional population structure

Freshwater habitats by their very nature are subdivided and populations of most species are linked by immigration and emigration. Such populations may conform to metapopulation or source-sink models[128]. In metapopulations, regional persistence depends on rates of colonization successfuly balancing rates of local extinction[107, 128]. A source-sink situation arises when colonists from a source population found unstable peripheral populations. Thus the source-sink and metapopulation models can be distinguished by uni- vs multidirectional gene flow. Both the models and empirical evidence to date suggest that regional stability in phylactolaemates is achieved by a dynamic equilibrium between colonization and extinction amongst a series of local sites. Yet very little is known about dispersal mechanisms, rates of dispersal and recruitment, levels of gene flow, and local extinction rates, and no data are available that can resolve whether a regional metapopulation structure or a source-sink situation obtains.

Karlson[71–73] and Karlson and Taylor[74] provide important insights about the significance of dimorphic statoblasts for population persistence. Inevitably, however, a number of questions remain. Do stream-dwelling plumatellids effect upstream dispersal that prevents eventual extinction through downstream transport of floatoblasts? What is the importance of occasional flooding in allowing gene flow to and from otherwise isolated sites? Are statoblast polymorphisms generally more adapted to effecting different degrees of dispersal in lentic habitats? What is the significance of dispersal through time effected by statoblasts, and how might polymorphism in hatching influence such temporal dispersal? With regard to the latter point, de Meester and de Jager[35] have found a significant genetic component in the hatching responses of *Daphnia magna* eggs, and Fell[40] describes variation in the timing of hatching by gemmules of freshwater sponges. Can stocks of statoblasts function in a manner analogous to seed banks[47] and resting egg banks of various aquatic zooplankters (e.g. see summary by Marcus et al.[83])? What is the significance of dispersal effected by larvae and the movement of gelatinous adult colonies? The restriction of movement to small colonies[109] suggests it plays a role in site selection. Does such movement correlate with reduced larval production and hence serve as a compensatory adaptation for infrequent bouts of sexual reproduction? Is movement of substrata an important means of dispersal as is indicated for some sessile, marine invertebrates[55]? Finally, what is the role of man in effecting introductions not only on local and regional scales (e.g. via muddy waders, fishermen's nets, plant introductions, etc.), but on global scales? Sporadic occurrences in remote places of some species (e.g. *Pectinatella magnifica* in Japan: Oda[99]) likely reflect introduction by humans.

The ecological viability of asexuality and the maintenance of sex

Given the two-fold cost of sex, a longstanding and important question in evolutionary ecology is what might account for the maintenance of sex. Although the question remains unresolved, a major contention is that the variation generated by sex is important for survival in the face of unpredictable environmental variation on both spatial and temporal scales[10,137]. In particular, natural enemies such as parasites are viewed to exert strong frequency dependent selection for rare genotypes and hence for the maintenance of sex[45]. Yet it seems that many populations of freshwater bryozoans may forego sex and are entirely clonal while others generate little variation through sex due to inbreeding. Similar patterns obtain for populations of other clonally propagating taxa ranging from colonial marine invertebrates[5,64] to terrestrial plants[124,125]. Are such populations thus doomed to extinction or can dispersal to new habitats allow clonal lineages to persist indefinitely? Recent simulation modelling[78] suggests that asexuality may persist when: 1) host population structure approximates a metapopulation; 2) hosts or parasites have high levels of dispersal; and 3) parasites disperse independently from their hosts. Since a metapopulation structure could obtain broadly in freshwater habitats and highly resistant stages offer great dispersal potential, the model may be particularly appropriate to asexuality in freshwater organisms. Since dispersal can occur in time and space, the role of statoblast dormancy in effecting temporal dispersal would merit some investigation. If sexuality is ultimately important, are some sexual populations 'hot spots' that generate significant levels of genetic variation and thereby allow for long term persistence? Are such populations associated with particular kinds of habitats?

The role of parasites in clonal populations

As freshwater bryozoans are infected by several known parasites a variety of predictions concerning the relationship between sex and parasites could be tested. For instance, is sex induced in parasitized populations? Do parasites differentially exploit the most common clonal type within habitats (i.e. are there host/parasite genotype interactions)? Do parasites represent inevitable agents of extinction in exclusively clonal populations? Does dispersal in time and/or space provide an escape from parasites? Are high levels of clonality in hosts correlated with reduced rates of recombination in parasites?

The importance of somatic mutation, cyclic clonality, and the lack of germ line sequestration

Accumulating evidence indicates that somatic mutation may introduce significant levels of genetic variation upon which selection can act in organisms with life cycles that entail high degrees of asexual proliferation (e.g. in clonal microorganisms[82], plants[124], *Daphnia*[9], aphids[12]). Given their high levels of clonality, what is the role of somatic mutation in the evolutionary ecology of freshwater bryozoans? Banta[9] pointed out long ago that clonal reproduction followed by mixis will increase the rate at which mutations are screened against a wide variety of potential genetic combinations. This is because mutations in a parthenogenetic lineage will come to be possessed by huge numbers of genetically identical individuals and because the effects of a given mutation are likely to vary depending on the particular complement of other genes with which it is associated (see also Silander's discussion[124] of facultative sexuality in vegetatively spreading plants). Such cyclic clonality will increase the chances of achieving genetic constitutions that are particularly favorable, and may endow cyclically clonal organisms with relatively rapid microevolutionary responses to changes in conditions[9,81]. The incorporation of clonal reproduction in numerous life histories[58] provides further demonstration of a population genetic advantage conferred by the expression of both modes of reproduction[17,50,53]. Freshwater bryozoans would seem to offer an ideal system for studying how clonal reproduction alternated with bouts of sex influences rates of local adaptation in cyclically clonal forms as local populations vary in the degree to which sexual and asexual reproductive modes are expressed.

For modular colonies, however, the potential for extended interaction of pre- and post-mutational tissues could lead to somatic cell parasitism[26,28] thereby entailing intergenomic conflict within colonies in a manner functionally analogous to fusion amongst non-clonemates. Such intergenomic conflict could then influence the rates at which beneficial and negative somatic mutations are fixed in populations.

Fission, fusion and chimerism

Why do some gelatinous freshwater bryozoan species undergo colony fission? It is notable that species that undergo fission are also capable of movement.

Does fission minimize the cost of movement for a given biomass? Or does fission serve to reduce feeding interference and thus maximize energetic gains as is indicated for some soft corals[84] and didemnid ascidians[119,127].

The frequent occurrence of two different karyotypes in colonies newly-hatched from statoblasts suggests that permanent chimerism may be asexually maintained in phylactolaemates[7]. Such chimerism could arise through fusion between non-clonemates or through karyotypic rearrangements within distinct cell lines[7] (the ectoderm and peritoneum remain separate during both budding and statoblast formation). Little, however, is known of the significance and extent of such chimerism. Thus, what is its frequency in the field? What is the importance of fusion of colonies hatched from various statoblast types? Does fusion only occur amongst colonies that have recently emerged from statoblasts or can larger colonies fuse? Can colonies derived from larvae fuse? Is the primary advantage of fusion the increase in fitness that accrues with increased colony size or is it the case that chimerism provides a new more complex set of physiological properties that benefit both genotypes by increasing phenotypic plasticity at the chimera level[44]? If so, can fusion be important in generating general-purpose genotypes (see next section)? Alternatively, if bryozoans lack a self/non-self recognition system, is fusion simply unavoidable, and is there evidence for somatic cell parasitism in chimeric colonies?

Clonal adaptation and the ecology of clonal types

Are clones adapted for particular ecological conditions and are there general-purpose genotypes? What is the extent of ecological divergence amongst clones and does clonal displacement occur (see review by Carvalho[30])? Evidence suggests clonal adaptation may be common in taxa ranging from freshwater crustaceans[29,31] and marine anthozoans[4] to flowering plants[135]. For some groups, there is evidence that general-purpose genotypes are exclusively parthenogenetic forms that maintain a coadapted genome and so persist in harsh environmental conditions such as high latitudes[8,32,80]. Does dispersal and gene flow of such forms represent an important source of material for both the short- and long-term maintenance of populations on regional scales? If clones are well-adapted to particular ecological conditions, what is their evolutionary significance? Do clones ultimately senesce or can adaptive somatic mutation and repair preclude aging? (See Silander[124] for discussion of senescence in clonal plants.)

The application of new techniques

Recent advances in analytical molecular approaches provide a novel and powerful set of tools which can help to tackle a number of the questions posed above. Demographic and life history questions in modular organisms are generally difficult to address because partial mortality, fusion and fission distort any simple relationship between age and size[59]. Molecular methods allow clones to be identified with a reasonable degree of certainty, thus enabling the researcher to estimate clonal population structure, relatedness, host/parasite genotype interactions, gene flow, population divergence, etc. The method employed will depend on the question being asked as different techniques can provide very different information. A high degree of resolution is required in the identification of clones or determining parentage and is best achieved by analysis of multilocus minisatellite fingerprints, microsatellites, or RAPD-generated fingerprints. Allele frequencies are better estimated by protein electrophoresis, single-locus minisatellites, or microsatellites as not all molecular methods are capable of distinguishing codominant markers. For questions where less resolution is required (e.g. in studying divergence amongst populations or species), DNA hybridization or analysis of ribosomal RNA or mitochondrial DNA might be more appropriate. A thorough examination of the techniques available is beyond the scope of this paper; we refer the reader to Avise[3] for an up-to-date treatment of the subject.

The importance of systematics

The taxonomy of phylactolaemates is in great need of revision. Species discrimination relies heavily on statoblast morphology since colonies themselves often show a high degree of environmentally-induced phenotypic plasticity. However, it is evident that statoblasts can vary in dimensions depending on habitat and rearing conditions[104,132,147], and numerous researchers have questioned the reliability of statoblast surface texture for taxonomic purposes (see review in Wood and Backus[147]). In addition, the apparent rarity of sex and consequent high degree of clonality in many phylactolaemate populations provide further complications to traditional taxonomic approaches if clonal lineages persist, diverge, and occasionally hybridize. Potter's research[111] suggests that *Cristatella mucedo* in North America has two distinct genome sizes, thus there may be two species that are not easily distinguishable morphologically. Backus and Mukai[7] have documented extensive chromosomal heteromorphism that may indicate hybridization amongst different clonal lineages in *Pectinatella gelatinosa*.

Since an adequate taxonomy is fundamental to further study of any group, and in view of the above-mentioned problems, current taxonomies should be reexamined using other characters (the *Plumatella* complex is in particular need of revision). Molecular approaches should provide a powerful means of resolving degrees of divergence and identifying species-level differences.

Endnote

In anticipation that the reader may yet draw the conclusion that freshwater bryozoans are a relatively obscure and unusual group, and to counterbalance our introductory 19th century quotation with a modern one we close by quoting John Harper[48]:

> "*Molecular growth, the rarity of senescence, curious reproductive schedules, the ability of a genet to function in bits, the absence of segregated germ plasm, and the effects that branching structure have on the capture of resources – all set modular organisms apart from those with unitary structure. The same set of properties brings most of the plant kingdom and a neglected part of the animal kingdom [see Hughes and Cancino*[58] *for review of the high incidence of clonality in the animal kingdom] into a common category for generalization about life-cycle biology and evolution. Moreover, it is in the nature of modular organisms that they provide exquisite experimental tools for the field and laboratory study of fundamental biological problems. It is odd that so much of the study of ecology and evolution has been based on the behavior of unitary ogranisms.*"

Acknowledgements. We wish to thank P. D. Taylor for cheerfully helping to locate and provide reference material, and P. M. Hammond, R. N. Hughes, C. Little, J. S. Ryland, T. Städler, and T. S. Wood for constructive comments on the manuscript.

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