Lessons in modularity: the evolutionary ecology of colonial invertebrates

ROGER N. HUGHES

School of Biological Sciences, University of Wales, Bangor, Gwynedd, LL57 2UW, U.K.
E-mail: r.n.hughes@bangor.ac.uk

SUMMARY: Benthic colonial invertebrates share with higher plants a modular construction and a sessile adult life. Both types of organism show parallel evolutionary responses to common selective forces, but in contrast to the long-established focus on plants, comparable study of colonial invertebrates has developed relatively recently, largely owing to the application of new techniques in image processing and molecular biology. Species whose life cycles are readily completed under laboratory conditions and whose colonies are easily propagated from cuttings provide powerful models for experimentally investigating fundamental evolutionary problems, including metabolic allometry, the manifestation of ageing and the origin of allorecognition systems. Free of the confounding influences of behavioural manipulation and costs of copulation, colonial invertebrates whose water-borne sperm fertilize retained eggs lend themselves well to the experimental study of cryptic female choice, sperm competition and sexual conflict. In these respects, it will be productive to adopt and extend theoretical frameworks developed for flowering plants to guide experimental investigation of modular animals. Since mate choice occurs at the cellular level in modular animals, reproductive isolation is uncorrelated with morphology and cryptic speciation is likely to be widespread.

Keywords: ageing, allorecognition, colonial architecture, cryptic female choice, metabolic allometry, sex allocation.

RESUMEN: Lecciones en modularidad: la ecología evolutiva de invertebrados coloniales. – Los invertebrados coloniales bentónicos comparten con las plantas vasculares una construcción modular y una vida adulta sésil. Ambos tipos de organismo muestran respuestas evolutivas paralelas a fuerzas selectivas comunes, pero en contraste a la atención establecida desde hace tiempo sobre las plantas, estudios comparables realizados sobre invertebrados coloniales se han desarrollado en tiempos relativamente recientes, debido principalmente a la aplicación de nuevas técnicas de proceso de imagen y biología molecular. Especies cuyos ciclos de vida pueden ser completados en condiciones de laboratorio y cuyas colonias se propagan facilmente a partir de cortes proporcionan modelos potentes para investigar experimentalmente problemas fundamentales evolutivos, incluyendo alometría metabólica, la manifestación del envejecimiento y el origen de sistemas de alorreconocimiento. Libre de las influencias que pueden inducir a confusión de la manipulación del comportamiento y de los costes de cópula, los invertebrados coloniales cuyo esperma, transportado por el agua, fertiliza huevos retenidos, constituyen adecuados organismos experimentales para el estudio de la selección críptica por parte de las hembras, competéncias espermática y conflicto sexual. Respecto a estos temas, será productivo adoptar y extender marcos teóricos desarrollados para plantas con flores para guiar investigación experimental de animales modulares. Puesto que la elección de pareja tiene lugar a nivel celular en animales modulares, el aislamiento reproductor no está correlacionado con la morfología, con lo que la especiación críptica debe ser amplia.

Palabras clave: envejecimiento, aloreconocimiento, arquitectura colonial, elección críptica, alometría metabólica, alocación de sexo.

INTRODUCTION

The architectural resemblance between benthic colonial invertebrates and rooted higher plants once led zoologists, e.g. Johnston (1847), to use the term zoophyte for "…any one of numerous species of invertebrate animals which more or less resemble plants in appearance, or mode of growth, as the

corals, gorgonians, sea anemones, hydroids, bryozoans, sponges, etc….” (Webster's Dictionary, 1913). From perspectives largely developed by Harper (1977), we now recognize that the similarity of form between zoophytes and plants is a consequence of modularity, whereby common challenges of permanent fixture to the substratum are met. A strictly sessile life requires environmental pressures and risks to be accommodated by adaptive growth, containment of damage and regeneration of lost parts. Modularity facilitates such processes, but also has other biologically important corollaries including the decoupling of aggregate body size from the functionally constrained dimensions of organ systems, partial relaxation of metabolic allometry and enhanced potential for clonal reproduction (Hughes, 1989). Sessile animals and plants face common problems associated with mating: how to achieve fertilization, exercise mate-choice or optimize sex allocation (Charnov, 1982). Adult behavioral responses are denied, apart perhaps from chemical induction of spawning, and much depends on processes occurring at the cellular level, with implications concerning the evolution of allorecognition systems.

Physical convenience has, until recently, allowed botanists to surpass zoologists in theoretical and experimental investigation of modularity. Image-processing technology that facilitates non-destructive morphometric measurement in the laboratory and field, and the development of molecular markers that can be used for ascertaining clonal identity and sexual parentage, are however accelerating the study of modular animals. Because modular colonial invertebrates can be propagated from cuttings, they offer excellent material for experimental work in the laboratory and field. Consequently, fundamental biological problems are being studied using modular invertebrates as models and selected elements of progress are summarized below (population processes, population genetics and colonial resource allocation are not included, but are reviewed by Karlson (2002), Okamura (2002) and Forbes (2002) respectively). Although attention will be confined to sessile forms, it is appropriate here to acknowledge the pioneering work of Mackie (1963, 1986) on the implications of modularity in motile, pelagic, colonial invertebrates.

COLONIAL ARCHITECTURE

Diverse forms can be generated by assembling a limited range of modules in different ways. Such architectural flexibility is the key to adaptive growth in modular colonies, reflecting not only taxon-specific assembly rules but also intra-colonial modification to local conditions. Astogeny, the process and pattern of modular iteration to form a colony, as distinct from ontogeny, the development of a component module (Pachut et al., 1991), has long been the subject of descriptive modeling. First-generation models treated modular iteration as a simple branching process, in which colonial architecture could be specified by the budding angle and linear growth between branching events. Simulation models fell into three categories (Bell, 1986): 'blind' models assumed fixed parameters controlling astogeny (Cheetham and Hayek, 1983; Cheetham et al., 1980, 1981), 'sighted' models allowed parameters to change in response to proximity of neighbouring branches (Gardiner and Taylor, 1982; McKinney and Raup, 1982) or to environmental factors (Graus and Macintyre, 1976), while 'self-regulatory' models incorporated endogenous, size-dependent changes in parameter values (Braverman and Schrandt, 1965). Second-generation models, reviewed in depth by Lasker and Sánchez (2002), have variously incorporated fractal geometry, allometric scaling and diffusion-limitation theory to simulate patterns of astogeny. Using gorgonians as a model system, Lasker and co-workers have accomplished what is currently the most incisive experimental and theoretical study of ontogeny and astogeny in a modular animal. Typical of modular invertebrates, gorgonian colonies obey determinate growth, ceasing to increase beyond a characteristic size (Kim and Lasker, 1998). To simulate this self-limitation, Lasker et al. (2003) found it useful to envisage two levels of modularity: the polyp and the branch. Each level undergoes its own ontogeny and astogeny, which graphical modeling and phylogenetic contrasts suggest are independent between levels (Sánchez and Lasker, 2003) and which is further justified by evidence of physiological compartmentalization, discussed under allometry, below. Rather than bifurcating, as assumed by many earlier models above, 'mother' branches produce 'daughter' branches subapically, at characteristically spaced 'internodes'. Daughter branches are themselves destined to become the next generation of mother branches. Colonial growth may be regarded as a process of 'self-organized criticality' in which the ratio of total branches (daughter plus mother) to mother branches per generation is held constant at a value that could, for example, represent the excess

resource-gathering capacity over expenditure necessary to trigger more branching (Sánchez *et al.*, 2004). General allometries will cause resource surplus to decline until branching is no longer triggered, setting an upper limit to colony size. For a given ratio of total branches to mother branches, colony form and size may also depend on growth rate through heterochrony (Sánchez *et al.*, 2004). This process of evolutionary change in the relative timing of developmental events (Smith, 2003) yields particularly well to experimental study in non-branching hydroids (Blackstone and Yund, 1989; Blackstone and Buss, 1993). Of course, any intrinsic process of growth limitation, such as discussed above, may be forestalled by external forces such as storms and tidal currents that cause mechanical failure of colonies at sizes below their potential maxima, indeed this may be the norm for certain species (Coma *et al.*, 2004).

Incorporation of threshold parameters, as in the previous type of model, implies the interaction of endogenous and exogenous factors controlling successive levels of ontogeny and astogeny. Although exogenous control has been widely studied, e.g. the influence of temperature and food supply on budding rate and sexual development of bryozoan colonies (Hunter and Hughes, 1995), less attention has been paid to the technologically more challenging endogenous control, notwithstanding the pioneering studies by Braverman and Schrandt (1965), Blackstone (1997,1999) and Buss (2001). Yet characterizing endogenous controlling mechanisms and their interaction with exogenous factors is crucial for advancing beyond the scope of previous, essentially descriptive, models of astogeny. In this vein, Blackstone *et al.* (2004) have applied in vivo fluorescence microscopy, showing that metabolic signals, emanating from mitochondria at polyp-stolon junctions, allow hydroid colonies to grow adaptively by increasing the frequency of polyp initiation in food-rich areas and decreasing this frequency in poorer areas. An exciting challenge will be to link endogenous signaling mechanisms to the expression of developmental genes (Buss, 2001). Elucidating the operation of developmental gene families in basal taxa such as hydroids is of fundamental interest, because the same gene families have shaped metazoan evolution since the Precambrian (Conway-Morris, 1998). Coloniality, however, is a derived state (Rosen, 1979) and the role of ancestral developmental genes in astogeny remains to be determined.

ALLOMETRY

Complete independence of modules throughout astogeny could in principle avoid functional allometry at the colonial level. Modules, however, usually remain physiologically interconnected and, whether interconnected or not, may interfere with each other's resource-gathering activity, imposing allometric constraint on the colonial energy budget (Winston, 1979; Cheetham and Hyek, 1983; Okamura, 1984; McFadden, 1986; Grünbaum, 1995; Kim and Lasker, 1998; Okamura and Ekman, 1999). Translocation of resources among interconnected modules (Murdoch, 1978; Gladfelter, 1983; Best and Thorpe, 1985; Blackstone and Buss, 1993; Miles *et al.*, 1995; Taylor, 1997; Oren *et al.*, 1997; Gateño *et al.*, 1998) is likely to follow a gradient from source to sink (Harvell and Helling, 1993; Miles *et al.*, 1995; Oren *et al.*, 1997). Sources are modules whose resource capture exceeds their own demand and sinks are modules in negative balance caused, for example, by ontogeny, budding, sexual reproduction or regeneration (Miles *et al.*, 1995; Oren *et al.*, 1997; Hughes *et al.*, 2002; Fine and Loya, 2003). Limitations of diffusion, circulation, or other modes of transport, may constrain translocation distance, potentially introducing allometry (Sebens, 1979) and encouraging partial compartmentalization into blocks within which source-to-sink coupling remains effective (Lasker and Sánchez, 2002). Such compartmentalization affords physiological justification for the hierarchical levels of modularity proposed by Lasker *et al.* (2003), discussed above under colonial architecture.

A celebrated physiological allometry is the -0.25 'law' describing the relationship between specific metabolic rate and body mass in Metazoa (Bertalanffy, 1960; Hemmingsen, 1961; Zeuthen, 1970). Despite its fundamental nature, there lacks a firm theoretical understanding of metabolic allometry (Peters, 1983) and although negative allometry undoubtedly applies to individual polyps or zooids as it does to unitary animals, there is little basis for predicting its manifestation in aggregations of such primary modules. Nevertheless, if primary modules attain physiological independence during astogeny, colonial metabolic rate should equal the product of the number of modules and the characteristic metabolic rate per module. The latter will obey negative allometry, but specific metabolic rate of a colony will remain constant throughout astogeny and equal to that of its primary modules. On the other hand, if

modules remain physiologically interdependent during astogeny, metabolic allometry may apply to the colony as to the module. Evidence of translocation within colonies of cnidarians and bryozoans, discussed above, suggests that complete physiological independence among primary modules is unlikely to arise. Degree of physiological interdependence, however, may vary in as yet unknown ways according to colonial architecture and modular polymorphism. Two-dimensional laminar colonies with monomorphic modules might be expected to exhibit the least physiological interdependency and therefore to offer the most likely candidates for metabolic isometry. Hughes and Hughes (1985) demonstrated metabolic isometry in colonies of the bryozoan *Electra pilosa*, although Muñoz and Cancino (1989) found that metabolic isometry during periods of modular quiescence changed to allometry during periods of feeding activity in *Cauloramphus spiniferum*. Peck and Barnes (2004), however, reported metabolic isometry that was independent of zooidal activity in *Isosecuriflustra tenuis* and *Kymella polaris*. In contrast to these two laminar species, the bush-like *Camptoplites bicornis* showed metabolic allometry (Peck and Barnes, 2004), suggesting greater physiological interdependence of modules in colonies with three-dimensional architecture. Further understanding of such differences in metabolic allometry associated with colonial architecture will require quantification of physiological integration, perhaps using in vivo fluorescent markers and confocal microscopy to complement radio-labeling of metabolites, together with the characterization of interference among modules in their capacity to capture resources.

AGEING

The classical concept of ageing stems from Weismann's (1885) proposal that the metazoan body is a disposable vehicle for the indefinite hereditary perpetuation of 'germ plasm' or 'germ-line'. To protect and nurture the germ line, the soma performs biological functions requiring specialized differentiation of its component cells, which irreversibly lose their own reproductive potential. Ecological factors acting against a background of phylogenetic constraints impose an optimum somatic life span that maximizes hereditary transmission of the germ-line (Stearns, 1992). The soma becomes evolutionarily irrelevant beyond the optimum life span and herita-

ble, often dysfunctional, characters ignored by natural selection begin to express themselves as ageing (Medawar, 1952; Hamilton, 1966). All animals that ontogenetically segregate germ-line from soma, i.e. sexually reproducing unitary animals, will age if they survive long enough. Certain taxa, however, do not segregate cell lineages in this way but maintain supplies of primordial stem cells that can differentiate into specialized somatic cells or gametes as required (Buss, 1987). A somatic reservoir of omnipotent primordial cells promotes regenerative capacity and hence reproduction by fragmentation, fission or budding (Hughes, 1989). In contrast to the progeny of sexual reproduction derived directly from the ageless germ-line, the progeny of asexual reproduction partially inherit the parental condition. It might be expected, therefore, that asexually reproducing unitary animals should be immune to ageing (Bell, 1984) and there is good evidence of this in hydra (Martínez, 2002).

But how do the above considerations apply to colonial invertebrates? Astogeny proceeds by a form of asexual reproduction in which successive generations of modules remain attached within a more or less integrated colony. It is abundantly evident that colonial growth is ultimately limited by allometric constraints (Sebens, 1979; Lasker and Sánchez, 2002). If the colony does not divide into daughter colonies or cannot rejuvenate itself by shrinkage and regeneration, it becomes analogous to an aclonal animal and likewise should undergo senescence. Colonial fragmentation and regeneration, however, are characteristic of numerous taxa (Jackson and Coates, 1986; Hughes and Jackson, 1980), raising the possibility of escape from senescence (Gardner and Mangel, 1997). Martínez (2002) argues that since colonial taxa probably have aclonal ancestry, modules are likely to retain phylogenetic susceptibility to senescence, but that in order to service the growing colony, their life span should extend beyond the ancestral limit. Cycles of modular degeneration-regeneration typical of bryozoans, certain hydroids, compound ascidians and perhaps other taxa may be a secondarily evolved means of matching modular life span to the needs of the colony (Martínez, 2002). For example, feeding zooids of the epiphytic bryozoan *Celleporella hyalina* function only for 3-4 weeks before degenerating (Hughes and Cancino, 1987a), a period presumably corresponding to the ancestral, unitary life span. Within 1-2 weeks of degenerating, zooids regenerate from primordial cells and by undergoing several

cycles of degeneration-regeneration zooids collectively support the colony during its normal existence of 3-9 months before destruction by disintegration of the substratum or overgrowth by space competitors (Cancino, 1986). Moreover, colonies protected from natural destruction seem potentially immortal: clones established from the larval progeny of wild colonies have been maintained for 9 years in laboratory culture, yet show no sign of losing fitness (personal observation). Extension beyond the natural life span depends on two factors: the degenerative-regenerative cycling of polyps described above and the artificial propagation of colonies, whereby size-dependent constraints on colonial function (Cancino and Hughes, 1987b; Lasker and Sánchez, 2002) are circumvented, as in horticulture, by repeatedly taking cuttings. Under natural circumstances however, colonial senescence prevails in most taxa (Karlson, 2002).

ALLORECOGNITION

Contact between growing edges of colonies may be intra- or inter-clonal. Intra-clonal (isogeneic) contact occurs when a previously subdivided colony re-aggregates through growth (Hughes and Jackson, 1980) or when edges meet as a colony wraps itself around a three-dimensional substratum (Feldgarden and Yund, 1992). Since they involve genetically identical tissues, intra-clonal contacts should be histocompatible, resulting in fusion as long as physical circumstances, such as a favourable contact angle (Jackson, 1979; Karande and Swami, 1988), will allow. Inter-clonal (allogeneic) contact occurs when conspecific larvae settle sufficiently close together for resulting colonies to grow into contact. Unless larvae are themselves the product of amictic processes conserving the parental genome (Stoddart, 1983; Ayre and Resing, 1986; Ayre and Miller, 2004), neighbouring colonies will be genetically distinct and their fusion will generate a chimera. Although fusion might confer space-competitive and reproductive advantages through increased colony size (Hughes and Jackson, 1985; Wulff, 1986), chimera formation runs the risk of cell-lineage competition, in which the somatic and/or germ cell lineage of one partner replaces that of the other (Buss, 1982, 1987; Stoner et al., 1999). Loss of inclusive fitness (Hamilton, 1964) through cell-lineage competition should be relatively slight among siblings, increasing exponentially with decreasing

relatedness. It might be expected, therefore, that genetic systems should have evolved which discourage fusion as kinship decreases (Grosberg, 1988). Such expectation is reasonable, however, only if kin commonly grow into contact. Philopatric settlement of larval kin is documented for the cnidarian *Hydractinia symbiolongicarpus* (Hart and Grosberg, 1999), the bryozoan *Bugula neritina* (Keough, 1984) and the ascidian *Botryllus schlosseri* (Grosberg and Quinn, 1986). As predicted, histocompatibility measured by fusion frequency is positively correlated with kinship in the above species. Application of Mendelian genetics to the results of fusion trials among pedigree offspring has shown that histocompatibility in *B. schlosseri* is controlled by a single, highly polymorphic fusibility/histocompatibility (Fu/HC) locus, often with >100 alleles per population (Sabaddin, 1982; Grosberg and Quinn, 1986; Rinkevich et al., 1995). Fusion requires only that at least one Fu/HC allele be shared. In accordance with Mendelian probabilities, such 'partial matching' becomes exponentially rarer within successively reduced levels of kinship. Although fusion is further influenced by heritable position within a competitive hierarchy (Rinkevich et al., 1993; Stoner et al., 1999; see also Hughes, 2002 for a review), it seems reasonable to suppose that the Fu/HC locus evolved to confine cell-lineage competition to kin (Burnet, 1971; Buss, 1982). Similar argument may apply to the genetic control of histocompatibility in *H. symbiolongicarpus*, which Mokadi and Buss (1996) suggest is based on a single, highly polymorphic locus as in *B. schlosseri*, but which perhaps is based on lesser polymorphism among several loci (Grosberg et al., 1996).

The extent of kin-recognition and philopatric settlement of kin among benthic colonial organisms is unknown and indeed may not be typical: further work on this is urgently required. The bryozoan *Celleporella hyalina* settles randomly and kin-recognition is unlikely to be of evolutionary significance in this species (Hughes et al., 2004). Nevertheless, fusion frequency in *C. hyalina* follows a qualitatively similar relationship to kinship as occurs in *B. schlosseri* and *H. symbiolongicarpus*. Rather than confining cell-lineage competition to kin, genetic control of histocompatibility in species such as *C. hyalina* that lack kin-recognition may have evolved to minimize cell-lineage competition by differentiating self from non-self. Confining fusion to self (complete matching) would eliminate cell-lineage competition altogether, but Mendelian

genetics introduce error, expressed in fusion compatibility among a proportion of kin, the cost of which in terms of inclusive fitness decreases in parallel with decreasing relatedness (Feldgarden and Yund, 1992). An alternative but untestable hypothesis is that partial matching in species such as *C. hyalina* is a phylogenetic legacy from ancestral populations in which kin recognition was important. Although only self-fusion has been recorded in certain sponges and corals (Neigel and Avise, 1983a,b; Wulff, 1986), further investigation is required to exclude the possibility of partial matching and hence fusibility among kin in such species.

Evolutionary models such as the above assume that there is a cost to allogeneic fusion, most likely in terms of cell-lineage competition. In the absence of such competition, discrimination against allogeneic fusion is not predicted. Accordingly perhaps, allogeneic fusion occurs frequently among unrelated colonies of the ascidian *Diplosoma listerianum* (Bishop and Sommerfeldt, 1999). Zooids *of D. listerianum* retain physical independence, shifting and mingling within the growing chimera. Lacking vascular interconnections, there is no apparent opportunity for cell-lineage competition. Such modular independence, however, is probably exceptional among colonial invertebrates.

MATING COMPATIBILITY AND CRYPTIC FEMALE CHOICE

Colonial invertebrates mate by releasing waterborne sperm that fertilize water-borne eggs in broadcasters or retained eggs in spermcasters (Pemberton *et al.,* 2003). Lacking opportunity for morphological or behavioural signaling between adults, sessile invertebrates rely on cellular compatibility mechanisms of mate selection. Although as yet undocumented for any broadcasting colonial invertebrate, mate choice must be achieved through intergametic (haploid-haploid) molecular processes such as the bindin system that controls the attachment of sperm to egg surface in sea urchins (Zigler and Lessios, 2001). Intergametic mate choice might also occur in some spermcasters, but in *D. listerianum*, rejected sperm are phagocytosed in the lower regions of the oviduct, well away from stored, unfertilized eggs. Mating incompatibility in *D. listerianum* therefore involves interaction between haploid sperm and diploid oviducal tissue, analogous to the pollen-style interaction of flowering plants (Bishop, 1996) and

comparable to 'cryptic female choice' in motile animals (Birkhead, 1998). The analogy between spermcasting modular invertebrates and flowering plants may extend even further. Accumulation of sperm is achieved by multiple receptor modules per colony just as pollen is accumulated by multiple pistils per plant (Bernasconi *et al.,* 2004). Haploid gene expression making some sperm more competitive than others is normally suppressed in unitary animals, thereby preventing selfish genes from reducing the number of viable sperm in the ejaculate. By contrast, haploid gene expression is not suppressed in pollen. Individual pollen grains are scattered widely and pistils usually become loaded from several sources. In such a random mixture, haploid gene expression may play an important role in the outcome of competition among donors. Additionally, deleterious mutations are purged when expressed in haploid pollen. Similar principles should apply to spermcasting modular animals and the possibility of haploid gene expression during any interaction between captured sperm and the tissues of recipient colonies deserves concerted investigation.

In routinely outbreeding populations, mating among close kin is liable to invoke inbreeding depression, whence a negative relationship between sexual reproductive compatibility and kinship is to be expected. Such a negative relationship is known from pedigree trials in *Botryllus primigenus* (Oka, 1970), *H. symbiolongicarpus* (Grosberg and Hart, 2000) and *C. hyalina* (Hoare and Hughes, 2001). The reciprocity between mating and fusion compatibility is striking and perhaps suggests a common genetic system, or linked systems, controlling mating and fusion in opposite directions with respect to coancestry. The balance of albeit scanty evidence, however, favours the alternative hypothesis of independent genetic control of mating and fusion compatibility. An ingenious analysis of fusion frequencies among offspring of mated colonies sharing a single allorecognition allele led Grosberg and Hart (2000) to conclude that allorecognition loci do not control mating compatibility in *B. schlosseri*, nor in *H. symbiolongicarpus*. Indirect evidence for common genetic control of fusion and mating compatibility in *C. hyalina* is equivocal, since whereas rejection frequency increases from 0% among sibs to 50% among half-sibs, mating compatibility, expressed as embryo production, increases from 28% among sibs to 38 % among half sibs (Hoare and Hughes, 2001). Furthermore, allosperm received from sibs has no effect on intra-colonial

sex ratio, whereas allosperm from half sibs increases femaleness equally to that from unrelated partners (Hughes *et al.,* 2002). Nevertheless, as a possible explanation for kin fusion in *C. hyalina,* Hughes *et al.* (2004) suggest that the genetic system controlling allorecognition perhaps originally evolved in the context of mating compatibility, serving as a mechanism for avoiding inbreeding, later being coopted to govern fusibility under reciprocal rules of compatibility. The genetics and genomics of mating and fusion compatibility in colonial invertebrates deserve concerted study, since they may reveal the early evolutionary history of allorecognition, including the origin of the vertebrate MHC (Oka, 1970; Burnet 1971; Weissman *et al.,* 1990).

Mate choice in *C. hyalina* appears to be concerned solely with avoiding inbreeding depression, since there is no evidence of selective mating among unrelated colonies (Hughes *et al.,* 2003). *D. listerianum* on the other hand discriminates not only against autosperm but also among unrelated allosperm sources (Bishop *et al.,* 1996; Pemberton *et al.,* 2003; Pemberton *et al.,* 2004). Fitness advantages of mate choice beyond kinship are unknown in colonial invertebrates, but might include heterozygous advantage (Saavedra and Guerra, 1996), dominance in cell-lineage competition (Stoner *et al.,* 1999) and in spermcasters such as *D. listerianum,* female control of somatic-gametic investment (Pemberton *et al.,* 2004). Rewarding possibilities for studying the evolutionary implications of cryptic mate choice (Cordoba-Aguilar and Contreras-Garduno, 2003) are afforded by the experimental breeding of pedigree clones of colonial invertebrates and the development of suitable genetic markers (Hoare *et al.,* 1998; Craig *et al.,* 2001; Maclean *et al.,* 2004; Pemberton *et al.,* 2004).

Any mating system that relies on the dispersal of water-borne sperm must cope with vagaries of turbulence, advection, dilution and limited sperm longevity (Grosberg, 1991; Levitan and Petersen, 1995). Spermcast mating may be an evolutionary solution to such problems common to diverse sessile invertebrates, which as shown in *D. listerianum* and *C. hyalina,* may be able to take up water-borne sperm entrained in the feeding current and store it for considerable periods (Bishop, 1998; Pemberton *et al.,* 2004). Sperm accumulated in this way are likely to originate from multiple donors, with consequent manifestations of sperm competition and female choice. Simplicity of the spermcast mating system offers great potential for investigating the genetic benefits of multiple paternity, since there are none of the distracting costs or benefits of copulation with multiple partners that may additionally contribute to fitness in motile animals (Pemberton *et al.,* 2003). As with any other system of internal fertilization, however, spermcast mating exposes males to challenges at the gametic level, such as frequency-dependent fertilization success among sperm of mixed origin and order-dependent success of sequentially stored sperm (Parker, 1990; Bernasconi *et al.,* 2004). Laboratory mating trials with *D. listerianum* have shown that colonies represented at lower frequency in simultaneously administered sperm mixtures achieve disproportionately greater mating success. This 'rare male effect' remains unexplained, but perhaps could be due to changes in mating compatibility during the individual ontogeny of female modules. Such non-genetic female choice operating at the modular level might promote fitness by increasing genetic diversity within sibships (Pemberton *et al.,* 2003). In contrast to copulating animals, in which sperm displacement or removal confers greater paternity on the last to mate (P_2 sperm precedence), earlier mating confers paternity advantage (P1 precedence) in *D. listerianum* (Bishop *et al.,* 2000) and in *C. hyalina* (Manríquez, 1999). Presumably, P_1 precedence results from queuing, although the physical basis of this will remain obscure until the mechanisms of sperm storage in such species are better known.

CRYPTIC SPECIATION

Cryptic or sibling species (Mayr, 1942) are reproductively isolated yet are impossible, or at best extremely difficult, to distinguish from one another morphologically. Mate recognition at the cellular level in colonial invertebrates, just as in free-spawning unitary species (Palumbi, 1992), obviates selection for morphological distinction of mating types, increasing the probability of cryptic speciation (Knowlton, 1993). Genetic markers have revealed cryptic species complexes in the bryozoan genera *Alcyonidium* (Thorpe *et al.,* 1998) and *Bugula* (Mackie *et al.,* 2002), but this probably is just the tip of an iceberg involving all major taxa of colonial invertebrate. Molecular phylogeny combined with comparative morphology and breeding tests has resolved the 'cosmopolitan' bryozoan *C. hyalina* into at least 20 clades that originated in bursts of Miocene and Pleistocene radiation interspersed by morphological stasis

(Gómez *et al.,* in preparation). Although multivariate analysis of morphological characters used in classical taxonomy of the genus can separate most, though not all, major clades within the *C. hyalina* complex, differences are too slight for practical identification from morphology alone. Nevertheless, breeding tests confirm that molecular clades are reproductively incompatible and so represent valid biological species (Mayr, 1942). Thus if *C. hyalina* is representative, conventional taxonomy has underestimated the biodiversity of sessile colonial invertebrates and hence a considerable proportion of the marine biota by at least an order of magnitude.

The evolution of mating incompatibility and hence speciation in colonial invertebrates presumably is driven by similar selection forces to those bearing upon flowering plants, though perhaps under differential phylogenetic constraint. In plants, mating incompatibility seems likely to be an expression of pleiotropic effects of genetic systems that evolved to limit self fertilization (Levin, 1978; Palumbi, 1993). Application of genomics to flowering plants and modular animals may illuminate the above problem by identifying key gene expression during interactions between male gametes and female gametes or tissues and indeed may reveal principles transcending differences between kingdoms (Bernasconi *et al.,* 2004).

SEX ALLOCATION

Hermaphroditism (monoecy) is widespread, though by no means universal, among colonial invertebrates just as it is among higher plants, suggesting parallel adaptation to sessile adult life, perhaps through maximizing mating opportunity (Ghiselin, 1969). Investment in male and female functions, however, need not be equal and circumstances promoting biased sex allocation can be predicted by evolutionarily stable strategy models based on 'gain curves' (Charnov, 1982). The male gain curve describes changes in fitness gained through the male function as allocation to maleness increases and may be linear or decelerating, depending on factors such as local competition for mates. Shape of the female gain curve is influenced by factors such as competition for resources among progeny.

Scope for assessing mate availability is limited among sessile compared with motile animals. A potentially important signal of mating opportunity, however, could be the uptake of allosperm. *C.*

hyalina has morphologically distinct male and female zooids, the males being simple sperm containers and the females of a more complex design for placental brooding. These sexual zooids subsist entirely on metabolites translocated from adjacent feeding zooids, but whereas investment in males can be repaid almost immediately by the production of sperm, investment in females can be repaid only when larvae are released after protracted brooding. Hence it is worth a colony investing in females only when fertilization is assured and, in self-incompatible populations that appear to be in the majority, this amounts to the reception of allosperm. Accordingly in laboratory experiments, colonies have been found to retard the production of female zooids until allosperm is acquired, while continuing to invest normally in males (Hughes *et al.,* 2002). Withholding female allocation in this way avoids paying the 'fixed costs' (Heath, 1977) of constructing and sustaining female zooids until repayment is possible in the form of embryo production. Potential for delay is not unlimited, however, and colonies eventually produce female zooids even in continued reproductive isolation (Hughes *et al.,* 2002). Here again, modular colonies prove to be powerful models for experimental evolutionary ecology, since sex allocation is free of complications found in motile animals. The cost of mating is negligible since mating is achieved by capture of sperm entrained in the feeding current. There are no costs of sexual display or mate acquisition and the risk of disease transmission is probably negligible.

The necessarily greater duration of allocation to the female function than to the male in brooding species such as *C. hyalina* may influence optimal sex allocation not only according to mating opportunity as discussed above, but also under conditions of environmental stress (Day and Aarssen, 1997). In response to diverse stressors *C. hyalina* quickly elevates the production of male zooids while leaving female production unchanged. If stress signals imminent colonial deterioration or death, this act of 'reproductive bailout' will increase reproductive success by maximizing the chance of siring offspring of non-stressed colonies located elsewhere (Hughes *et al.,* 2003).

In principle, quasi-behavioural responses could occur if, for example, genets were to adjust the timing of their own spawning according to the activity of neighbours, or even to manipulate the spawning activity of neighbours.

CONCLUSIONS

Modular, colonial invertebrates predominate on stable-substratum communities of the shallow seas (Jackson, 1977) and so represent a major component of global biodiversity. Modularity and sessile adult life are common to aquatic colonial invertebrates and terrestrial higher plants, which therefore may be expected to show parallel responses to similar selective forces. Historically, terrestrial plants have received the lion's share of attention from evolutionary biologists, but recent advances in image processing, development of molecular markers and artificial propagation have made colonial invertebrates more amenable to experimentation. Though still in its infancy, the evolutionary ecology of modular invertebrates is a rapidly expanding field. Great advances are being made in understanding how physiological allometry at the modular level interacts with that at the colonial level and how such interaction directs the architectural development of a growing colony. Species whose colonies are readily propagated from cuttings and whose larvae settle successfully in the laboratory afford powerful models for fundamental evolutionary research, for example on the manifestation of senescence and allorecognition. Sperm-cast mating, in which waterborne sperm fertilize retained eggs, avoids confounding complications associated with manipulative behaviour and copulation in motile animals, so enhancing the suitability of colonial invertebrates for experimentally testing theories of sex allocation, mate selection, sperm competition and sexual conflict. Cellular level mate recognition promotes cryptic speciation in colonial invertebrates as in other benthic animals using water-borne gametes to achieve mating. Therefore, to avoid serious underestimation of the biodiversity of such taxa, it becomes necessary to use molecular techniques, and if possible breeding tests, to complement morphologically based taxonomy (Sáez and Lozano, 2004).

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