

Reproduction of Cnidaria¹

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Abstract: Empirical and experimental data on cnidarian reproduction show it to be more variable than had been thought, and many patterns that had previously been deduced hold up poorly or not at all in light of additional data. The border between sexual and asexual reproduction appears to be faint. This may be due to analytical tools being insufficiently powerful to distinguish between the two, but it may be that a distinction between sexual and asexual reproduction is not very important biologically to cnidarians. Given the variety of modes by which it is now evident that asexual reproduction occurs, its ecological and evolutionary implications have probably been underestimated. Appropriate analytical frameworks and strategies must be developed for these morphologically simple animals, in which sexual reproduction may not be paramount, that during one lifetime may pass through two or more phases differing radically in morphology and ecology, that may hybridize, that are potentially extremely long-lived, and that may transmit through both sexual and asexual reproduction mutations arising in somatic tissue. In cnidarians, perhaps more than in any other phylum, reproductive attributes have been used to define taxa, but they do so at a variety of levels and not necessarily in the way they have conventionally been considered. At the species level, in Scleractinia, in which these features have been most studied, taxa defined on the basis of morphology, sexual reproduction, and molecular characters may not coincide; there are insufficient data to determine if this is true throughout the phylum. At the class level, transverse fission occurs in members of all three major taxa but is rare outside Scyphozoa, the group of which it is considered characteristic (pending more research, its absence in Cubozoa should be ascribed to poor knowledge). Understanding the role of transverse fission in the ecology and reproductive biology of hydrozoans and anthozoans could shed light on scyphozoan evolutionary history, and elucidating its morphogenesis in all groups is essential to determining if it is homologous across the classes. Only by comparing aspects of reproduction among cnidarians of various taxa will idiosyncratically adaptive strategies be distinguished from reproductive characters that reflect evolution and so are phylogenetically informative.

Résumé : Les données empiriques et expérimentales montrent que la reproduction des cnidaires est plus variable qu'on ne l'avait cru précédemment et plusieurs déductions au sujet des patterns de reproduction n'ont pas été confirmées à la lumière des données récentes ou alors ne l'ont été que partiellement. La démarcation entre la reproduction sexuée et la reproduction asexuée n'est pas nette. Il se peut que les outils analytiques qui servent à les distinguer ne soient pas assez puissants, mais il se peut aussi que la différence entre les deux types de reproduction n'ait pas une grande importance biologique pour les cnidaires. Étant donné la diversité des modes de reproduction asexuée, il est probable que ses effets écologiques et évolutifs aient été sous-estimés. Il importe de créer des cadres analytiques et des stratégies appropriés à ces animaux simples chez lesquels la reproduction sexuée n'a pas nécessairement une importance centrale et qui peuvent, durant leur vie, subir deux phases ou plus au cours desquelles ils sont radicalement différents morphologiquement et écologiquement, qui peuvent s'hybrider, qui peuvent avoir une longévité exceptionnelle et qui peuvent transmettre des mutations des tissus somatiques par reproduction sexuée ou asexuée. Chez les cnidaires, peut-être plus que dans tout autre phylum, les caractères relatifs à la reproduction ont servi à définir les différents taxons, mais à des niveaux divers et pas nécessairement de façon conventionnelle. Chez les Scleractinia, dont les structures relatives à la reproduction ont été bien étudiées, les taxons définis au niveau spécifique en fonction de la morphologie, de la reproduction sexuée et des caractéristiques moléculaires ne coïncident pas nécessairement, mais les données existantes ne permettent pas de vérifier cette affirmation dans tout le phylum. Au niveau de la classe, la fission transversale existe chez les membres des trois principaux taxons, mais cette fission est rare, sauf chez les scyphozoaires, le groupe considéré comme le plus caractéristique (en attendant les résultats des recherches futures, l'absence de fission chez les

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cubozaïres est attribuée à un manque de connaissances). La compréhension du rôle de la fission en écologie et en biologie de la reproduction chez les hydrozoaires et les anthozoaires permettra sans doute de faire la lumière sur l'évolution des scyphozoaires. La clarification de sa morphogénèse chez tous les groupes est essentielle pour déterminer si la fission transversale est homologue chez toutes les classes. Seule la comparaison des divers aspects de la reproduction chez différents taxons de cnidaires permettra de distinguer les idiosyncrasies adaptatives stratégiques des caractères reproducteurs qui reflètent l'évolution et ont donc valeur d'information phylogénétique.

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Introduction

Even in a phylum in which vegetative processes are as prominent and important as they are in Cnidaria, "reproduction" is often used only when gametes are involved (e.g., Fadlallah 1985; Sier and Olive 1994). A large portion of this review is concerned with asexual reproduction, in contrast with most previous reviews of cnidarian reproduction, in which, with emphasis on the individual, cellular/histological and physiological aspects of sexual reproduction were highlighted. From my consideration of the organism in space and time, I see the line between sexual and asexual reproduction in these animals as faint, and I infer that sexual processes may be less significant to the ecology and evolution of cnidarians than has been thought.

Asexual reproduction inevitably leads to some consideration of regenerative processes because, as Hoeksema (1989, p. 20) asserted for fungiid corals, "asexual reproduction is always the result of regeneration". Indeed, genes active in regeneration are likely also to be active in asexual reproduction (Grimmelikhuijzen 2000). Processes of asexual reproduction or the patterns it produces are important to the classification of most modular organisms (Boardman et al. 1973; Rosen 1979), including cnidarians; many studies of their taxonomy contain information on reproduction. In colonial taxa, the morphology of the colony (as the word is generally employed in biology; for a discussion of terminology see Rosen 1979) can be systematically diagnostic (e.g., Cornelius 1995; Wallace 1999; Zilberberg and Edmunds 1999), and even in solitary scleractinian corals, mode of asexual reproduction is potentially an important taxonomic character (Cairns 1988). In addition to the ability to propagate vegetatively, which is hardly unique to them, many cnidarians alternate between polypoid and medusoid phases, an aspect of reproduction that has systematic implications. (Nomenclatural, biological, and philosophical aspects of this alternation, including whether the widely used term metagenesis is appropriate for it, were discussed by Cornelius 1990.) Thus, among the studies I review are some that focus primarily on taxonomy and systematics. I also address some aspects of development for, as Davey et al. (1984, p. 1) wrote in justifying the addition of "and Development" to the title of the *International Journal of Invertebrate Reproduction* with volume 7 of the serial, "Particularly among the lower invertebrates and most particularly among the marine forms, it becomes very difficult to separate reproduction from development in any realistic way". Likewise, some publications on ecology contain reproductive information; for example, Hall and Hughes (1996, p. 950) considered data from six species of corals on the Great Barrier Reef in assessing "how modularity influ-

ences reproductive strategies and the evolution of life histories in clonal animals". Therefore, this review is of literature extending beyond the strictly reproductive.

The literature

In addition to having been the subject of many previous reviews, reproduction by members of the phylum Cnidaria has been addressed in some reviews in which the major theme was not reproduction. In this review, I focus on publications since about 1990 (but my coverage is not exhaustive), primarily those having to do with phenomena above the cellular level; most are in English. I attempt to identify themes of current research and trace some prevailing ideas to their intellectual roots. Access to much of the earlier literature, and discussion of its contents, are available through the previous reviews.

Among the earliest in English are chapters by Mergner (1971) and Campbell (1974) in volumes dealing with multiple facets of invertebrate reproduction. Each volume of the series *Reproductive Biology of Invertebrates* concerns a particular reproductive phenomenon; most have a chapter on cnidarians (Beams and Kessel 1983; Miller 1983; Fautin et al. 1989; Fautin 1992; Shostak 1993; Harrison and Jamieson 1999; Grimmelikhuijzen 2000), but some, such as Volume 3, which deals with accessory sex glands (Adiyodi and Adiyodi 1988), lack one. Although most chapters in *Traité de Zoologie* are organized along taxonomic lines, the chapter by Van de Vyver (1994) is entitled "Reproduction sexuée—embryologie". The book by Strathmann (1987), which focuses on methodology, summarizes data on sexuality, spawning, and development of marine invertebrates, including cnidarians, of the northeast Pacific Ocean, and the *Atlas of Marine Invertebrate Larvae* (Young et al. 2002) contains a chapter on Cnidaria (Martin and Koss 2002).

In some reviews, reproduction is but one subject among many. For example, each comprehensive treatise on invertebrate zoology contains information on cnidarian reproduction. The volume of Hyman (1940) that includes cnidarians is encyclopedic in its coverage of the literature to that time. Reproduction is discussed by Tardent (1978) in the chapter on Cnidaria in the series *Morphogenese der Tiere* and by Werner (1993) in *Wirbellose Tiere*, as it is in chapters on extant groups of Cnidaria in *Traité de Zoologie* (Chevalier 1987; Doumenc and Van Praët 1987; Herbets 1987; Pax et al. 1987; Tiffon 1987; Tixier-Durivault 1987; Bouillon 1994; Carré and Carré 1994; Franc 1994a, 1994b; Goy 1994). Aspects of reproduction, especially gametogenesis, embryogenesis, and tissue proliferation and reorganization, are treated in Volume 2 of *Microscopic Anatomy of Invertebrates* in the

chapters on Hydrozoa (Thomas and Edwards 1991), Scyphozoa and Cubozoa (Lesh-Laurie and Suchy 1991), and Anthozoa (Fautin and Mariscal 1991). Shick (1991) and Arai (1997) considered generalized life cycles and details of reproductive biology in books dealing with sea anemones and scyphozoans, respectively.

Taxonomically oriented overviews of Cnidaria such as *Die Tierwelt Deutschlands* (Broch 1928; Krumbach 1928; Pax 1928) and regional field guides (e.g., Stephenson 1928, 1935; Cornelius 1995; Fabricius and Alderslade 2001) contain discussions of aspects of reproduction. Chapters by Bayer (1956), Hyman (1956), and Wells (1956) in Volume F of *Treatise on Invertebrate Paleontology* all include a section on reproduction; some of the other chapters concerned with both extant and extinct taxa contain explicit or implicit information on reproduction. Data on reproduction of even fossil taxa are included because in cnidarians, perhaps more than in any other phylum, reproductive attributes define taxa. This is true of higher taxa, like the production of ephyrae in the Scyphozoa, and lower taxa, like the distinction between the sea anemone genera *Tealanthus* and *Isotealia* being largely the nature of the secondary mesenteries, which are fertile in the former and sterile in the latter (Carlgren 1949).

Presentations on cnidarian reproduction were made at virtually all of the nine international coral reef symposia, six international coelenterate symposia, and four hydrozoan workshops held to date, some of them in sessions devoted to the subject. These were predominantly the results of primary research (e.g., Miller 1976; Fadlallah 1985; Benayahu 1991; Kubota 1997; Bavestrello et al. 2000) but some were syntheses (e.g., Chia 1976; Cairns 1988; Cornelius 1992; Fautin 1997; Willis et al. 1997). The Fifth International Coral Reef Congress, held in Tahiti in mid-1985 (Gabrie and Salvat 1985), had what was probably the most extensive session of any of these conferences on cnidarian reproduction. The proceedings of the most recent coral reef symposium, held in Bali in October 2000, have not yet been published, but the two previous ones are Richmond (1993) and Lessios and Macintyre (1997); the proceedings of the two most recent coelenterate symposia are Williams et al. (1991) and den Hartog (1997); and the proceedings of the most recent hydrozoan workshop is Mills et al. (2000).

Most other reviews of reproduction of which I am aware concern scleractinians, the cnidarian taxon in which the greatest amount of relevant research has been carried out during the past two decades or so. These reviews cover aspects of gamete production through larval development (Fadlallah 1983; Harrison and Wallace 1990; Richmond 1997), some with a geographical focus (Richmond and Hunter 1990; Shlesinger et al. 1998). Cutting through the subject of cnidarian reproduction in alternative ways, Ryland (1997b) reviewed reproduction of zoanthids and Leitz (1997) reviewed mechanisms of settlement and metamorphosis throughout the phylum, with emphasis on cellular events.

Overview

Knowledge of reproduction is most extensive for members of the largest class of Cnidaria, Anthozoa, although that was not true before the late 20th century. Recent research has

been carried out on anthozoans of every order, including the previously understudied groups Antipatharia (sexual reproduction: Parker et al. 1997; sexual and asexual reproduction: Miller and Grange 1997), Ceriantharia (sexual reproduction: Hinsch and Moore 1992), Coenothecalia (sexual reproduction: Babcock 1990), Corallimorpharia (sexual reproduction: Holts and Beauchamp 1993; Chen et al. 1995a, 1995b; Chadwick-Furman et al. 2000; asexual reproduction: Chadwick and Adams 1991; Chen et al. 1995a; Chadwick-Furman and Spiegel 2000), Gorgonacea (sexual and asexual reproduction: Coma et al. 1995a), and Zoanthidea (sexual reproduction: Babcock and Ryland 1990; Soong et al. 1999; Ryland 2000; asexual reproduction: Ryland 1997a; Soong et al. 1999). Pennatulacea remains poorly studied, recent research on its reproduction centering on biological and anatomical aspects of gametogenesis (Rice et al. 1992; Tyler et al. 1995; Eckelbarger et al. 1998). Research on the better known groups has included some on places or taxa from which data were few, such as deep-sea actinians (e.g., Van Praet 1990; Van Praet et al. 1990; Bronsdon et al. 1993, 1997) and high-latitude octocorals (e.g., Brito et al. 1997; Schleyer et al. 1997), or on novel structures (e.g., Excoffon and Zamponi 1999).

Knowledge of non-anthozoans has been enhanced, although not as dramatically, during the past decade. Information is least adequate on the class with the fewest members: data for Cubozoa are only beginning to accumulate (e.g., Hartwick 1991; Franc 1994a, in which the literature review extends only into the early 1980s; Matsumoto 1996; Stewart 1996), owing probably both to the small number of species and to the perceived dangers of working with these potentially lethal animals. Franc (1994b) and Arai (1997) reviewed knowledge of reproduction in all four orders of Scyphozoa: Coronatae, Rhizostomeae, Semaestomeae, and Stauromedusae. Classification of the higher taxa of Hydrozoa is currently in a state of flux, Siphonophora being the only taxon clearly distinguishable by morphology and other biological attributes, as well as by molecules (e.g., Bouillon et al. 1992; Schuchert 1993; Collins 2000). Reproduction has been studied in all major lineages, in part because in Hydrozoa, more than in any other class of Cnidaria, aspects of reproduction may be essential taxonomic features. Knowledge concerning the reproduction of siphonophores was summarized briefly by Kirkpatrick and Pugh (1984); the extensive review of this taxon by Mackie et al. (1987) contains little information on reproduction. The hydras were the best studied cnidarians until rather late in the 20th century, presumably largely because of the ease of keeping them. Their reproduction continues to be studied (e.g., Grassi et al. 1995), but most research has shifted from understanding cnidarians to using them as "model systems for developmental biologists" (Grimmelikhuijzen 2000, p. 51). Although in many ways hydra could hardly be a more atypical cnidarian (e.g., Carré and Carré 2000), research such as that by Cartwright et al. (1999) has explored whether what is known for hydras applies more broadly within Hydrozoa. Reproductive data for other hydrozoans continues to accumulate at a rate consistent with that of the past.

Deduction, i.e., the search for general explanations of particular observations, is a major activity of science. Recent data reveal that cnidarian reproduction is more variable than

had been thought. In drawing together literature documenting this remarkable variability, I reconsider some of the generalizations that were deduced from the previously limited data. I try to analyze apparent exceptions and assess how representative the new data are, seeking patterns, primarily ecological or taxonomic. Foremost among previous generalizations are life cycles of the sort found in text books and treatments designed for other than cnidarian specialists (e.g., Grimmelikhuijzen 2000; Martin and Koss 2002). There are some known exceptions even to one of the most tenable of such generalizations, that of Hyman (1956, p. F16) that "Adult Scyphozoa reproduce exclusively by the sexual method" (I assume that by "adult" she meant "medusoid") (for example, see da Silveira and Morandini 1997; Jarms 1997). Some recently studied species are exceptions to relatively robust general patterns, but some generalizations appear to have been derived from few studies that, by chance or because of unrecognized bias, dealt with atypical species (species that were selected for research perhaps because they were responsive to experimental manipulation, or their periodicities coincided with scientists' field seasons). Foremost among these, in cnidarian reproductive biology, is that of Wells (1956, p. F346), who was not alone in writing of scleractinian reproduction, "Viviparity is the rule".

Insights from mass spawning

Not only is viviparity not the rule, the spawning of gametes may be highly episodic. One of the best known phenomena of cnidarian reproduction, and certainly among the most dramatic, is mass spawning. First reported by Marshall and Stephenson (1933), the phenomenon has been intensively studied since Harrison et al. (1984) documented the simultaneous release of gametes by 32 species of scleractinians on the Great Barrier Reef. Species have continued to be added to the inventory (e.g., Babcock et al. 1986) until it appears now that most of the 350+ species of scleractinians on the Great Barrier Reef participate in mass-spawning events to some extent (Harrison and Wallace 1990). So do animals of other taxa, including alcyonarians (Babcock et al. 1986; Alino and Coll 1989) and zoanthids (Ryland and Babcock 1991). I found no data, however, for cnidarians other than anthozoans.

Because of its limited scope, early research on scleractinian reproduction, which was reviewed by Harrison and Wallace (1990) and Richmond and Hunter (1990), led to generalizations such as that of Wells. Since those reviews were published, reports have appeared on more species from more places, including Okinawa (Hayashibara et al. 1993; Kinzie 1993; Shimoike et al. 1993), Taiwan (Fan and Dai 1995, 1996, 1998; Soong and Cho 1998), Hong Kong (Lam 2000), the high latitudes of Australia (Wilson and Harrison 1997), the Mediterranean Sea (Fine et al. 2001), the Gulf of Mexico (Gittings et al. 1992), Bermuda (Wyers et al. 1991), parts of the Caribbean that had not previously been studied (e.g., Acosta and Zea 1997), the eastern Pacific Ocean and Galápagos Islands (by Glynn and collaborators, e.g., Glynn et al. 1991, 2000), and Brazil (Pires et al. 1999).

It has been difficult to derive general patterns from this mass of data. For example, in addition to the Great Barrier

Reef, synchronous spawning of corals occurs in the Gulf of Mexico (Gittings et al. 1992; Hagman et al. 1998), the Caribbean (Van Veghel 1993), and off Western Australia (Babcock et al. 1994), but not in the Red Sea (Shlesinger and Loya 1985); mass spawning seems to be less synchronous in southern Japan than elsewhere (Hayashibara et al. 1993). Even where mass spawning does occur, not all colonies of a species participate in the event (e.g., Van Veghel 1993; Babcock et al. 1994), and Shimoike et al. (1993) reported that shaded portions of some colonies of *Acropora* spawn a night or more after unshaded portions. On the Great Barrier Reef, spawning occurs progressively later in the year with increasing latitude (Babcock et al. 1986; Oliver et al. 1988), which Sier and Olive (1994) also found for *Pocillopora verrucosa* in the Maldives and Dai et al. (1993) for many species in Taiwan, but Fan and Dai (1995, 1998) did not find for *Echinopora lamellosa* and *Merulina ampliata*, respectively, attributing differences in spawning times to local effects. Nor is there a latitudinal shift in timing of mass spawning on Australia's west coast (Babcock et al. 1994).

Analyses of triggers of spawning and release of medusae by individual species have a long history. Some recent publications in this area include those by Mills (2001) and Mendes and Woodley (2002). An example of a study concerned expressly with reef-forming scleractinians that participate in mass-spawning events is that of Gorbunov and Falkowski (2002).

The phenomenon of mass spawning was unexpected in part because offsets in spawning times between closely related species are common (Palumbi 1994). For example, congeneric hydrozoans in Japan release medusae at slightly different, although overlapping, times (Kubota 1997); the three species of the Brazilian endemic reef-forming coral *Mussismilia* broadcast gametes in broad asynchrony (Pires et al. 1999); and in Taiwan, although three putative species of the hydrozoan coral *Millepora* overlap in releasing medusae, there is more synchrony within than between species (Soong and Cho 1998). The inference had been that asynchrony protects against hybridization; mass spawning therefore seems to provide an opportunity for hybridization (e.g., Babcock 1995; Kinzie 1996; Fautin 1997; Willis et al. 1997; Wallace 1999). Other means by which hybridization of synchronously spawning species may be avoided have been considered. For example, Babcock (1995) discussed how species-specific chemical gamete attractants might function, but remarkably few have been identified: one each in a scleractinian and an octocoral (Coll et al. 1994, 1995, respectively). (Sperm attractants are known in other cnidarians (Miller 1983).) In fact, for reef-forming corals of the Great Barrier Reef, fertilization rates are high between some colonies that, based on morphology, belong to different species of three genera, including the most speciose one, *Acropora* (Wallace and Willis 1994; Willis et al. 1997), and among seven morphospecies of *Platygyra* that spawn virtually simultaneously (Miller and Babcock 1997), viable larvae are produced. Karyotypic data from 10 species of *Acropora* support the hypothesis that hybridization can occur in corals (Kenyon 1993). In the Caribbean, molecular data also provide evidence of hybridization: between two sympatric species of *Acropora* that spawn simultaneously (Van Oppen et al. 2000; Vollmer and Palumbi 2002) and for

five sympatric morphospecies of *Madracis* (Diekmann et al. 2001).

Reproductive attributes of what is ostensibly a single species can vary in one place as well as from place to place. The simultaneously hermaphroditic scleractinian *Pocillopora damicornis* broadcasts and broods in Western Australia (Ward 1992), where it releases most of its planulae during new moons in summer, but on the northern Great Barrier Reef most planulae are released during full moons in winter (Tanner 1996). In Hawai'i, planulae are released monthly during full moon (Jokiel 1985). Glynn et al. (1991) inferred that this species is exclusively a broadcast spawner in the eastern Pacific Ocean. *Goniastrea aspera* spawns and broods in Okinawa (Sakai 1997) but only spawns on the Great Barrier Reef (Babcock et al. 1986); it spawns gametes of the two sexes separately in Okinawa (Sakai 1997) but egg-sperm bundles are released on the Great Barrier Reef (Babcock 1984). *Pocillopora verrucosa* is a broadcasting simultaneous hermaphrodite in the Red Sea (Fadlallah 1985; Shlesinger and Loya 1985), the Maldives (Sier and Olive 1994), South Africa (Kruger and Schleyer 1998), and Okinawa (Kinzie 1993), whereas it is reportedly a brooder in Enewetak (Stimson 1978). The octocoral *Anthelia glauca* produces considerably more oocytes in South Africa (Kruger et al. 1998) than in Israel (Benayahu 1991).

Ostensible intraspecific variability in reproductive attributes may be evidence that the organisms identified as conspecific really are not, i.e., that cryptic species exist (Babcock 1995), an explanation that is also consistent with the observation of mating incompatibility between colonies of single morphospecies of *Acropora* and *Montipora* (Wallace and Willis 1994; Willis et al. 1997). On the other hand, apparent hybridization could be interpreted as reflecting intraspecific morphological variability. Indeed, the current conundrum concerning scleractinians, in which these features have been most studied, is that species defined on the basis of morphology, reproduction, and molecular characters may not coincide (Wallace and Willis 1994; Willis et al. 1997). Szmant et al. (1997) summarized the current state of knowledge concerning the group for which there is the greatest amount of data in this regard, which may constitute either a single variable species of *Montastraea*, *M. annularis*, or three species.

Asexual reproduction

Although broadcasting predominates in scleractinians, internal brooding (also referred to as viviparity) is widespread among them and other anthozoans; it appears to occur in proportionally fewer medusozoans (for a discussion of the term Medusozoa see Cornelius 1990). Some internally brooded anthozoan young result from sexual reproduction (Ayre and Resing 1986), but the assumption that all do was refuted first in the sea anemones *Actinia tenebrosa* (see Ottaway and Kirby 1975; Black and Johnson 1979) and *Actinia equina* (see Carter and Thorpe 1979; Gashout and Ormond 1979; Orr et al. 1982) and shortly thereafter in scleractinians, both zooxanthellate (*P. damicornis*: Stoddart 1983) and azooxanthellate (*Tubastrea*: Ayre and Resing 1986). The process that gives rise to them has been termed vegetative or somatic embryogenesis (e.g., Shick 1991), but despite a growing list of

anthozoan species that exhibit the phenomenon (e.g., *Cereus pedunculatus*: Shaw 1989; *Actinia bermudensis*: Monteiro et al. 1998), the source of the propagules, which are morphologically indistinguishable from sexually produced ones, is unresolved (Kinzie 1996; Yanagi et al. 1996, 1999; Fautin 1997). The origin of the brooded young in the deep-sea sennaeostome *Stygiomedusa gigantea* (= *fabulosa*) is equally enigmatic (Arai 1997).

Shaw et al. (1987) and Shaw (1989) proposed that at least some asexually produced planulae in actinians result from apomictic parthenogenesis. Parthenogenetic development in the brooding octocoral *Alcyonium hibernicum* was also inferred by Hartnoll (1977), and in the spawning octocoral *Plexaura A* by Brazeau and Lasker (1989) because they found only females. Harrison and Wallace (1990) cited one study in which asexually derived brooded young of a scleractinian were thought to be parthenogenetic, but concluded that is unlikely to be a general explanation of the phenomenon. Given the variability in other aspects of cnidarian reproduction, I also consider it improbable that a single process is responsible for all asexually derived "planulae".

In the black coral *Antipathes fiordensis*, "Parts of the polyp (presumably the tentacles) will drop off the colony forming large, ciliated and highly mobile 'planulae'" (Miller and Grange 1997, p. 360). Likewise, the planuloid buds produced by rhizostome scyphistomae are clearly asexual and multicellular in origin, and differ morphologically from sexually produced planulae (Hofmann and Honeggar 1990; Hofmann and Gottlieb 1991; Van Lieshout and Martin 1992). Coronate ephyrae may transform into what Jarms (1997) termed planuloids; a planuloid (two in the case of *Nausithoe marginata*) may transform into a polyp. Hydrozoan frustules are typically planuliform (Bouillon 1994). A propagule that arises ultimately from a single cell (an ovum in the case of parthenogenesis) and one that arises from a multicellular Anlage have different implications for evolution, and for individual as well as population genetics (Orive 2001 and publications cited therein): an individual that develops from a single cell initially contains only one genome, whereas, because somatic mutation may result in chimeras (Fautin 1997; Orive 2001), an individual that develops from more than one cell may initially contain more than one genome.

Planuloid buds are one among numerous types of buds produced by scyphozoans (Van Lieshout and Martin 1992). Hofmann and Honeggar (1990) compared and contrasted budding in *Cassiopea* spp. and *Hydra* spp.: the distal portion of a *Hydra* bud forms the oral region, so a fully differentiated polyp detaches, whereas the distal portion of the bud forms the pedal end in *Cassiopea*, so a detached bud lacks a hypostome and tentacles. In both, a bud arises as a protrusion from the parental body wall, morphogenesis that is consistent with the only recent explicit definition of "bud" which I could find, that of Bouillon (1994, p. 217) for the French equivalent: "le bourgeon est une hernie de la paroi ecto-endodermique de l'organisme". This also appears to be the working definition of the formation of polyps by polyps in Cubozoa (e.g., Arneson and Cutress 1976), Hydrozoa, and Scyphozoa. Sibly and Calow (1982) considered ephyrae to be buds (although they did not expressly define "bud"), and Bouillon (1994) found the budding of medusae to be re-

markably similar to that of polyps in Hydrozoa. Although budding has been most studied in hydras, I found no definition of bud in the chapter "Terminology for morphology and cell types" by Campbell and Bode (1983) despite reference to buds, and a "budding region" being delimited, nor in Tardent (1988), whose detailed morphogenetic analysis is consistent with a bud's being an outgrowth of the body wall.

Ryland (1997a) employed "budding" for a zoanthid in the manner generally used in Hydrozoa and Scyphozoa, and both forms of budding (marginal and inverse) reported by Chadwick-Furman and Spiegel (2000) appear to conform to it. However, in other anthozoans it has been applied to diverse sorts of vegetative reproduction. For example, it has been used for regeneration of parts of alcyonacean colonies that survived a storm (Dai 1991) and for the development of new fungiid polyps from remnants of tissue that were too small to regenerate the parent polyp (Krupp et al. 1992; Kramarsky-Winter and Loya 1996). Kramarsky-Winter et al. (1997) classed as budding the expulsion from a colony of individual scleractinian polyps complete with calices. In the table in which he summarized "modes of asexual reproduction in Scleractinia", Cairns (1988) synonymized intratentacular budding with fission; under extratentacular budding, he included fragmentation. Gudo and Hubmann (2001) described a type of intratentacular budding in a rugose coral that they termed parricidal increase because the original corallite died in the process of giving rise to four daughter polyps. Dahan and Benayahu (1997) and Fabricius and Alderslade (2001) included budding among the modes by which octocorals propagate. Anemones of at least one species belonging to the group Boloceroidea swallow and incubate their own autotomized tentacles, which regenerate into small individuals (Cutress 1979), and tentacles of others may begin to regenerate small individuals while still attached to the parent (Pearse 2002), a process Cutress (1979, p. 101) referred to as tentacle budding. Shick (1991) and Chia (1976) classified these as the only instances of budding among actinians, a usage followed by Hand and Uhlinger (1995). Although Shick (1991, p. 251) remarked that "The occurrence of budding seems related moreover to the ability of these anemones to autotomize tentacles in response to predators", he listed "tentacular autotomy and regeneration" as a mode of asexual reproduction distinct from budding. Stephenson (1928, p. 95) stated of actinians, "True budding is not a characteristic of the group", attributing records of it to aberrations in other sorts of vegetative reproduction or early development; tentacle regeneration in boloceroideans seems not to have been recognized at the time. Budding appears not to be used as a synonym of asexual reproduction in non-anthozoans: four of the nine modes of asexual reproduction listed by Bouillon (1994) do not include "bourgeon" or "bourgeonnement".

Colony development is through processes commonly referred to as asexual reproduction (e.g., Bouillon 1994; Cornelius 1995; Tyler et al. 1995; Ivanova-Kazas 1996), although Walker and Bull (1983, p. 137) restricted asexual reproduction "to an increase in the number of individual animals or colonies [excluding] the case of enlargement of a colony by increase in the number of zooids", a usage also followed by Richmond (1997), for example. However, it seems that most, if not all, vegetative processes that produce colonies may also result in separate individuals (Wells 1956; Bell 1982). In this

review I concentrate on the latter; colony formation in some taxa has been discussed extensively, by Marfenin (1997) for hydroids, Wallace (1999) for scleractinian corals, and Fabricius and Alderslade (2001) for octocorals, for example. The modes of vegetative propagation that have long been recognized may be divided into two sorts, those which follow the stereotypic metagenetic life cycle (that is, polyps producing medusae) and those which do not (medusae producing medusae or polyps, and polyps producing polyps). Formation of a medusa by a cubozoan polyp is not reproductive, since the entire polyp reportedly metamorphoses (Arneson and Cutress 1976).

Strobilation (transverse fission) is the process by which a scyphozoan polyp produces medusae (summarized by Arai 1997), although the process can produce polyps in some scyphozoans (e.g., da Silveira and Morandini 1998), and it is not confined to Scyphozoa (Nyholm 1959). A report by Bavestrello et al. (2000) was the second of strobilation in a hydrozoan (identified only as a member of the superfamily Bougainvillioidea), the first, in an unnamed hydroid, having been by Hand and Jones (1957). Transverse fission occurs in at least four orders of Anthozoa (thus a polyp produces a polyp): Cerfontaine (1909) documented it in a cerianthid, Cairns (1988) considered it to be a key innovation in solitary scleractinians, it is known in five species of actinians (Hand and Uhlinger 1995), and Soong et al. (1999) described it in the zoanthid *Sphenopus marsupialis*. Transverse fission in *Gonactinia prolifera* has been considered a "primitive" trait (Schmidt 1970): after a whorl of tentacles forms partway along the column, the anemone divides, so the newly formed tentacles are at the apex of the new individual (e.g., Stephenson 1935; Chia et al. 1989). In the ostensibly closely related *Nematostella vectensis*, the column divides transversely before a whorl of tentacles develops at the new apical end (Hand and Uhlinger 1995), which is typically how it occurs in *S. marsupialis*, but occasionally "new mouths and tentacles developed for the lower parts before complete separation" (Soong et al. 1999, p. 337). Transverse fission in *Anthopleura stellula*, a member of what is considered to be a derived group of actinians, occurs only under exceptional circumstances: it has been documented in captivity, under conditions of low salinity (Schmidt 1970). Likewise, Cerfontaine's (1909) account of spontaneous division in *Cerianthus oligopodus* was in captive animals that had not been attended.

"Longitudinal fission is the most widespread form of vegetative proliferation among sea anemones", according to Shick (1991, p. 253). Mire (1998) and Mire and Venable (1999) analyzed cellular aspects of fission in the anemone *Haliplanella lineata*. Longitudinal fission is also common in Scleractinia (Cairns 1988), Corallimorpharia (Chadwick-Furman and Spiegel 2000), and Scyphozoa (Arai 1997). The octocoral *Alcyonium rudyi* propagates by binary fission (McFadden 1997), as do some other octocorals (Dahan and Benayahu 1997; Fabricius and Alderslade 2001). Frey (1970) reported that branched cerianthid tubes may be evidence of asexual reproduction.

Fragmentation of solitary scleractinians can clearly serve for asexual propagation (e.g., Hoeksema 1989). Colony fragmentation has been studied as a reproductive strategy in colonial scleractinians (e.g., Highsmith 1982; Wallace 1985; Smith and Hughes 1999; Lirman 2000), but whether it should be considered an adaptation for vegetative propagation has

been questioned (Hughes et al. 1992; Smith and Hughes 1999). As in scleractinians, fragmentation occurs in colonies of at least some species of alcyonaceans (Tursch and Tursch 1982; Dahan and Benayahu 1997; Fabricius and Alderslade 2001) and zoanthids (Acosta et al. 2001). Colonies of some gorgonian species seem not to fragment at all (e.g., *Acabaria biserialis*, even though it is an excellent colonizer of open surfaces: Zeevi Ben-Yosef and Benayahu 1999). In other species, fragments are rare and their survival rate is low (*Paramuricea clavata*: Coma et al. 1995a), but in still others, fragmentation appears to be important to propagation (e.g., *Junceella fragilis*: Walker and Bull 1983), at some places or times to the virtual exclusion of other modes of recruitment (e.g., *Plexaura kuna*: Coffroth and Lasker 1998). Shick (1991) questionably listed "regeneration of fragments" in his table "Modes of asexual reproduction in sea anemones (Actiniaria)", but also included basal laceration, which involves regeneration from a small piece that typically includes all three body layers (Stephenson 1928).

The formation of polyp balls reported by Rosen and Taylor (1969) in the scleractinian *Goniopora* seems much like the addition of polyps to a colony except that the skeletal elements of the ball are separated from those of the main colony, so the resultant polyps detach easily. This appears similar to the phenomenon of "polyp expulsion" described by Kramarsky-Winter et al. (1997), although a polyp ball consists of 1–30 polyps, whereas polyp expulsion apparently results in the ejection of single polyps. By contrast, polyp bail-out (Goreau and Goreau 1959; Sammarco 1982) results in a naked scleractinian polyp that can then presumably form a skeleton. Polyp bail-out has a counterpart in hydroids: a hydranth is released and becomes pelagic, then settles and redifferentiates. Only two instances are known in thecate but the phenomenon is more common in athecates (Gravier-Bonnet 1992).

Stolons or runners are put out by some alcyonarians (summarized by Dahan and Benayahu 1997; Fabricius and Alderslade 2001) and hydroids (Cornelius 1995). Arai (1997) categorized the production of stolons as a type of budding in Scyphozoa, but not all stolons are involved in reproduction: some effect locomotion. The tip of a scyphozoan stolon may form a cyst; whether formed from a stolon or otherwise, a cyst consists of some living cells surrounded by a cuticle that is considered to protect them through environmentally unfavorable conditions so that they can regenerate a polyp when favorable conditions return (Arai 1997; Cáceres 1997). However, the triggers of encystment and excystment are obscure (Brewer and Feingold 1991; Condon et al. 2001; Lucas 2001).

A life history that involves both polyp and medusa stages has led in Hydrozoa to a "bewildering array of modified and clearly derived morphologies and life-cycle patterns" (Cornelius 1992, p. 247). Bouillon (1994) identified nine categories of asexual reproduction in the class; for examples see also Cornelius (1990) and Boero et al. (1997). Buds of some hydromedusae produce polyps or other medusae (e.g., Mills 1987); Bavestrello et al. (1992) summarized reports of gonothecae arising from gonads of medusae, and medusae metamorphosing into polyps. Polyps can arise from the radial canals of *Eucheilota paradoxica* (see Carré and Carré 1990), and in *Turritopsis nutricula* a medusa can settle and

transform entirely into tissue that gives rise to polyps (Bavestrello et al. 1992). In some species the sexual phase is brief to non-existent (e.g., in the leptomedusan *Clytia mccradyi*, blastostyles develop in the position where gametes characteristically do; Carré et al. 1995).

Significance of reproductive features

Reproductive characters presumably reflect evolution; thus, many have been considered informative for taxonomy and systematics. However, some are being found to vary far more than had been suspected. The more responsive life cycles are to environmental conditions, the less informative they are for inferring evolution. The unsettled state of hydrozoan systematics is largely due to difficulties in reconciling medusa and polyp stages (e.g., Boero and Bouillon 1987, 1989; Boero et al. 1992). Understanding the survival advantages that led to the evolution of particular life cycles of hydrozoans is an immense challenge. Kubota (1993), Coma et al. (1996), and Nakayama and Numakunai (2000) have recently documented life-cycle variants. Among the most extreme departures from the "typical" pattern is that of *T. nutricula*, in which transformation of a mature medusa into a polyp may involve fully mature cells dedifferentiating, then redifferentiating (Piraino et al. 1996), and *Microhydrula limopsicola*, which may lack a sexual phase entirely (Jarms 1997). Life cycles of members of the other two medusozoan classes appear to vary less, but Jarms (1997) documented circumstances in which the sexual phase of some scyphozoans is skipped, da Silveira and Morandini (1998) reported that the scyphistoma of *Linuche unguiculata* can simultaneously produce ephyrae, which go on to reproduce sexually, and planuloids, which develop asexually into new polyps, and Jarms et al. (1999) inferred that the coronate *Periphylla periphylla* is holopelagic. Because anthozoans lack a medusa stage, the significance of reproductive features might seem easiest to discern in them, but as I wrote previously (Fautin 1991), patterns are difficult to find, perhaps because the anatomical and physiological simplicity of cnidarians makes them evolutionarily plastic. Indeed, early classifications and explanations based on few examples (e.g., Chia 1976) have proved unable to accommodate some new data.

A character useful for systematics in some other groups of organisms that is generally most easily accessible in reproductive cells is the karyotype. Known for few species of cnidarians, and despite technical problems (e.g., Wijsman and Wijsman-Best 1973; Shaw et al. 1987), it has proved to be of some value. In 10 species of *Acropora*, Kenyon (1993) inferred a polyploid series that supports some species being a result of hybridization. Shaw et al. (1987) also found evidence of polyploidy in the sea anemones of the genus *Sagartia*. Additional karyotypes for corals have been reported by Heyward (1985) and for anemones by Van-Praet and Colombara (1984), Fukui (1993, 1996), and Choe et al. (2000). Although both medusa and polyp in metagenetic species are assumed to be diploid (Boero et al. 1992), to my knowledge that has not been established. Tardent (1978) summarized data on 24 species of hydrozoans and one scyphozoan, Bouillon (1994) did so for 31 species of hydrozoans (the latest reference being 1973), and Rahat et al. (1985) and Kubota (1992) provided subsequent data on hydrozoans. Caution should be

used in gathering karyotype data on cnidarians in light of the finding that polyploid nuclei can occur in certain tissues of apparently diploid individuals of the siphonophore *Physalia* (Mackie et al. 1987).

Schmidt and Zissler (1979) used sperm morphology to analyze cnidarian phylogeny; Franzén (1956) was among the first to impute a phylogenetic signal to those cells. The generalizations of Schmidt and Zissler (1979), based on a small sampling of taxa, have not been supported. Rather than reflecting phylogeny, the morphology of cnidarian sperm appears to reflect ecology, a finding at odds with Eckelbarger's (1994, p. 152) generalization, based on an admittedly small sample, that "While animal gametes show enormous morphological and physiological variation, there is usually no obvious biological advantage or apparent adaptive significance to any given modification". Rouse and Pitt (2000) found that sperm structure did not correlate well with reproductive mode in Scyphozoa, but gonochoric corals share distinctive sperm morphology, regardless of taxonomic position (Harrison 1990; Steiner 1998; Harrison and Jamieson 1999). Harrison and Jamieson (1999), summarizing data from 138 species of cnidarians, found that sperm of brooding species are modified; however, since they had small samples for some taxa and none for the entire class Cubozoa and for six orders, they expected that exceptions to these generalizations will be found.

Based on ovarian morphology, Eckelbarger and Larson (1992, 1993) concluded that Scyphozoa is more closely related to Anthozoa than to Hydrozoa, but a variety of molecular and morphological data convincingly demonstrate the basal position of the Anthozoa relative to the derived Medusozoa (summarized by Bridge et al. 1995). The similarities perceived by Eckelbarger and Larson may be a consequence of the endodermal source of gametogenic tissue for Scyphozoa and Anthozoa, as opposed to the predominantly ectodermal source for Hydrozoa (Campbell 1974; Van de Vyver 1994). However, within the Scyphozoa, ovarian morphology does appear to reflect systematics: based on at least three species each, that of members of the orders Semaestomeae and Rhizostomeae fundamentally differs from that of Coronatae (Eckelbarger and Larson 1992), and, based on a single species, that of Stauromedusae differs from both (Eckelbarger and Larson 1993). On the other hand, monodisk strobilation and polydisk strobilation are not systematically consistent (Calder 1982); indeed, Pitt (2000) observed both within a single species, *Catostylus mosaicus*. The anthozoan order Ptychodactiaria was reduced to a suborder of Actiniaria when the sole feature characterizing it, the position in which gametes develop, was discovered to have been misinterpreted (Cappola and Fautin 2000).

Eckelbarger et al. (1998) inferred from the morphology of gametogenic tissue that the pennatulacean *Pennatula aculeata* is likely to spawn continuously rather than periodically. In reporting that his expectations about reproduction in the scleractinian *P. verrucosa*, based on taxonomic and skeletal parameters, were not borne out, Fadlallah (1985, p. 316) wrote, "any model that would explain the patterns observed must take into account a decidedly complex set of parameters such as taxonomic relatedness, colony morphology, polyp size and skeletal anatomy, and a suite of habitat characteristics". For scleractinians of the Red Sea, Shlesinger et al.

(1998, p. 698) concluded, "At present there seems to be no universal relationship between coral size, polyp size and/or egg size and mode of reproduction". Moreover, it has been suggested (Diekmann et al. 2002) that reproductive mode may influence the acquisition of endosymbiotic algae (zooxanthellae), which are intimately involved in nutrition and calcification of many cnidarians.

Certain reproductive attributes do appear to characterize at least some higher taxa of scleractinians; for example, Pocilloporidae is hermaphroditic (Harrison and Wallace 1990; Kinzie 1996), as are all three species of *Mussismilia* (Pires et al. 1999). Even exceptions (such as were predicted by Harrison and Jamieson 1999) may be informative if the pattern to which they do not conform is robust. Goffredo et al. (2000) inferred that hermaphroditism in the solitary scleractinian *Balanophyllia europaea* is derived, based on sperm morphology that is characteristic of gonochoric corals.

Reproductive features may also characterize species. A scleractinian species may have more than one mode of asexual reproduction; for example, Sakai (1998) documented both intratentacular and extratentacular budding in *G. aspera*. However, Stephenson (1928) cautiously claimed that a sea anemone species has, at most, one mode; although both pedal laceration and longitudinal fission have been documented in *Haliplanella luciae* (= *Diadumene lineata*) (see Shick 1976), thus far it is unique among actinians in that regard. Fautin and Chia (1986) distinguished the gonochoric sea anemone *Epiactis lisbethae* from the hermaphroditic *Epiactis prolifera* largely by sexuality. Two sympatric species of the scleractinian genus *Fungia* differ in "distribution pattern, reproductive timing, prevalence of budding and sex ratio" (Kramarsky-Winter and Loya 1998, p. 175).

Given the variety of modes by which we now know asexual reproduction can occur, its ecological and evolutionary implications have probably been underestimated. Its genetic consequences may be at least as important as those of sexual reproduction in ecological and even evolutionary time (Kinzie 1996; Fautin 1997; Vollmer and Palumbi 2002). McFadden (1997, p. 113) stated that in "species [in which] dispersal capabilities of asexual propagules may be similar to or even exceed that of sexual propagules...the population structure...may differ from the paradigm that has arisen based on studies of species with widely dispersed sexual propagules". For some species in some places, a significant source of recruits is through vegetative processes (e.g., fragmentation: Lirman 2000). Having studied *Zoanthus coppingeri* in the Great Barrier Reef region, Burnett et al. (1995, p. 672) wrote, "many of the more important groups on the GBR, such as the reef building corals, may show considerably more population structuring than has been described previously in strictly sexual species". Although Ayre et al. (1997) found the population of the hermatypic coral *P. damicornis* on the Great Barrier Reef to be panmictic, the population structure reflecting almost exclusively sexual recruitment, they recognized that populations on the geographic margins depend heavily on asexual/local recruitment. Particulars of the life cycle would be expected to affect distribution. Contrary to expectation, in their analysis of the 346 Mediterranean species of hydro-medusans, Boero and Bouillon (1993) found that the endemic fauna consists of approximately equal proportions of species possessing and lacking free medusae; they concluded

that having a free-living medusa stage makes a species more likely to spread, so colonists tend to have a medusa stage, but over a long time, environmental tolerance is more important in determining whether a species will persist.

Asexual reproduction produces what are implicitly or explicitly (e.g., McFadden 1991; Richmond 1997) expected to be genetically identical clonemates. Although initial reports were consistent with such an expectation (e.g., Shick 1976), as data have accumulated, intraclonal variability has been discovered (e.g., the biochemical composition of the anemone *H. lineata*: McManus et al. 1997). Position can affect fecundity: in a clone of the sea anemone *Anthopleura elegantissima* and a colony of the scleractinian *G. aspera*, marginal polyps produce fewer eggs than central ones (Francis 1976 and Sakai 1998, respectively). Environment affects the life cycle of the hydrozoan species *Laodicea indica*, which, when conditions are wet, passes from medusa to planula to hydroid and back to medusa, whereas when conditions are dry, the planula forms a gonotheca rather than a primary hydranth, and liberates one medusa (or, rarely, two) (Bouillon et al. 1991). Jokiel (1985) stressed the importance of environmental parameters in understanding patterns of scleractinian reproduction. Adaptations of animals to their local environment (e.g., Ayre 1995) might be explained by general-purpose genotypes (e.g., Shick 1976; Shick and Lamb 1977) or somatic mutation, perhaps accompanied by selection among genotypes (Fautin 1997), or some combination.

Quantification

An increasing number of studies on cnidarians provide quantitative data on both sexual and asexual reproduction. For species in which both occur, recognition is growing that they interact (e.g., Miller and Grange 1997) and that their relative proportions have profound life-history consequences, i.e., that there are trade-offs (e.g., Littlefield et al. 1991; Hughes et al. 1992). Given what is known about other aspects of reproduction in Cnidaria, the importance of sexual versus asexual reproduction is more likely to vary across the range of a species than to be a fixed attribute of the species.

Because a colony typically must be a minimum size to reproduce sexually (e.g., Hall and Hughes 1996; Kapela and Lasker 1999; Smith and Hughes 1999), its output from sexual reproduction can be affected by breakage of the skeleton (summarized, for example, by Zakai et al. 2000) or other damage (Oren et al. 2001). Typically such perturbations have negative effects (e.g., Kalafatiæ 1997; Schierwater and Hadry 1998), at least in part because resources are diverted for repair (Oren et al. 2001). The reverse does not necessarily occur: a symbiotic damselfish positively affected growth of the host coral colony (*Stylophora pistillata*) but seemed not to affect reproductive output (Lieberman et al. 1995). Even fragments larger than the minimum size for gamete formation may be incapable of reproducing sexually (Smith and Hughes 1999). The polyps being expelled from a coral colony lack gametogenic tissue, even when the polyps around them are gravid, but they "...are larger than sexually derived propagules [so] they begin their sessile lives at the juvenile stage, avoiding the rigours of larval development, settlement and metamorphosis" (Kramarsky-Winter et al. 1997, p. 137). Smith and Hughes (1999) concluded for three species of *Acropora*

on the Great Barrier Reef that adverse effects on sexual reproduction produced by fragmentation were not compensated for by any vegetative propagation that may have resulted. In Florida, colonies of *Acropora palmata* as well as fragments from them lacked gametes for 4 years from the time of damage (Lirman 2000).

Lirman (2000) reported that fragment size was unrelated to survival in *A. palmata* but, although there were differences among the species of *Acropora* studied by Smith and Hughes (1999), large fragments survived significantly better than smaller ones. A possibly confounding factor is that in the former study, fragments were generated naturally, whereas for the latter they were artificially created. Karlson (1988) found fragment size to be directly proportional to survival in *Zoanthus solanderi*. Substratum may also affect survival of asexual propagules (Karlson 1988; Lirman 2000). The rate of asexual reproduction in the field may vary with habitat (Anthony and Svane 1994), with density (Karlson et al. 1996), and with season (Chadwick-Furman and Spiegel 2000); in the laboratory it can vary with amount of food supplied (Hand and Uhlinger 1995).

Sexual aspects of reproductive effort in modular organisms were reviewed by Hall and Hughes (1996). Recent field studies on sexual reproductive effort in cnidarians include those by Brazeau and Lasker (1990) on the Caribbean gorgonian *Briareum asbestinum*, Szmant (1991) on two Caribbean scleractinians of the genus *Montastrea*, Coma et al. (1995b) on the Mediterranean gorgonian *P. clavata*, and Coma et al. (1996) on the Mediterranean hydroid *Campanularia everta*. Ward (1995) compared colonies of the coral *P. damicornis* in Western Australia that are hermaphroditic brooders with all-male colonies that do not brood; the latter grew 1.5 times faster and had more stored lipid following reproduction. Recent quantitative laboratory research on *Hydra* has been done by Grassi et al. (1995). Lucas and Lawes (1998) compared two populations of the scyphomedusa *Aurelia aurita* in England that differ in reproductive output.

Having a baseline allows assessment of the effects of exogenous factors on reproduction, a major life-history trait. Most studies deal with perturbations, including those by other organisms (e.g., Aceret et al. 1995) and by anthropogenic substances, both synthetic (Negri and Heyward 2001) and more natural (e.g., Reichelt-Brushett and Harrison 1999; Ward and Harrison 2000). Sier and Olive (1994) found so much variability in fecundity among colonies and, by implication, between years that they questioned whether fecundity should be used to monitor stress. Such variability is clear in the long-term data of Shaw (1989) for the sea anemone *C. pedunculatus*, those of Lucas et al. (1995) for the hydromedusan *Clytia hemisphaerica* (2 years only), those of Lasker et al. (1998) for the clonal gorgonian *P. kuna*, those of Ben-David-Zaslow et al. (1999) for the soft coral *Heteroxenia fuscescens*, and those of Hughes et al. (2000) for three species of the scleractinian *Acropora* (2 years only). Ward and Harrison (2000) reported on nutrient-enrichment experiments with scleractinians of the Great Barrier Reef. Colonies of *Acropora longicyathus* exposed to elevated N (alone and in combination with P) had fewer, smaller eggs and less spermatogenic tissue per polyp than the controls, whereas those exposed to elevated P alone had more, smaller eggs and more spermatogenic tissue than the controls, although these results were confounded

to some extent by transplanted colonies having smaller eggs than the parent colonies. The results from *Acropora aspera* were much less consistent, perhaps because of fewer colonies but apparently also because of less pattern; on some dates the number of eggs was higher than in controls, whereas on other dates the number was smaller, but overall, control colonies of *A. aspera* had higher fecundity than experimental transplants. Long-term observations on natural perturbations are few: Guzmán and Holst (1993) found less gametogenic tissue but no fewer reproductive colonies or less gametogenic tissue per polyp in the scleractinian *Siderastrea siderea* inhabiting areas that had been exposed to spilled oil 5 years previously in Panamá than in those in areas unaffected by the spill.

Conclusions

Empirical and experimental knowledge of reproduction by members of the phylum Cnidaria is accumulating rapidly. Interpretation of data relies to a greater or lesser extent on assumptions that may not be relevant to these animals, which are so unlike those for which much of the interpretative machinery was developed (Fautin 1997). This is as true for research in ecology or evolution as it is for that in reproductive biology. It is essential to develop analytical frameworks and strategies appropriate to animals in which sexual reproduction may not be paramount, that during one lifetime may pass through two or more phases differing radically in morphology and ecology, that may hybridize, that are potentially extremely long-lived, and that through both sexual and asexual reproduction may transmit mutations arising in somatic tissue. Attempts to deal with such complexities are beginning. Mathematical models include those by Orive (1995, 2001), who explicitly tested hers on data from scleractinians, and one by Pedersen and Tuomi (1995). Grosberg and Hart (2000) did experiments on mate selection for allorecognition polymorphisms in a colonial tunicate and a colonial hydroid, and the experiments of Hoare and Hughes (2001) on a bryozoan tested theories about hermaphroditism.

Much in this paper implies a rather faint border between sexual and asexual reproduction. This may be because the tools we currently have are not sufficiently powerful to allow us to distinguish between the two. A quarter century after it became virtually certain that not all propagules resembling planulae are the result of sexual reproduction, the source of many that are not is unresolved. More importantly, short of observing fertilization (if any) and development, there is no easy way to determine whether a propagule is sexual or asexual in origin. For example, using electrophoresis, Edmands (1995, p. 723) found the externally brooded young of the actinian *E. lisbethae* were clearly produced sexually, but those of *E. prolifera* "were all identical to their mothers, a result consistent with either asexual reproduction, self-fertilization or extreme biparental in-breeding".

But perhaps the border actually is faint. Finding that pedal laceration in the sea anemone *Metridium senile* varied with environment, Anthony and Svane (1994, p. 257) concluded that "properties of asexual proliferation possess both habitat-related and intrinsic components". In the only anemone that has been cultured through its entire life cycle (Hand and Uhlinger 1992), the gonochoric *N. vectensis*, Hand obtained

evidence that the intrinsic component is heritable. Siblings held under identical laboratory conditions may differ significantly in fission rate, but clonemates differ to only a minor extent (Hand and Uhlinger 1995). Hand repeatedly crossed fast-dividing males and females and slow-dividing males and females. After several successive generations of inbreeding, the progeny of the former crosses divided rapidly and the progeny of the latter seldom divided; five individuals did not divide in 4 years of observation (C. Hand, personal communication). Thus, the ability to proliferate asexually can be selected for or against. Presumably this mechanism could be manifested in colonial organisms that propagate vegetatively by fragmentation as much as in solitary organisms that divide.

There is evidence of a mechanism that would allow cnidarians to adjust the proportions of sexual and asexual reproductive effort even more rapidly. In documenting transverse fission by the anemone *A. stellula*, Schmidt (1970, p. 245) wrote, "The fission process spreads infectiously". In 2001, I was told by Julian Sprung (a marine aquarist and author of publications for home aquaria) that when he and other aquarists put into an aquarium an anemone of a species that typically undergoes frequent longitudinal fission, the division rate of anemones in the aquarium belonging to species that do not divide as frequently will increase. He therefore inferred that some chemical signal released by dividing anemones can stimulate division in heterospecific as well as conspecific anemones.

On the other side of the faint border, sex determination is problematic in cnidarians. Carré and Carré (2000) reviewed the subject in hydras, the group in which this subject has been most studied, but their own research was on a marine hydrozoan, *C. hemisphaerica*. There appear to be separate male and female germ cell lines in hydrozoans, which tend to be gonochoric (except for siphonophores), but environmental conditions can affect how sex is manifested. However, under all conditions, the experimental populations studied by Carré and Carré (2000) contained colonies of both sexes, which is evidence that environmental conditions do not completely determine sexuality in this animal.

A faint border may mean that a distinction between sexual and asexual reproduction is not very important to the biology of cnidarians (Budd 1990). Equivalence of the two, at some level, is supported by a gene studied by Miller and Steele (2000) that is expressed in interstitial cells most strongly during gametogenesis and budding. Although the paradigm is that sexual reproduction is essential to evolutionary success (reviewed by Fautin 1997), it is clear that the population dynamics of some cnidarians may be dominated by production and death of ramets, with new genets being rare (e.g., Billingham and Ayre 1997; Coffroth and Lasker 1998; Lirman 2000). Even sexual reproduction may proceed in ways that are considered atypical or maladaptive, such as selfing (Hinsch and Moore 1992; Edmands 1995; Brazeau et al. 1998).

Comparing aspects of reproduction among cnidarians is highly desirable. Phylogenetic commonalities can thereby be distinguished from idiosyncratically adaptive strategies. For example, the various modes of vegetative propagation can be assessed for their importance relative to sexual reproduction in an ecological analysis as well as for their value in tracing phylogenies. Such information is vital to research in other

fields as well, such as physiology. Particularly for comparative research, it is essential that terms be clearly defined as part of understanding underlying mechanisms. It is obvious from what I have written that “budding” is used for a wide variety of phenomena. Therefore, analyzing what has been termed budding is unlikely to provide ecological or evolutionary insights. However, an analysis restricted to Hydrozoa and Scyphozoa, in which the term appears to be used for the identical phenomenon, could provide understanding of ecology (e.g., under what conditions is it manifested?), evolution (e.g., is it homologous in the two classes?), or the interaction of the two.

Transverse fission is, to my mind, a reproductive phenomenon that is more interesting and promising for comparative analysis to shed light on both evolution and ecology. This distinctive mode of vegetative propagation has been documented in the three major classes of Cnidaria, but is rare outside Scyphozoa. Is its occurrence in other taxa evidence of an underlying potential for greater reproductive flexibility in cnidarians than is typically evident? If so, it should also be sought in Cubozoa. Understanding its morphogenesis in all groups is essential to determining if it is homologous across the classes. If not, the circumstances under which strobilation occurs and how it is controlled could be important to understanding ecology and reproductive biology. If so, understanding the conditions under which it is manifested in Hydrozoa and Anthozoa could shed light on scyphozoan evolutionary history. The fact that the strobilating polyp produces another polyp in Hydrozoa and Anthozoa but an ephyra (a medusa) in Scyphozoa may mean that the processes are not homologous (Schmidt (1970) considered transverse fission to be non-homologous even within Actiniaria). However, differences in the product of strobilation could shed light on factors that determine how polyp and medusa develop: ultimate ones (the ecological context) and proximate ones (which genes are active).

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