Sexual Reproduction of Scleractinian Corals

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Abstract Sexual reproduction by scleractinian reef corals is important for maintaining coral populations and evolutionary processes. The ongoing global renaissance in coral reproduction research is providing a wealth of new information on this topic, and has almost doubled the global database on coral reproductive patterns during the past two decades. Information on sexual reproduction is now available for 444 scleractinian species, and confirms that hermaphroditic broadcast spawning is the dominant pattern among coral species studied to date. Relatively few hermaphroditic or gonochoric brooding species have been recorded. Multispecific coral spawning has been recorded on many reefs, but the degree of reproductive synchrony varies greatly within and among species at different geographic locations.

Keywords

1 Introduction

This review provides an overview of global knowledge and emerging patterns in the reproductive characteristics of the 444 scleractinian species for which information on sexual reproduction is available, and updates the previous review by Harrison and Wallace (1990), with particular emphasis on new discoveries and data from the past 2 decades. Sexual reproduction in scleractinian corals has been widely studied in many regions of the world, and substantial new information has become available since earlier detailed reviews on this subject by Fadlallah (1983), Harrison and Wallace (1990), and Richmond and Hunter (1990), with more recent topic reviews provided by Richmond (1997), Harrison and Jamieson

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(1999), Kolinski and Cox (2003), Guest et al. (2005a), Harrison and Booth (2007), and Baird et al. (2009a).

Scleractinian reef-building corals are foundation species on coral reefs because they provide the complex three-dimensional structure and primary framework of the reef, and essential habitats and other important resources for many thousands of associated species (reviewed by Harrison and Booth 2007). These corals are distinguished from other members of the Class Anthozoa (Phylum Cnidaria) such as soft corals, by their continuous hard calcium carbonate crystal exoskeleton, which form the essential building blocks of the reef ecosystem when cemented together by crustose coralline algae. The term "coral" is used in this review to refer to these hard corals from the Order Scleractinia.

Although corals are widely distributed throughout the world's seas and deeper ocean environments, they are particularly significant in shallow tropical and subtropical seas where the mutualistic symbiosis between the coral polyps and their endosymbiotic dinoflagellates (zooxanthellae) fuels light enhanced calcification and rapid growth of reef-building corals, resulting in coral reef development. Corals can be broadly divided ecologically, but not systematically, into reef-building (hermatypic) corals and non-reef-building (ahermatypic) corals. Hermatypic corals create the primary reef framework and most hermatypic species in shallow warm-water habitats normally contain millions of zooxanthellae (i.e., zooxanthellate); in contrast, although ahermatypic corals also secrete complex aragonite exoskeletons they do not usually contribute significantly to reef formation, and mostly lack zooxanthellae (e.g., Yonge 1973; Schuhmacher and Zibrowius 1985; Cairns 2007). However, some azooxanthellate corals do contribute to reef-building and are therefore hermatypic, including some deeper-water and deep-sea colonial cold-water corals that form reefs or bioherms, which provide important habitats for many other species (e.g., Brooke and Young 2003; Waller and Tyler 2005; Friewald and Roberts 2005).

The total number of extant scleractinian "species" is not known, and estimating global coral species richness is complicated by a number of issues (e.g., Veron 1995, 2000; Cairns 1999, 2007; Harrison and Booth 2007). These include the limited exploration of deeper reef, mesophotic, and

deep-sea environments, as well as some shallow tropical reef regions where new species are likely to be found, and imperfect taxonomic resolution of highly variable species and potential cryptic species. Furthermore, the discovery of hybridization among some morphologically different coral morphospecies (e.g., Willis et al. 1992, 1997; Szmant et al. 1997; van Oppen et al. 2002; Vollmer and Palumbi 2002) challenges the application of the traditional biological-species concept based on reproductive isolation between different species, for some corals.

If we assume that the current primarily morphologically based taxonomy provides an appropriate indication of global coral species richness, there are probably at least 900 extant hermatypic scleractinian species (e.g., Wallace 1999; Veron 2000; J. Veron, personal communication). Of these, 827 zooxanthellate hermatypic coral species have been assessed for their conservation status (Carpenter et al. 2008). In addition, at least 706 azooxanthellate scleractinian species are known, including 187 colonial and 519 solitary coral species, with their most common depth range being 200–1,000 m (Cairns 2007). Of the more than 1,500 recognized coral species, aspects of sexual reproduction have now been recorded in at least 444 species, the vast majority being shallow-water zooxanthellate hermatypic coral species. This global knowledge base provides a wealth of information on the biology and ecology of coral reproduction that surpasses most other marine invertebrate groups, and corals therefore provide an important model for assessing life history and evolutionary theory.

This chapter focuses mainly on sexual reproductive characteristics in hermatypic species because these corals have been more extensively studied and are foundation species on coral reefs (Harrison and Booth 2007). Additional reference is made to sexual reproduction in some ahermatypic scleractinian species, and an overview of asexual reproduction in corals is provided below to highlight the diversity of reproductive processes exhibited by scleractinians.

2 Coral Life Cycle and Reproduction

Corals have a relatively simple life cycle involving a dominant benthic polyp phase and a shorter planula larval phase. The polyp phase is characterized by growth of tissues and skeleton that often includes one or more forms of asexual budding or reproduction; and repeated cycles of sexual reproduction (iteroparity) involving the production of gametes, fertilization, embryo development, and a larval phase that is usually planktonic and dispersive to some degree (Harrison and Wallace 1990). If the planula survives and successfully attaches and settles permanently on hard substratum (Fig. 1), it metamorphoses from the larval form into a juvenile polyp
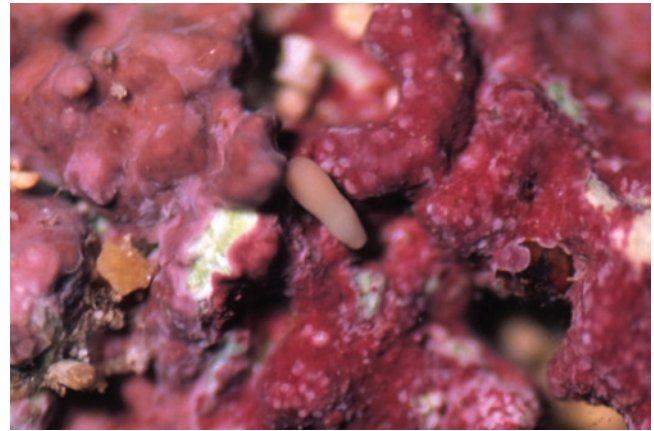

Fig. 1 A brooded *Isopora cuneata* planula searching reef substratum covered with crustose coralline algae for a suitable site for initial attachment and metamorphosis into a juvenile polyp (Photo: author)

that initiates the formation of the calcium carbonate exoskeleton. Subsequent growth during an initial presexual juvenile phase leads to development of the adult form that becomes sexually reproductive, which completes the life cycle (Harrison and Wallace 1990).

Asexual reproduction produces genetically identical modules that may prolong the survival of the genotype, whereas sexual reproduction enables genetic recombination and production of new coral genotypes that may enhance fitness and survival of the species. Four basic patterns of sexual reproduction are evident among corals, which include: hermaphroditic broadcast spawners, hermaphroditic brooders, gonochoric broadcast spawners, or gonochoric brooders. Hermaphroditic corals have both sexes developed in their polyps and colonies, whereas gonochoric corals have separate sexes; and corals with these sexual patterns either broadcast spawn their gametes for external fertilization and subsequent embryo and larval development, or have internal fertilization and brood embryos and planula larvae within their polyps (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990). However, not all coral species are readily classified into these basic patterns, as mixed sexual patterns or both modes of development are known to occur in some species.

2.1 Asexual Budding and Reproduction

Different modes of asexual production can be distinguished; asexual budding of polyps leads to the formation of coral colonies, while various forms of asexual reproduction result in the production of new modules that form physically separate but genetically identical clones (ramets) (reviewed by Highsmith 1982; Cairns 1988; Harrison and Wallace 1990;

Richmond 1997). Most hermatypic coral species (Wallace 1999; Veron 2000) and about 26% of the known ahermatypic azooxanthellate coral species (Cairns 2007) form colonies via asexual budding of polyps and are therefore modular, iterative colonial organisms. Budded polyps usually form by growth and internal division of existing polyps (intratentacular budding) or development of new polyps from tissues adjacent to, or between, existing polyps (extra-tentacular budding) (reviewed by Vaughan and Wells 1943; Wells 1956; Cairns 1988; Veron 2000). In most colonies, these budded polyps remain interconnected (Fig. 2), and the colony is partly integrated via nerve and muscular networks within the thin veneer of tissues that overly the skeleton they secrete (e.g., Gladfelter 1983; Harrison and Booth 2007).

Asexual budding produces genetically identical polyps within each colony; however, DNA damage and somatic mutations can genetically alter cell lineages and may induce development of neoplasms (tumors) within colonies (e.g., Coles and Seapy 1998). In a few coral species, gregarious settlement of larvae and allogenic fusion of newly settled primary polyps produce chimeras that result in colonies composed of different genotypes (e.g., Hidaka et al. 1997; Hellberg and Taylor 2002; Puill-Stephan et al. 2009). This would confer some advantages of initial increased size and reduced mortality of chimeras during the vulnerable juvenile polyp phase of the life cycle. The increased genetic diversity may also enhance colony survival unless negative interactions and competition between cell lineages from different genotypes occur (Puill-Stephan et al. 2009).

The formation of coral colonies through modular iteration of budded polyps, and associated growth of their supportive and protective exoskeleton, provide important ecological and
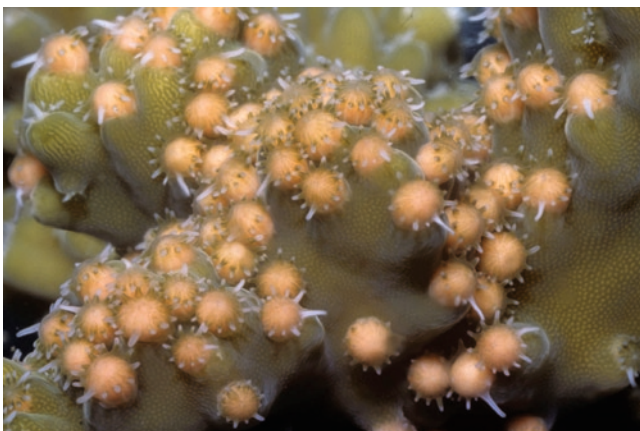

Fig. 3 Large colonies have increased sexual reproductive output, such as the *Acropora tenuis* colony seen here spawning many thousands of buoyant egg–sperm bundles on the Great Barrier Reef (GBR) during the crepuscular period just after sunset (Photo: author)

evolutionary advantages for colonial species. Colonial growth enables corals to grow much larger than most single polyps; thus, colonies can occupy more space and more effectively compete for resources by growing above the reef substratum or over other benthos, and colonies can survive the death of individual polyps and partial colony mortality (e.g., Jackson and Coates 1986; Rosen 1990; Hughes et al. 1992). Increased size reduces the mortality risk in juvenile corals and increases colony biomass and resource acquisition, leading to increased reproductive output as the number of gravid polyps and fecundity increases with size and age (Fig. 3); hence, larger colonies can dominate gamete production within coral populations, unless reproductive senescence occurs (e.g., Kojis and Quinn 1981, 1985; Babcock 1984, 1991; Szmant-Froelich 1985; Rinkevich and Loya 1986; Harrison and Wallace 1990; Hall and Hughes 1996; Goffredo and Chadwick-Furman 2003; Zakai et al. 2006).

Corals exhibit a wide range of asexual reproductive processes that produce new clonal solitary corals or colonies (Highsmith 1982; Cairns 1988; Harrison and Wallace 1990). These processes include colony fragmentation resulting from storm and wave impacts or other damage, colony fission, longitudinal and transverse division, polyp expulsion or polyp "bail-out," growth and detachment of polyp balls in some *Goniopora* colonies, and budding of polyps from an anthocaulus or regenerating tissues in fungiids and some other corals (e.g., Wells 1966; Rosen and Taylor 1969; Sammarco 1982; Krupp et al. 1992; Kramarsky-Winter and Loya 1996; Kramarsky-Winter et al. 1997; Gilmour 2002; Borneman 2006). In addition, asexual production of brooded planulae occurs in populations of the common reef coral *Pocillopora damicornis* (Stoddart 1983; Ayre and Miller 2004; Sherman et al. 2006), and in *Tubastrea coccinea* and

Fig. 2 Integration of polyp tissues enables activities such as sexual reproduction to be coordinated within colonies that develop from asexual budding of coral polyps. Coordinated behavior is shown in this colony of *Acropora arabensis*, where bundles of eggs and sperm bulge under the oral disk of each polyp in the "setting" phase just prior to synchronized spawning (Photo: author)

Tubastrea diaphana (Ayre and Resing 1986). *Oulastrea crispata* may also brood asexually produced planulae during periods when sexual reproduction has ceased (Nakano and Yamazoto 1992; Lam 2000).

Asexual reproduction can therefore produce genetically identical ramets that may occupy substantial space on reefs and in some cases may disperse widely. The extent and importance of asexual versus sexual reproduction varies greatly among different populations of corals and among different coral species (e.g., Ayre et al. 1997; Ayre and Hughes 2000; Miller and Ayre 2004; Baums et al. 2006; Whitaker 2006; Sherman et al. 2006; Foster et al. 2007). The range of reproductive processes and modes in corals partly reflects the extraordinary ability of cnidarian cell lines to differentiate, dedifferentiate, and redifferentiate (e.g., Campbell 1974; Holstein et al. 2003), which provides their tissues with remarkable developmental plasticity and adaptability.

3 Historical Perspectives on Coral Reproduction

The current, extensive global knowledge of coral reproduction is a product of many decades of research; hence, it is useful to provide a brief overview of previous and recent research as an historical and geographic context for the more detailed summaries of sexual reproductive characteristics in the remaining sections of this chapter. Harrison and Wallace (1990) reviewed the history of research on coral reproduction and noted that sexual reproduction in scleractinians had been studied for 200 years, since Cavolini (c. 1790, cited in de Lacaze-Duthiers 1873) observed *Astroides* planulae in the Mediterranean region.

Most of the early reproduction studies focused on coral species that brooded planula larvae within their polyps, while early reports of broadcast spawning of gametes were either overlooked or dismissed as aberrant by subsequent researchers (see Harrison and Wallace 1990). This led to the dogma that corals were typically or uniformly viviparous brooders (e.g., Duerden 1902a; Hyman 1940; Vaughan and Wells 1943; Wells 1956). That misconception was rapidly overturned by research in the early 1980s, which demonstrated that broadcast spawning of gametes was the dominant mode of development in the majority of coral species studied worldwide (Fig. 4). Much of that new information resulted from the discovery of mass coral spawning on the Great Barrier Reef (GBR), which included records of broadcast spawning in more than 130 coral species (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). This clearly established broadcast spawning as the dominant mode of reproduction among reef corals studied in the Pacific region, and significantly changed our understanding of reef coral
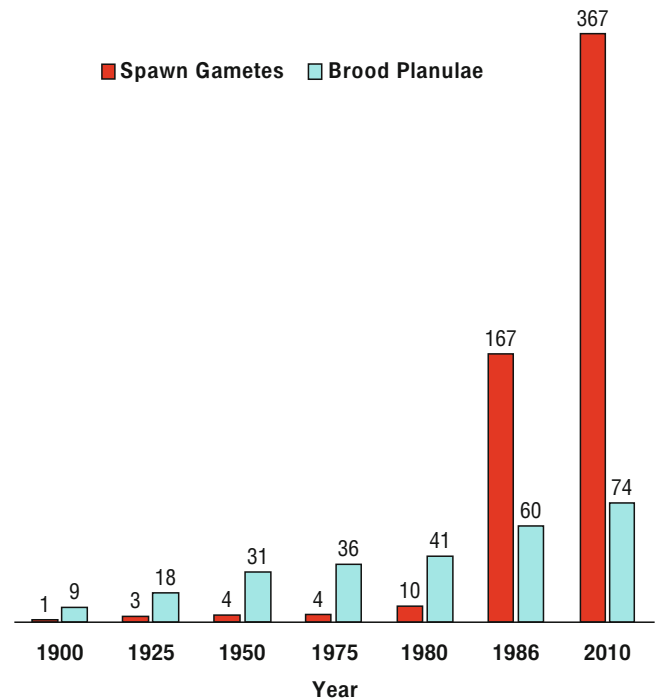

Fig. 4 Total number of coral species worldwide whose mode of development was recorded during different periods, from 1900 to the present. The trends highlight the historical bias towards brooding species prior to the 1980s, and the rapid increase in broadcast spawning species reported following the discovery of mass coral spawning on the GBR in the early 1980s. The species totals for broadcast spawning species (*red columns*) and brooding species (*pale blue columns*) include an additional ten species in 1986 (see Table 7.4 in Harrison and Wallace 1990), and an additional 13 species in 2010, in which both modes of development have been reported (see Table 4)

ecology. Somewhat different patterns of coral reproduction were evident in other reef regions in the Indo-Pacific (reviewed by Richmond and Hunter 1990; Harrison and Wallace 1990), and Szmant (1986) noted that brooding corals were relatively more abundant among coral species studied in the Atlantic region, and were characterized by small colony size.

By the late 1980s, at least 157 coral species were known to broadcast spawn gametes, while 50 species were recorded to brood their larvae, with another ten species recorded to have both modes of development (Fig. 4; see Harrison and Wallace 1990). Hermaphroditic broadcast spawners were by far the most common group recorded, gonochoric broadcast spawners were moderately common, while hermaphroditic brooders and gonochoric brooders were relatively uncommon (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990). Strong systematic trends were evident in sexual patterns, arrangement of gametes in polyps and sperm structure, whereas the mode of reproduction was more variable and a relatively plastic life history trait (Harrison 1985).

Table 1 Summary of global information on sexual patterns and mode of development for 444 scleractinian species

Sexual pattern Mode of development	Hermaphroditic	Mixed or contrasting sexuality reported	Gonochoric	Unknown sexual pattern	Total species
Spawn gametes	258	6	78	12	354
Spawn gametes and brood	8	1	4	–	13
Brood	25	5	15	16	61
Unknown mode of development	4	–	12	–	16
Total species	295	12	109	28	444

Information on reproductive characteristics was obtained primarily from analysis of all the available known publications on sexual reproduction in corals, with some additional data from summaries in other reviews (Fadlallah 1983; Harrison 1985; Harrison and Wallace 1990; Richmond and Hunter 1990; Richmond 1997; Harrison and Booth 2007; Baird et al. 2009a), conference abstracts, research reports and postgraduate theses, plus extensive information made available to the author from many colleagues around the world over the past 30 years, some of which is unpublished.

4 Recent Advances in Coral Reproduction Research

Over the last 20 years, research on coral reproduction has continued to grow substantially and has expanded into many reef regions that were not previously well represented, including equatorial and tropical regions of high coral species richness and biodiversity, and some subtropical reef regions (reviewed by Richmond 1997; Guest et al. 2005a; Harrison and Booth 2007; Baird et al. 2009a). This more recent research has resulted in substantial new information and has almost doubled the number of coral species for which sexual reproductive data are now available, from more than 230 species in the late 1980s (Harrison and Wallace 1990; Richmond and Hunter 1990) to at least 444 species by 2010 (Table 1). The current global data generally confirm and extend many of the trends and patterns highlighted in earlier studies, and some recent advances in our understanding of sexual reproduction in corals are summarized in Table 1.

4.1 Biogeographical Patterns of Coral Reproduction

As expected, multispecific coral spawning has now been recorded in many reef regions, but the scale of spawning and the degree of reproductive synchrony varies greatly within and among populations of different coral species in different regions, resulting in varied patterns of reproduction among coral assemblages (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990; Richmond 1997; Kolinski and Cox 2003; Guest et al. 2005a; Harrison and Booth 2007; Baird et al. 2009a). The global data show that reproductive patterns in different coral assemblages form a continuum, ranging from highly synchronized mass spawning events involving many colonies of many species from different families, through to a wide range of other synchronous multispecific

spawning patterns involving fewer species and corals (summarized in Harrison and Wallace 1990; Richmond 1997; Harrison and Booth 2007; Mangubhai and Harrison 2009; Baird et al. 2009a). At the other extreme of this continuum, 24 coral species studied in the northern Gulf of Eilat in the Red Sea exhibit temporal reproductive isolation (Shlesinger and Loya 1985; Shlesinger et al. 1998). In contrast, more recent research has recorded highly synchronous maturation of gametes among many *Acropora* species on reefs 250 km south of Eilat in the Egyptian Red Sea, which is likely to result in large multispecific spawning events (Hanafy et al. 2010).

Coinciding with the increased range of reproductive patterns now evident among coral assemblages, some confusion has arisen over the use of the terms "mass spawning" and "multispecific spawning." For example, a few publications have described synchronous spawning by colonies of one or a few coral species in the Gulf of Mexico and Caribbean region as mass spawning (e.g., Gittings et al. 1992; Hagman et al. 1998a; Beaver et al. 2004; Bastidas et al. 2005), or have used the terms mass spawning and multispecific spawning interchangeably (e.g., Guest et al. 2005a), leading to different interpretations and application of these terms (e.g., Mangubhai and Harrison 2008a, 2009; cf. Guest et al. 2005a; Baird and Guest 2009). Harrison and Booth (2007) distinguished between the larger-scale synchronous mass spawning events currently known from some reefs on the GBR and Western Australia (WA), from other smaller-scale multispecific spawning events involving fewer species and corals. This distinction has the advantage of differentiating between reproductive patterns involving reproductive synchrony among fewer corals and species (i.e., multispecific spawning), from the largest synchronous mass spawning events recorded so far, and most recently published papers have tended to differentiate the terms "multispecific spawning" and "mass spawning."

By definition, multispecific spawning refers to synchronous spawning by two or more species, whereas the term mass spawning was initially used to describe the highly synchronous nocturnal spawning of many coral colonies of many

species from a range of scleractinian families on the GBR (Harrison et al. 1983, 1984; Willis et al. 1985; Babcock et al. 1986; Wallace et al. 1986; Oliver et al. 1988; Harrison 1993). Synchronous spawning by more than 20–30 coral species involving many or most colonies of extensively sampled and monitored populations has been recorded on peak mass spawning nights after full moon periods in the austral late spring and early summer months on some GBR reefs, with split-spawning over consecutive lunar cycles occurring in some populations in some years (Willis et al. 1985; Babcock et al. 1986; Harrison and Wallace 1990). Mass spawning therefore represents an extreme form of multispecific spawning (Harrison and Booth 2007; Mangubhai and Harrison 2009). Willis et al. (1985) partly defined mass spawning as "the synchronous release of gametes by many species of corals, in one evening between dusk and midnight" to emphasize the large number and diversity of coral taxa participating in these events, but implicit in this definition was that it involves synchronous spawning by many individual corals in many of these species (e.g., Rosser and Gilmour 2008). Similar large-scale mass-spawning events have been reported among corals on some tropical and subtropical WA reefs in the austral autumn period involving synchronous spawning by up to 24 coral species from a wide range of genera and families (Simpson 1985, 1991; Simpson et al. 1993; Babcock et al. 1994). More recent research on some WA coastal and offshore reefs has confirmed a larger primary mass spawning period in autumn, with a smaller but ecologically significant multispecific spawning period involving fewer species and colonies occurring during late spring or early summer (Rosser and Gilmour 2008; Gilmour et al. 2009; Rosser and Baird 2009).

It is also important to note that some corals on GBR and WA reefs also, or only, spawn or release planulae during nonmass spawning periods. For example, some species reproduce on other lunar nights or during different lunar phases, or at other times of the year, and some corals exhibit biannual or multiple cycles of gametogenesis and breeding during the year (e.g., Marshall and Stevenson 1933; Kojis and Quinn 1982; Harriott 1983a, b; Harrison et al. 1984; Willis et al. 1985; Wallace 1985; Babcock et al. 1986; Kojis 1986a; Willis 1987; Harrison and Wallace 1990; Stobart et al. 1992; Tanner 1996; Baird et al. 2002, 2009a; Wolstenholme 2004; Rosser and Gilmour 2008; Gilmour et al. 2009; Rosser and Baird 2009; among others). Therefore, the mass coral spawning paradigm does not, and was never intended to, encompass all coral reproductive data from these regions. Future studies are likely to increase both the numbers of coral species known to have highly synchronous gametogenic and breeding patterns that participate in mass spawning events, as well as increase the numbers of species that do not participate or only partially spawn during mass spawning events. Broader scale surveys of *Acropora*

assemblages at various sites along the GBR have also revealed a high degree of synchronous maturation of gametes in some *Acropora* populations, but less synchronous maturation and breeding periods in some other populations (e.g., Oliver et al. 1988; Hughes et al. 2000; Baird et al. 2002, 2009a, b).

Mass coral spawning is likely to occur in some other reef regions with diverse coral assemblages where gametogenic cycles and maturation are highly synchronized within and among populations of many species during brief seasonal breeding periods. Large multispecific coral spawning events have been increasingly recorded in some other Indo-Pacific regions, and some of these may prove to be of a similar scale compared to the GBR and WA mass spawning events, when further data on both the numbers of corals and the range of species that spawn synchronously become available.

Diverse reproductive patterns ranging from highly synchronized gamete maturation and multispecific spawning by more than ten coral species and many corals occurring during one or a few nights, through to less synchronous multispecific spawning by fewer corals and species and more extended breeding seasons have now been recorded from many Indo-Pacific regions, including: Japan (e.g., Heyward et al. 1987; Shimoike et al. 1992; Hayashibara et al. 1993; van Woesik 1995; Nozawa et al. 2006; Mezaki et al. 2007; Baird et al. 2009b), Taiwan (Dai et al. 1992; see also Kawaguti 1940), the Philippines (Bermas et al. 1992; Vicentuan et al. 2008), Palau (Kenyon 1995; Penland et al. 2004, and unpublished data; see also Kawaguti 1941a, b), Yap (Kenyon 1995), Guam (Heyward 1988a; Richmond and Hunter 1990; Richmond 1997), Singapore (Guest et al. 2002, 2005a, b), Thailand (Piromvaragorn et al. 2006; Kongjandtre et al. 2010), Indonesia (Edinger et al., unpublished data in Tomascik et al. 1997; Baird et al. 2009a), Papua New Guinea (Oliver et al. 1988; Baird et al. 2009a), Solomon Islands (Baird et al. 2001), Fiji and Western Samoa (Mildner 1991), Line Islands (Kenyon 2008), French Polynesia (Carroll et al. 2006), subtropical eastern Australia (Wilson and Harrison 1997, 2003; Harrison 2008), Egyptian Red Sea (Hanafy et al. 2010), and some other Indo-Pacific regions (e.g., Richmond 1997; Baird et al. 2009a). However, as noted for the GBR and WA reproductive patterns, other coral species are known to spawn or planulate at other times in these regions (reviewed by Harrison and Wallace 1990; Richmond and Hunter 1990; Richmond 1997; see also Kinzie 1993; Fan and Dai 1995, 1999; Dai et al. 2000; Bachtiar 2000; Diah Permata et al. 2000; Fan et al. 2002, 2006; Wallace et al. 2007; Villanueva et al. 2008; among others). In the South Pacific region, coincident spawning records after full moon periods in the austral spring and summer seasons occur on reefs throughout the GBR up to 1,200 km apart (e.g., Willis et al. 1985; Babcock et al. 1986; Oliver et al. 1988), and north to the Solomon Islands (Baird et al. 2001), and east to French Polynesia (Carroll et al. 2006).

Latitudinal trends in the seasonal patterns and timing of reproduction are evident in some Pacific regions. For example, peak reproduction tends to occur in late spring to early summer in lower latitude tropical reefs, with progressively later peaks in reproduction occurring in subtropical and higher latitude reefs (e.g., van Woesik 1995; Wilson and Harrison 1997, 2003; Nozawa et al. 2006; Mezaki et al. 2007; Harrison 2008; Baird et al. 2009b).

Less synchronous and more protracted spawning seasons have been recorded among hundreds of colonies of 20 *Acropora* species on equatorial reefs in Kenya where spawning occurred over 2–5 months within populations of different species, and gamete release in *Acropora* and some faviid species extended over a 9-month period from August to April (Mangubhai and Harrison 2006, 2008a, b, 2009; Mangubhai 2009). Although coincident spawning was recorded in colonies of two *Acropora* species, and some degree of multispecific spawning is likely to occur on these equatorial reefs, most species exhibited protracted and relatively asynchronous spawning with some level of temporal reproductive isolation between species (Mangubhai and Harrison 2006, 2008a, 2009). Similar patterns of asynchronous spawning over multiple lunar phases within populations of some coral species and some pulsed multispecific spawning events have recently been recorded from diverse coral assemblages in the Maldives (Harrison and Hakeem 2007, and unpublished data). These data support earlier hypotheses of protracted breeding seasons and less synchronous spawning nearer the equator (e.g., Orton 1920; Oliver et al. 1988), whereas more synchronous reproduction has been recorded among some species in other equatorial reefs (e.g., Baird et al. 2002; Guest et al. 2002, 2005a, b; Penland et al. 2004). Baird et al. (2009a) analyzed latitudinal trends in spawning synchrony using data from some Indo-Pacific *Acropora* assemblages and concluded that spawning synchrony peaked at midlatitudes on the central GBR and was lower near the equator (Singapore and Kenya), and lowest at subtropical eastern Australian reefs in the Solitary Islands. Hence, some reduction in spawning synchrony is apparent in at least some *Acropora* assemblages at high and low latitudes compared with midlatitude tropical GBR reefs.

Corals also successfully reproduce in more extreme temperate latitude environments such as in Kuwait (Harrison 1995; Harrison et al. 1997; Fig. 2), and at higher latitude regions where populations are at, or near, their latitudinal limits (e.g., van Woesik 1995; Wilson and Harrison 1997, 2003; Harii et al. 2001; Nozawa et al. 2006; Harrison 2008). Therefore, as noted by van Woesik (1995), there is no indication that these coral populations in marginal reef and cooler temperate environments are nonreproductive pseudopopulations.

Reproductive patterns documented in Hawaiian corals range from brooding throughout the year in a few species, to seasonal peak reproduction in spring and summer months for broadcast spawning and some brooding species, and although some species have overlapping spawning periods, there is no evidence of large multispecific or mass spawning events (e.g., Edmondson 1929, 1946; Harrigan 1972; Stimson 1978; Krupp 1983; Richmond and Jokiel 1984; Jokiel 1985; Jokiel et al. 1985; Heyward 1986; Hodgson 1988; Hunter 1988; Richmond and Hunter 1990; Harrison and Wallace 1990; Kenyon 1992; Schwartz et al. 1999; Neves 2000; reviewed by Kolinski and Cox 2003). Slightly different reproductive patterns are evident among the 14 coral species studied in the Equatorial Eastern Pacific region (EEP), where only two brooding species have been recorded, and extended breeding seasons occur in thermally stable environments but shorter seasonal breeding occurs during warm periods in seasonally varying upwelling environments (e.g., Glynn et al. 1991, 1994, 1996, 2000, 2008; Colley et al. 2002, 2006; reviewed by Glynn and Colley 2009). Some coral species in the EEP exhibit unusual or contrasting reproductive characteristics compared with other regions. For example, *Pavona varians* is a sequential hermaphrodite in the EEP but is recorded as gonochoric in other regions (see Table 3), and *P. damicornis* populations in the EEP do not brood planulae in contrast to most other regions (see Table 4).

Reproductive patterns have been widely studied in the Caribbean and other western Atlantic regions (reviewed by Szmant 1986; van Woesik et al. 2006). Multispecific spawning by a small number of coral species has been recorded on some reefs in the Caribbean (e.g., van Veghel 1993; Steiner 1995; de Graaf et al. 1999; Sanchez et al. 1999; Bastidas et al. 2005; Rodríguez et al. 2009), in the Gulf of Mexico (e.g., Gittings et al. 1992; Hagman et al. 1998a, b; Vize 2006), and subtropical Bermuda (Wyers et al. 1991). Long-term spawning records from the Gulf of Mexico show that the timing of spawning for species is highly consistent between years, but most species have unique spawning "windows" during the main spawning nights when no other coral species have been observed to spawn (Vize et al. 2005). In other western Atlantic corals, gametogenesis and spawning patterns are often synchronous within species or populations exhibit split-spawning over consecutive lunar cycles, but some species spawn at different lunar phases or different seasons and exhibit some degree of temporal reproductive isolation (e.g., Wyers 1985; Szmant 1986, 1991; Soong 1991; Steiner 1995; Acosta and Zea 1997; de Graaf et al. 1999; Mendes and Woodley 2002a; Vargas-Angel and Thomas 2002; Alvarado et al. 2004; Bastidas et al. 2005; Vargas-Angel et al. 2006; van Woesik et al. 2006; Rodriguez et al. 2009). An unusual feature of the western Atlantic coral fauna is that it contains a high proportion of brooding species (Szmant 1986) and reproductive patterns among Atlantic brooding species

Table 2 Summary of sexual patterns and mode of development for 444 scleractinian species, grouped according to families and molecular clades

Reproductive character	Sexual pattern		Mode of development				
Clade: Family "Complex" clade	H	Mixed or H/G	G	SG	SG+B	B	Total species sex/mode recorded
II. Dendrophylliidae	4	–	16	9	1	10	23
III. Poritidae	1	2	24	19	–	13	32
IV. Pachyseris	–	–	3	3	–	–	3
V. Euphyllidae etc.	2	2	3	6	–	2	8
VI. Acroporidae	155	–	–	150	–	6	157
VII. Agariciidae	3	3	5	9	–	4	13
VIII. Astrocoeniidae	–	–	2	2	–	–	2
IX. Siderastreidae	1	–	3	2	–	2	4
Flabellidae	–	1	7	2	–	4	8
Fungiacyathidae	–	–	1	1	–	–	1
Micrabaciidae	–	–	–	–	–	1	1
Totals for "complex"	166	8	64	203	1	42	252
"Robust" clade							
X. Pocilloporidae etc.	16	–	–	4	3	11	19
XI. Fungiidae etc.	5	3	22	22	5	–	31
XII. Meandrinidae	–	–	5	5	–	–	5
XIII. Oculinidae etc.	1	–	5	4	–	–	6
XIV.	–	–	3	4	–	–	4
XV. Diploastrea	–	1	–	1	–	–	1
XVI. Mont. cavernosa	–	–	1	1	–	–	1
XVII. "Faviidae" etc.	74	–	–	76	1	1	78
XVIII+XIX+XX.	16	–	–	17	–	–	17
XXI. Mussidae etc.	13	–	–	7	2	4	14
Caryophylliidae	4	–	7	8	1	2	13
Rhizangiidae	–	–	2	2	–	1	3
Totals for "Robust"	129	4	45	151	12	19	192
Total species	295	12	109	354	13	61	444

Systematic groupings of species and genera are aligned with clades identified by Fukami et al. (2008) and other recent phylogenetic analyses and groupings (e.g., Romano and Cairns 2000; Fukami et al. 2004b; Le Goff-Vitry et al. 2004; Kerr 2005; Benzoni et al. 2007; Nunes et al. 2008; Huang et al. 2009; Baird et al. 2009a) *H* hermaphroditic, *G* gonochoric; *Mixed or contrasting sexual patterns reported* (see Table 3); *SG* broadcast spawn gametes, *B* brood planulae, *SG+B* both modes of development reported (see Table 4)

range from synchronous seasonal planulation through to year-round planulae release (e.g., Wilson 1888; Duerden 1902a, b; Vaughan 1910; Lewis 1974; van Moorsel 1983; Szmant-Froelich et al. 1985; Tomascik and Sander 1987; Delvoye 1988; Soong 1991; Johnson 1992; McGuire 1998; Vermeij et al. 2003, 2004; Goodbody-Gringley and Putron 2009).

A wide range of reproductive patterns and differences in periods of spawning and planula release have also been recorded among South Atlantic corals from Brazil (e.g., Pires et al. 1999, 2002; Francini et al. 2002; Neves and Pires 2002; Lins de Barros et al. 2003; Neves and da Silveira 2003). The endemic gonochoric brooding coral *Siderastrea stellata* exhibits remarkably synchronous maturation of oocytes over a 20° range of latitude from equatorial to southern tropical locations, although planulation appears to begin slightly earlier at the southernmost site that is influenced by cold water upwelling (Lins de Barros and Pires 2007).

4.2 Environmental Influences on Coral Reproduction

Sexual reproductive processes in corals appear to be strongly influenced by various environmental factors that act as proximate factors regulating and synchronizing reproductive cycles and gamete maturation, and as ultimate causes that exert evolutionary selective pressure through enhanced reproductive success (reviewed by Harrison and Wallace 1990). For example, synchronized spawning within coral populations leads to higher concentrations of gametes that promotes enhanced fertilization success (e.g., Oliver and Babcock 1992; Willis et al. 1997; Levitan et al. 2004), which increases planula production and the probability of successful reproduction among corals that spawn together.

Earlier studies indicated that seasonal changes in sea temperature, day length, wind or current patterns, lunar cycles of

Table 3 Scleractinian species in which mixed or contrasting sexual patterns have been reported

Clade: Family species	Sexual pattern	Location and comments (References)
III. Poritidae		
Porites astreoides	H	Puerto Rico (e.g., Szmant-Froelich 1984; Szmant 1986)
	Mixed: H, f	Jamaica; 26H, 28f, 1m?; H colonies had f, m or H polyps (Chornesky and Peters 1987)
	Mixed: G, H	Panama; 79% of 168 colonies f, 4% m, 17% H (Soong 1991)
Porites brighami	G, H?	Hawaii (Kolinski and Cox 2003)
V. Euphyllidae etc.		
Galaxea fascicularis	Mixed: f and "H" colonies	GBR; pseudo-gynodioecious, have female, and H colonies with functional sperm+eggs that cannot be fertilized (Harrison 1988)
Galaxea astreata	Mixed: f and "H" colonies	GBR; pseudo-gynodioecious, have female, and H colonies with functional sperm+eggs that cannot be fertilized (Harrison 1988)
VII. Agariciidae		
Agaricia agaricites	G	Virgin Islands, Puerto Rico (Peters 1984)
	Mixed: G, H	Curaçao; 41m, 25f, 12H (Delvoye 1982, 1988)
	H	Curaçao (G.N.W.M. van Moorsel, personal communication in Fadlallah 1983)
Agaricia humilis	Mixed : H, G	Curaçao; 37H, 8m, 13f (Delvoye 1982, 1988)
	H	Curaçao (G.N.W.M. van Moorsel, personal communication in Fadlallah 1983)
	H	Jamaica (E. Chornesky, personal communication in Harrison and Wallace 1990)
Pavona varians	G	Eilat, Red Sea (Shlesinger et al. 1998)
	G	Hawaii (Mate 1998; Kolinski and Cox 2003)
	H sequential cosexual	Eastern Pacific; sequential cosexual H, some G colonies (Glynn et al. 2000; Glynn and Colley 2009)
Flabellidae		
Monomyces rubrum	H	South Africa, Maldives; polyps H, some have only m or f gametes, suggested protandrous hermaphrodite (Gardiner 1902a, b; 1904)
	G	New Zealand (Heltzel and Babcock 2002)
XI. Fungiidae		
Fungia scutaria	G (some H?)	Hawaii; likely G, >20 corals sampled with no evidence of H, but eggs from isolated corals fertilized, so some H? (Krupp 1983)
	G or H?	Eilat, Red Sea; small corals m, large corals f, so may exhibit protandrous sex change (Kramarsky-Winter and Loya 1998)
Heliofungia actiniformis	H sequential?	Palau; Abe (1937) concluded that this species is probably hermaphroditic with sperm developing before eggs in the same individual
	G	GBR (Willis et al. 1985; Babcock et al. 1986)
	G	GBR (Babcock et al. 1986)
Sandalolitha robusta	H	Hawaii; colonies change sex between years, indicating bidirectional sex change and sequential hermaphroditism (B. Carlson, personal communication)
XV.		
Diploastrea heliopora	G	GBR (Harrison 1985; Babcock and Harrison, unpubl. data in Harrison and Wallace 1990)
	H sequential	Singapore; 4 H colonies and 1 m colony recorded, and polyps in H colonies were either m or f with sequential development (Guest 2004)

H hermaphroditic, *G* gonochoric, *m* male, *f* female, numbers refer to numbers of colonies or solitary corals recorded with different sexes or sexual patterns, *?* uncertain, *GBR* Great Barrier Reef

night irradiance, and daily periods of light and dark may act as proximate cues operating on progressively finer time scales to synchronize reproductive cycles and breeding among many corals (e.g., Yonge 1940; Szmant-Froelich et al. 1980; Babcock 1984; Harrison et al. 1984; Jokiel et al. 1985; Simpson 1985; Fadlallah 1985; Willis et al. 1985; Babcock et al. 1986; Kojis 1986b; Hunter 1988; Oliver et al. 1988; Harrison and Wallace 1990; among others). More recent hypotheses have been proposed that correlate reproductive patterns with environmental factors that may act as additional or alternative proximate or evolutionary controls on sexual reproduction in corals. These include a combination of warm temperature and absence of heavy rainfall (e.g., Mendes and Woodley 2002a), solar insolation cycles (Penland et al. 2004; van Woesik et al. 2006), and the duration of regional calm periods that may enhance fertilization and larval retention (van Woesik 2009). However, as noted by Harrison and Wallace (1990), correlation does not prove causality; hence, rigorous manipulative experiments are required to unequivocally demonstrate the extent to

Table 4 Coral species in which both broadcast spawning (SG) and brooding (B) modes of development have been reported

Clade/Family: Species	Mode	Location and comments (References)
II. *Tubastrea coccinea*	B + SG	GBR (D. Ayre, personal communication in Harrison and Wallace 1990); planulae produced asexually (Ayre and Resing 1986)
	B	Hawaii (e.g., Edmondson 1929, 1946; Yonge 1932; Richmond 1997)
	B	Eastern Pacific; sperm release observed (Glynn et al. 2008)
X. *Pocillopora damicornis*	B	GBR (e.g., Stephenson 1931; Marshall and Stephenson 1933; Harriott 1983b; Muir 1984 – asexual planulae; Tanner 1996)
	B	Pacific region (e.g., Edmondson 1929, 1946; Kawaguti 1941a; Atoda 1947a; Harrigan 1972; Vandermeulen and Watabe 1973; Stimson 1978; Richmond 1982, 1987; Stoddart 1983; Richmond and Jokiel 1984; Jokiel 1985; Hodgson 1985; Dai et al. 1992; Diah Permata et al. 2000; Fan et al. 2002, 2006; Villanueva et al. 2008)
	SG	Eastern Pacific; no brooded planulae (e.g., Glynn et al. 1991)
	SG	Gulf of California; no B (Chavez-Romo and Reyes-Bonilla 2007)
	B + SG?	WA; broods asexual planulae, inferred to spawn gametes (Stoddart 1983; Stoddart and Black 1985; Ward 1992)
Pocillopora meandrina	B	Enewetak; recorded as *P. elegans* (Stimson 1978)
	SG	Hawaii (Stimson 1978; Fiene-Severns 1998; Kolinski and Cox 2003)
Pocillopora verrucosa	B	Enewetak (Stimson 1978); Philippines (Villanueva et al. 2008)
	SG	Hawaii (Kinzie 1993)
	SG	Red Sea (Shlesinger and Loya 1985; Fadlallah 1985; Shlesinger et al. 1998)
	SG	Indian Ocean (Sier and Olive 1994; Kruger and Schleyer 1998)
XI. *Fungia fungites*	SG	GBR (e.g., Willis et al. 1985; Babcock et al. 1986)
	B	Japan (Loya et al. 2009)
Heliofungia actiniformis	B	Palau (Hada 1932; Abe 1937)
	SG	GBR (e.g., Willis et al. 1985; Babcock et al. 1986)
Leptastrea purpurea	SG	Japan (Hayashibara et al. 1993); Palau (Penland et al., unpublished data)
	SG	Hawaii (G. Hodgson, unpublished data cited in Kolinski and Cox 2003)
	B	(P. Schupp, personal communication cited in Baird et al. 2009a)
Psammocora stellata	SG	Eastern Pacific (Glynn and Colley 2009)
	B?	Hawaii; planulae collected (Kolinski and Cox 2003)
Oulastrea crispata	SG + B	Japan and Hong Kong (Nakano and Yamazoto 1992; Lam 2000)
XVII. *Goniastrea aspera*	B	Palau (Abe 1937; Motoda 1939)
	SG + B	Japan (Sakai 1997; Nozawa and Harrison 2005)
	SG	Indo-Pacific: GBR (e.g., Babcock 1984; Harrison et al. 1984; Babcock et al. 1986); Japan (e.g., Heyward et al. 1987; Hayashibara et al. 1993; Mezaki et al. 2007); Taiwan (Dai et al. 1992); Palau (Penland et al. 2004); WA (Simpson 1985; Gilmour et al. 2009)
XXI. *Favia fragum*	B + SG?	Jamaica; mainly brooded planulae, occasionally spawned eggs and sperm – possibly abnormal (Duerden 1902a)
	B	Caribbean – Western Atlantic (e.g., Vaughan 1908, 1910; Matthai 1919, 1923; Lewis 1974; Szmant-Froelich et al. 1985; Szmant 1986; Soong 1991; Carlon and Olson 1993; Brazeau et al. 1998; Goodbody-Gringley and Putron 2009)
Manicina areolota	B + SG?	Bahamas; mainly brooded planulae, initially spawned abundant eggs and sperm – possibly abnormal (Wilson 1888)
	B	Caribbean – Western Atlantic (e.g., Duerden 1902a, c; Boschma 1929; Yonge 1935; Johnson 1992)
Caryophylliidae		
Caryophyllia smithii	B	Golfe du Lion; released advanced embryos (de Lacaze-Duthiers 1897)
	SG	England (e.g., Thynne 1859; Hiscock and Howlett 1977; Tranter et al. 1982)

Early reports of brooding in six other species are probably incorrect (see Table 7.4 in Harrison and Wallace 1990), hence are not included

GBR Great Barrier Reef, *WA* Western Australia, *?* uncertain

which different environmental factors regulate sexual reproductive cycles in corals.

Some corals have recently been shown to sense moonlight (Gorbunov and Falkowski 2002) via photosensitive cryptochromes (Levy et al. 2007), while other research has provided new insights into biochemical processes influencing gametogenesis and spawning (e.g., Atkinson and Atkinson 1992; Tarrant et al. 1999, 2004; Twan et al. 2006).

These biochemical and molecular approaches provide exciting prospects for further research to understand how corals perceive and integrate information on environmental cues (e.g., Vize 2009) to regulate their reproductive cycles.

Ongoing research is providing increasing evidence that sexual reproductive processes in corals are highly sensitive to a wide range of natural and anthropogenic stressors that cause sublethal stress, reduce fecundity, and impair reproductive

success (reviewed by Loya and Rinkevich 1980; Harrison and Wallace 1990; Richmond 1993, 1997; Fabricius 2005). Environmental factors known to stress corals and negatively affect sexual reproduction include: thermal stress (e.g., Kojis and Quinn 1984; Edmunds et al. 2001; Nozawa and Harrison 2002, 2007; Bassim et al. 2002; Krupp et al. 2006; Negri et al. 2007; Meyer et al. 2008; Randall and Szmant 2009; Yakovleva et al. 2009), ultraviolet radiation (e.g., Gulko 1995; Wellington and Fitt 2003; Torres et al. 2008), coral bleaching (e.g., Szmant and Gassman 1990; Omori et al. 2001; Ward et al. 2002; Baird and Marshall 2002; Mendes and Woodley 2002b), lowered salinity (e.g., Edmondson 1946; Richmond 1993; Harrison 1995; Vermeij et al. 2006; Humphrey et al. 2008), and increased sedimentation and turbidity (e.g., Kojis and Quinn 1984; Jokiel 1985; Gilmour 1999; Fabricius et al. 2003; Humphrey et al. 2008).

Sublethal and toxic levels of pollutants also impair or prevent successful coral reproduction, including increased nutrients (e.g., Tomascik and Sander 1987; Ward and Harrison 1997, 2000; Harrison and Ward 2001; Bassim and Sammarco 2003), oil pollutants and dispersants (e.g., Loya 1976; Rinkevich and Loya 1977, 1979c; Loya and Rinkevich 1979; Peters et al. 1981; Guzmán and Holst 1993; Harrison 1993, 1995; Negri and Heyward 2000; Lane and Harrison 2002), trace metals (e.g., Heyward 1988b; Reichelt-Brushett and Harrison 1999, 2000, 2004, 2005; Negri and Heyward 2001), herbicides and insecticides (e.g., Negri et al. 2005; Markey et al. 2007), and mixtures of pollutants in storm water runoff (e.g., Richmond 1993). These stress effects are likely to be exacerbated by climate change impacts, including modified thermal environments that may disrupt reproductive cycles in corals and inhibit larval settlement and postsettlement survival. Furthermore, increased carbon dioxide absorption resulting in decreased seawater pH and aragonite saturation state ("ocean acidification") is likely to interfere with initiation of calcification in newly settled coral polyps and reef-building by hermatypic corals (e.g., Albright et al. 2008; Jokiel et al. 2008). As coral reproduction appears to have a narrower tolerance to stress than other life functions (Harrison and Wallace 1990), it is essential to maintain ecologically appropriate environmental conditions to enable successful reproduction by corals in future.

4.3 Molecular Perspectives on Coral Reproduction

Important research advances have also occurred in relation to other aspects of sexual reproduction in reef corals, and these coincide with the development of powerful molecular methods for analyzing genetic structure in populations, and phylogenetic and systematic relationships among taxa. Of particular significance is the discovery that hybridization and genomic introgression can occur among some morphologically different coral "species" (e.g., Willis et al. 1992, 1997; Miller and Babcock 1997; Szmant et al. 1997; Hatta et al. 1999; van Oppen et al. 2001, 2002; Vollmer and Palumbi 2002, 2004; Fukami et al. 2004a; Richards et al. 2008; among others), which has important implications for coral taxonomy and our understanding of scleractinian evolution (reviewed by Veron 1995, 2000; Willis et al. 2006; Harrison and Booth 2007). For example, the Caribbean coral *Acropora prolifera* is now recognized to be a first generation hybrid of *Acropora palmata* and *Acropora cervicornis* (van Oppen et al. 2001; Vollmer and Palumbi 2002, 2004). More complex patterns of hybridization versus reproductive isolation occur in some other corals, such as in the *Montastrea annularis* species complex in the Caribbean. Hybridization between *Montastrea* species in this complex has been demonstrated in cross-fertilization experiments in some regions, whereas subtle differences in the timing of gamete release and regional differences in gametic incompatibility between species provide mechanisms for reproductive isolation among these sympatrically spawning species in other Caribbean regions (e.g., Szmant et al. 1997; Knowlton et al. 1997; Levitan et al. 2004; Fukami et al. 2004a).

Advances in molecular research and oceanographic models have also enabled more detailed analyses of gene flow and connectivity among populations of reef corals in different regions. These studies have demonstrated a wide range of larval retention and dispersal patterns in both brooding and broadcast spawning corals, ranging from highly localized larval settlement and recruitment in some cases, through to ecologically significant gene flow and connectivity among coral populations on different reefs over distances of tens to many hundreds of kilometers (e.g., Ayre et al. 1997; Ayre and Hughes 2000, 2004; Nishikawa et al. 2003; Baums et al. 2006; van Oppen and Gates 2006; Underwood et al. 2007, 2009; Hellberg 2007; Miller and Ayre 2008; Noreen et al. 2009; reviewed by Jones et al. 2009).

This more recent genetic research coincides with substantially increased knowledge of coral larval settlement competency periods and settlement rates. Rapid settlement of brooded planulae after release from polyps has been well documented for many brooding species and is likely to enhance localized settlement (e.g., Duerden 1902a, b; Atoda 1947a, b; Harrigan 1972; Rinkevich and Loya 1979a, b; Gerrodette 1981; Richmond 1985, 1987, 1988; Harrison and Wallace 1990; Carlon and Olson 1993; Harii et al. 2001). Recent research has demonstrated that planktonic planulae of some broadcast spawning species can temporarily attach to hard substrata or benthic algae after a few days planktonic development before becoming fully competent to settle (e.g., Harrison 1997, 2006; Nozawa and Harrison 2002, 2005; Miller and Mundy 2003), and this precocious attachment is

likely to enhance larval retention and settlement on, or near, their natal reef. Thus, planulae settlement competency varies within and among species such that although some planulae may settle locally, some planulae can be transported between reefs over larger geographic scales (e.g., Oliver and Willis 1987; Sammarco and Andrews 1988; Willis and Oliver 1990; Harrison and Wallace 1990; Sammarco 1994; Harrison and Booth 2007; Gilmour et al. 2009; Jones et al. 2009; among others). Furthermore, some brooded planulae and some planulae from broadcast spawning corals remain competent to settle for more than 2–3 months (e.g., Richmond 1987; Wilson and Harrison 1998; Harii et al. 2002; Nozawa and Harrison 2002, 2005), while a few planulae can survive for more than 200 days (Graham et al. 2008), which increases their potential for mesoscale and long-distance dispersal. Occasional long-distance larval dispersal is likely to contribute to the broad biogeographic ranges of some coral species (Harrison 2006).

Molecular research is also providing important new perspectives on the phylogenetic relationships of corals, which challenge the conventional systematic classification and arrangement of many scleractinian families and suborders that are based on skeletal morphology (e.g., Vaughan and Wells 1943; Wells 1956). Pioneering molecular studies identified two highly genetically divergent scleractinian clades – the "complex" coral clade and the "robust" coral clade that have different skeletal morphologies (Romano and Palumbi 1996, 1997). The "complex" clade corals tend to have relatively porous and more lightly calcified complex skeletons with a wide range of branching and other growth forms, whereas "robust" clade corals tend to have relatively robust and heavily calcified skeletons with mostly plate-like or massive growth forms (Romano and Palumbi 1996). Subsequent molecular research has provided further strong support for these divergent clades and has shown that many conventionally defined scleractinian suborders, families and even some genera are polyphyletic, and many groups contain representatives of both complex and robust clades, leading to a radical reappraisal of coral systematics and phylogeny (e.g., Romano and Cairns 2000; Chen et al. 2002; Fukami et al. 2004b, 2008; Le Goff-Vitry et al. 2004; Kerr 2005; Medina et al. 2006; van Oppen and Gates 2006; Benzoni et al. 2007; Nunes et al. 2008; Huang et al. 2009). These molecular phylogenetic hypotheses provide new opportunities for assessing the evolution of reproductive traits in corals (Baird et al. 2009a), which are described in detail in the remaining sections of this chapter.

5 Patterns of Sexual Reproduction

Information on sexual reproductive characteristics is available for at least 444 scleractinian species (Table 1). Among the 400 coral species in which both the sexual pattern and mode of development are known, hermaphroditic broadcast spawners remain the dominant category with 258 species (64.5%), gonochoric broadcast spawners are moderately common with 78 species (19.5%), while hermaphroditic brooders (25 species) and gonochoric brooders (15 species) are relatively uncommon (Table 1). In addition, 12 coral species exhibit mixed patterns of sexuality or have contrasting sexual patterns reported, both modes of development have been reported in 13 coral species, and a few species brood asexually derived planulae. Therefore, not all coral species can be strictly categorized in the four main patterns of sexual reproduction defined by the two main sexual patterns and modes of development (see Tables 1–4).

6 Sexual Patterns

Fadlallah (1983) and Harrison and Wallace (1990) reviewed the terminology associated with patterns of sexuality applicable to corals and noted the complexity of interpreting sexual patterns in some species. Most corals studied to date are either hermaphroditic or have separate sexes (gonochoric). Hermaphroditic coral species typically produce both male and female gametes in the polyps of colonies or solitary corals during their lifetime, and within this group, simultaneous and sequential hermaphroditism can be distinguished. A total of 295 solely hermaphroditic coral species have been reported to date (Tables 1 and 2). This represents 70.9% of the 416 species for which the sexual pattern is known; hence, hermaphroditism is clearly the dominant sexual pattern among coral species studied so far. In addition, some hermaphroditic colonies or solitary corals occur among the 13 species in which mixed or contrasting sexual patterns have been reported (Table 3).

Hermaphroditic coral species occur in 13 different families and clade groups identified by Fukami et al. (2008). Hermaphrodites dominate the families Acroporidae (155 species), faviids, and associated corals in clade group XVII (74 species), Pocilloporidae (16 species), and the 29 mussid and related coral species now grouped in clades XVIII–XXI (Fukami et al. 2008), where all species studied to date are hermaphroditic (Table 2).

Simultaneous hermaphrodites develop mature ova and mature sperm at the same time within the same individual (Policansky 1982), and the vast majority of known hermaphroditic coral species are simultaneous hermaphrodites that develop both ova and sperm within each polyp (Fig. 5). Interestingly, *Astroides calycularis* and *Cladopsammia rolandi* colonies were reported to be hermaphroditic, but different polyps were typically only female or male (monoecious pattern), with some *A. calycularis* polyps occasionally hermaphroditic (de Lacaze-Duthiers 1873; 1897).

Fig. 5 The great majority of corals studied to date are broadcast spawning simultaneous hermaphrodites, such as *Favites* brain corals that develop both eggs and sperm within each polyp, which are spawned in buoyant egg–sperm bundles (Photo: author)

Fertilization trials indicate that most simultaneous hermaphroditic corals are completely or partially self-sterile, although self-fertilization occurs in a few species (e.g., Heyward and Babcock 1986; Willis et al. 1997; Knowlton et al. 1997; Hagman et al. 1998b; Hatta et al. 1999; Carlon 1999; Miller and Mundy 2005).

Sequential hermaphrodites have ova and sperm that develop or mature at different times, and these may be used in the same breeding season (sequential cosexual), or individuals may exhibit true sex change over successive breeding seasons or over their lifetime (Ghiselin 1974; Policansky 1982). The four agariciid species *P. varians*, *Pavona gigantea*, *Pavona chiriquiensis*, and *Gardineroseris planulata* are sequential cosexual hermaphrodites (but with some gonochoric colonies) in the eastern Pacific region, and have multiple cycles of gamete development during breeding seasons whereby maturation of the sexes alternates, and early development of one sex coincides with maturation of the other sex (Glynn et al. 1996, 2000; Glynn and Colley 2009). The endemic Brazilian coral *Mussismilia hispida*, and three deep-sea *Caryophyllia* species also display cyclical sequential hermaphroditism, whereby gametes of both sexes occur on mesenteries but only gametes of one sex develop and mature at a time, followed sequentially by maturation and spawning of the other sex (Neves and Pires 2002; Waller et al. 2005). *Diploastrea heliopora* colonies in Singapore are hermaphroditic (with one male colony recorded), but individual polyps are either female or male with sequential patterns of egg and sperm development (Guest 2004).

Some corals produce only sperm during their initial growth and sexual development, but subsequently mature as simultaneous hermaphrodites and are therefore adolescent protandric hermaphrodites (e.g., Rinkevich and Loya 1979a; Kojis and Quinn 1985; Kojis 1986a; Harrison and Wallace 1990; Hall

and Hughes 1996). This initial sex allocation to male function is in accordance with sex allocation theory (e.g., Charnov 1982), and indicates a lower investment of energy and other resources in producing only sperm during the early growth stages of colony growth, thereby enabling a larger investment in growth and survival until the mortality risk is lower and allocation to both female and male function is sustainable. Furthermore, variation in sex allocation can also occur in adult corals, as demonstrated by a long-term study of sexual reproduction in colonies of *Stylophora pistillata*, which showed that some hermaphroditic colonies with high fecundity became male or were sterile in subsequent breeding seasons, and vice versa (Rinkevich and Loya 1987).

True protandrous sex change from initial male function in small corals to female function in larger corals has recently been demonstrated for some fungiid mushroom corals, including *Fungia repanda*, *Fungia scruposa*, *Ctenactis echinata,* and *Ctenactis crassa*, and the two *Ctenactis* species exhibit bidirectional sex change (Loya and Sakai 2008; Loya et al. 2009). A similar observation of bidirectional sex change has been recorded in colonies of another fungiid *Sandalolitha robusta* (B. Carlson, personal communication). Another fungiid species, *F. scutaria*, is predominantly male at small sizes whereas large individuals are all females, which suggests that these fungiids are also protandrous hermaphrodites (Kramarsky-Winter and Loya 1998). Abe (1937) also suggested that sperm develop before eggs in individual *Heliofungia actiniformis* corals (Table 3), and the recent reports of protandrous sex change in other fungiids provide support for this conclusion. Protandry was previously reported in the flabellid coral *Monomyces rubrum* (Gardiner 1902a, b), although Matthai (1914) disputed this interpretation.

These observations indicate that sex change and labile sex allocation may be a feature of reproduction in some other fungiids and perhaps some other corals that are generally recorded as gonochoric (Table 3, Fig. 6). Sex allocation theory predicts that these patterns of sex change occur in response to differential male and female fitness as size and age increase (Charnov 1982). The labile sex allocation in fungiids resembles patterns known in dioecious plants that respond to changing environmental conditions, and different energy costs associated with male versus female function (Loya and Sakai 2008).

Gonochoric coral species are less commonly reported than hermaphroditic coral species and are characterized by colonies or solitary corals that have separate sexes and are therefore functionally only male or female during their lifetime (dioecious). A total of 109 coral species have been recorded as gonochoric (Tables 1 and 2), which represents 26.2% of the 416 scleractinian species for which the sexual pattern is known. Gonochoric coral species have been recorded in 16 families and clades (Table 2). Families and

Fig. 6 Fungiid mushroom corals have some individuals that spawn sperm (**a**), and some that spawn eggs (**b**), and have been generally classified as gonochoric species with separate sexes. However, some fungiids are now known to change sex during their lifetime and are therefore sequential hermaphrodites (Photos: author)
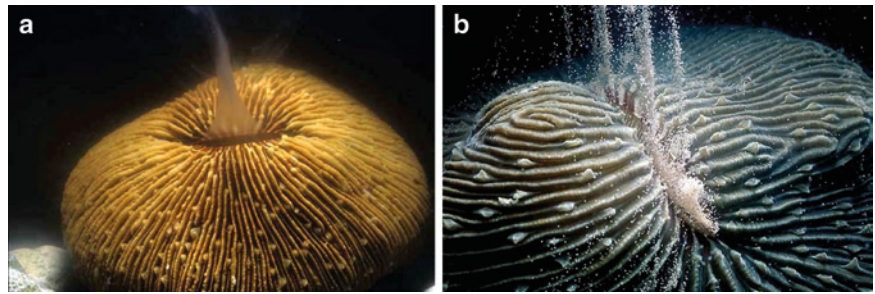
clades that have mainly gonochoric species recorded include the Dendrophylliidae (16 gonochoric species), Poritidae (24 gonochoric species), Flabellidae (seven gonochoric species), and Fungiidae (22 gonochoric species); but these families also have smaller numbers of hermaphroditic species recorded (Table 2). Families and clade groups in which all species studied so far are gonochoric include three *Pachyseris* species in clade IV, Astrocoeniidae (two species), Fungiacyathidae (only one species studied), Meandrinidae (five species), Rhizangiidae (two species), and clade XIV (three species).

Strong evidence for gonochorism occurs in some species of *Porites* (e.g., Kojis and Quinn 1982; Harriott 1983a; Soong 1991; Glynn et al. 1994; Shlesinger et al. 1998), *Turbinaria mesenterina* and some *Pavona* species (Willis 1987; Glynn and Colley 2009), and *Montastrea cavernosa* (e.g., Szmant 1991; Soong 1991), where male colonies and female colonies were repeatedly sampled with no evidence of sex change. In some other gonochoric species, large numbers of colonies or solitary corals have been sampled (e.g., Szmant-Froelich et al. 1980; Fadlallah 1982; Fadlallah and Pearse 1982a, b; Fine et al. 2001; Waller et al. 2002; Heltzel and Babcock 2002; Brooke and Young 2003; Goffredo et al. 2006; Lins de Barros and Pires 2007) and usually contain only male or female gametes, with no relationship between sex and coral size that would suggest protandry or protogynous hermaphroditism. However, in many gonochoric species, the evidence for separation of sexes is based primarily on limited sampling of a few corals or observations of spawning.

Some primarily gonochoric coral species also exhibit a low or variable incidence of hermaphroditism in some polyps or colonies within the population (see Table 1 in Fadlallah 1983; Table 7.3 in Harrison and Wallace 1990; Table 1 in Richmond and Hunter 1990). In cases where the hermaphrodites are relatively rare, the species can be considered to exhibit stable gonochorism (*sensu* Giese and Pearse 1974) and are classified as gonochoric (Tables 1 and 2).

In 12 other coral species, mixed or contrasting sexual patterns have been reported (Tables 1 – 3). In some of these species, different populations are either gonochoric or hermaphroditic, or populations contain mixtures of females, males, and hermaphrodites (Table 3). These species may have labile gonochorism (*sensu* Giese and Pearse 1974). Alternatively, some of these species may be sequential

hermaphrodites with asynchronous or partly overlapping oogenic and spermatogenic cycles that were sampled when only one sex was evident in some corals in the population (Fadlallah 1983; Harrison and Wallace 1990). It is also possible that the different sexual patterns reported between populations of some species from different reef regions reflect taxonomic problems, or morphologically similar cryptic species that have evolved contrasting sexual patterns.

More unusual mixed sexual patterns have been recorded in a few other coral species. *Porites astreoides* colonies from Jamaica were either female or hermaphroditic, which is a gynodioecious sexual pattern (Chornesky and Peters 1987). In Panama, most colonies of this species were female, with a few males recorded, and 17% of 168 colonies were hermaphroditic, in which spermaries and eggs sometimes occurred in different polyps (Soong 1991). In contrast, *P. astreoides* from Puerto Rico were simultaneous hermaphrodites (Szmant-Froelich 1984; Szmant 1986). *Galaxea fascicularis* and *Galaxea astreata* were originally described as simultaneous hermaphrodites; however, subsequent research demonstrated that these species have populations composed of female colonies that spawn pinkish-red eggs, and hermaphroditic colonies that produce sperm and lipid-filled white eggs (Harrison 1988). Hermaphroditic *G. fascicularis* colonies produce functional sperm that can fertilize the spawned pigmented eggs from female colonies (Fig. 7). However, the white eggs contain unusually large lipid spheres and are not able to be fertilized, and function to lift the sperm bundles up to the water surface where the buoyant pigmented eggs accumulate, thereby potentially enhancing fertilization success (Harrison 1988). This pseudogynodioecious sexual pattern in at least some *Galaxea* species is therefore functionally gonochoric.

These more complex sexual patterns, documented sex change and the variable incidence of hermaphroditism in some gonochoric species highlight the need for detailed and careful analysis of reproductive patterns in corals, as the assumption that coral species are always simply hermaphroditic or gonochoric species is not supported by the range of sex allocation and sexual patterns evident. Unambiguous determination of sexual patterns requires long-term observations or repeated sampling of marked or mapped corals, and preferably large-scale sampling within different populations to characterize patterns at the species level.

Fig. 7 *Galaxea fascicularis* populations have female colonies that spawn pigmented eggs (**a**), and other colonies that spawn functional sperm and white eggs that cannot be fertilized (**b**), and therefore have a pseudo-gynodioecious sexual pattern (Photos: author)
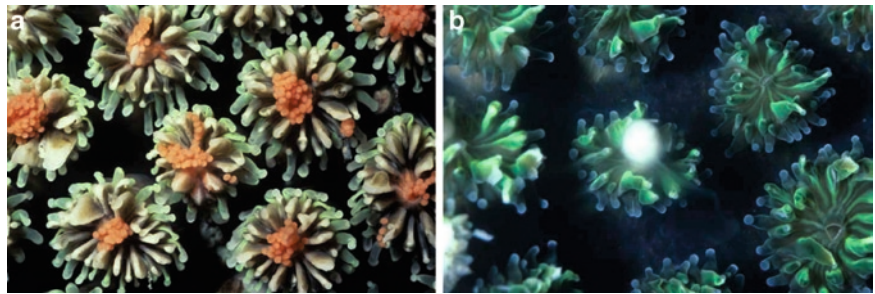
6.1 Systematic Trends in Sexual Patterns

Harrison (1985) noted that strong systematic trends were evident in sexual patterns and some other reproductive characteristics of corals. Subsequent reviews have expanded and provided further support for systematic trends in some reproductive characteristics based on conventional systematic classifications (Harrison and Wallace 1990; Richmond and Hunter 1990; Harrison and Jamieson 1999) and recent molecular phylogenies (Baird et al. 2009a). The available data indicate that sexual patterns are generally consistent within most coral species and genera studied to date, and in some families or clade groups. For example, sexual patterns are consistent in ten families and clades where at least two species have been studied (Table 2). However, as noted above, exceptions to these systematic trends are still evident within some species (Table 3) and genera, and an increasing number of families and clades now have both hermaphroditic and gonochoric species recorded (Table 2). Interestingly, similar proportions of species with hermaphroditic, gonochoric, and mixed or contrasting sexual patterns occur within both the "complex" and "robust" divergent coral clades (Table 2). Of the 105 coral genera for which sexual patterns have been recorded to date, 50 genera have only hermaphroditic species recorded, 38 genera have only gonochoric species recorded, while the remaining 17 genera have both sexual patterns or mixed sexuality recorded.

Baird et al. (2009a) concluded that the consistency of systematic trends in sexual patterns increased when global reproductive data are aligned with the revised molecular phylogeny of Fukami et al. (2008) and the "supertree" phylogeny of Kerr (2005), compared with the traditional morphological systematic organization. However, they noted that these molecular phylogenetic systematic arrangements do not resolve differences in sexuality within five of the families or clades defined by molecular groupings (Tables 1 and 2 in Baird et al. 2009a). In addition, when sequential hermaphrodites and species with mixed or contrasting sexuality (Table 3) are distinguished from gonochoric sexuality among species studied from the families Agariciidae (e.g., Delvoye 1982, 1988; Glynn et al. 1996, 2000; Glynn and Colley 2009) and Fungiidae (e.g., Loya and Sakai 2008), these families are

not uniformly gonochoric (Tables 2 and 3). Furthermore, *Monomyces rubrum* may be a protrandrous hermaphrodite (Gardiner 1902a, b), and recent studies have indicated that *Pseudosiderastrea tayamai* (see Harii et al. 2009) and *Cladocora caespitosa* (see Kruzic et al. 2008) are hermaphroditic; hence, the sexual pattern in these species also contrasts with other members of these three families (Table 2). Overall, sexual patterns are consistent in 12 of the 21 families and clades listed by Baird et al. (2009a) that have had the sexual pattern of more than one species documented – the other nine families have species with hermaphroditic, gonochoric, and mixed or contrasting sexuality recorded. Therefore, systematic trends in sexuality are only consistent in some scleractinian families and clades currently defined by molecular phylogenies (Table 2), which implies that contrasting sexual patterns have evolved in a range of clades. The exceptions to stable systematic patterns in sexuality are interesting as they highlight taxa that should be targeted for further research to confirm their phylogenetic relationships and the evolution of hermaphroditism versus gonochorism in the Scleractinia (Harrison and Wallace 1990).

Molecular data indicate that *Alveopora* should be transferred from the Poritidae to the Acroporidae (Fukami et al. 2008), and this is in accordance with their sexual pattern; *Alveopora* species studied so far are hermaphroditic (e.g., Shlesinger and Loya 1985; Babcock et al. 1994; Harii et al. 2001; Nozawa et al. 2006), like all the Acroporidae, whereas most Poritidae are gonochoric (Table 2). Likewise, the transfer of the gonochoric species *Montastrea cavernosa* (e.g., Szmant-Froelich 1984; Szmant 1986), from the Faviidae to a separate clade (Fukami et al. 2008), results in a consistent hermaphroditic sexual pattern within all faviid species studied to date, including other *Montastrea* species (Table 2). Baird et al. (2009a) noted that the early record of *Isophyllia sinuosa* as being possibly gonochoric contrasted with other mussids that are hermaphroditic; however, Duerden (1902a) stated that only oocytes were seen in one colony, and hence, the sexual pattern of this mussid is not known and is not included in the summary tables in this chapter.

At present, the molecular relationships of many coral taxa have not yet been analyzed, and the phylogenetic relationships of some groups are uncertain or vary somewhat between

studies and between molecular and morphological groupings (e.g., Kerr 2005; Fukami et al. 2008; Huang et al. 2009). Therefore, the recent molecular-based systematic groupings represent important new hypotheses that need to be further developed and tested using additional molecular and morphological data, to provide a comprehensive new systematic classification of the Scleractinia. Once this is achieved, it will provide a stronger basis for understanding systematic trends and evolution of sexual patterns in corals.

Szmant (1986) noted the dominance of hermaphroditic coral species and suggested that hermaphroditism might be the ancestral pattern in corals. However, analysis of scleractinian sperm morphology and ultrastructure has shown that the more primitive conical type of sperm is mostly associated with gonochoric coral species (e.g., Harrison 1985, 1990; Steiner 1991, 1993; Harrison and Jamieson 1999), which suggests that gonochorism is ancestral in the Scleractinia (Harrison 1985, 1990). Gonochorism is considered to be the ancestral condition of hexacorallian Anthozoa, including scleractinians (Daly et al. 2003), and Baird et al. (2009a) concluded that a phylogenetic analysis of reproductive traits also strongly supported gonochorism as the ancestral sexual state in corals.

7 Mode of Development

Corals have two different primary modes of development: broadcast spawning of gametes from their polyps into the sea for external fertilization and development (spawners); or brooding of embryos and planula larvae within their polyps that are subsequently released, usually at an advanced stage of development (brooders). Brooding corals also spawn sperm, and among hermaphroditic brooders, the spawned sperm may enable self-fertilization of eggs within polyps of the same coral in some species (e.g., Brazeau et al. 1998; Gleason et al. 2001; Okubo et al. 2007), or fertilize eggs within polyps of other colonies of the same species leading to outcrossing (e.g., Ayre and Miller 2006).

The vast majority of coral species studied to date are broadcast spawning species (Fig. 8); hence, external fertilization leading to planktonic larval development is the dominant mode of development (Tables 1 and 2). Of the 428 coral species for which the mode of development has been recorded, 354 species (82.7%) are broadcast spawners, whereas 61 species (14.3%) are brooders (Tables 1 and 2). In at least another 13 coral species (3%), both modes of development have been recorded (Table 4), including at least two of the three species known to brood asexually generated planulae (e.g., Stoddart 1983; Ayre and Resing 1986). The number of broadcast spawning coral species has more than doubled since the late 1980s (Harrison and Wallace 1990; Richmond and Hunter 1990), whereas relatively few new

Fig. 8 Most corals studied so far are broadcast spawning simultaneous hermaphrodites, such as *Favia* brain corals that forcibly eject egg–sperm bundles from the polyps during brief annual spawning events (Photo: author)

records of brooding species have emerged in the last 20 years (Fig. 4).

Among the 13 coral species in which both modes of development have been reported (Table 4), some species clearly spawn gametes and brood planulae, while some species have different modes of development recorded in different regions. This may reflect differences between populations or may have arisen from unrecognized or unresolved taxonomic differences between the corals identified as the same species from different regions (see Stimson 1978). The early records of spawning in the Caribbean brooding species *Favia fragum* and *Manicina areolata* may be an artifact and were regarded as abnormal (see Wilson 1888; Duerden 1902a, b).

Initial spawning of gametes followed by brooding of some eggs and embryos that are retained in the polyps has been shown to occur in some *Goniastrea aspera* colonies in Japan (Sakai 1997; Nozawa and Harrison 2005). In contrast, colonies of this faviid species have only been observed to spawn gametes on the GBR and WA reefs, whereas this species was reported to brood and release planulae in Palau (Table 4).

Five fungiid coral species have both spawning and brooding modes of development recorded (Table 4), whereas other members of this family all spawn gametes (Table 2). *Heliofungia actiniformis* is of particular interest, as this is the only coral species known so far in which both modes of development have been recorded, and contrasting sexual patterns have been reported (Tables 1 to 4).

Both modes of development have been reported in three species of *Pocillopora* (Table 4), whereas three other *Pocillopora* species are reported to spawn gametes (Glynn et al. 1991; Kinzie 1993; Glynn and Colley 2009). The variable modes of development recorded in *P. damicornis* are particularly interesting, as this is one of the most widely studied brooding coral, and planulae in some populations are

produced asexually (Table 4). Evidence for brooding of asexual planulae and inferred sexual reproduction via production and spawning of eggs and sperm in some populations of *P. damicornis*, is provided by histological and genetic studies (e.g., Stoddart 1983; Muir 1984; Stoddart and Black 1985; Ward 1992; Ayre and Miller 2004; Whitaker 2006; Sherman et al. 2006). In contrast, histological studies of *P. damicornis* colonies in Japan indicated that brooded planulae developed from eggs, and may be produced sexually (Diah Permata et al. 2000). A different reproductive pattern occurs in eastern Pacific and Gulf of California populations of *P. damicornis*, which are characterized by the production of eggs and sperm and inferred spawning of mature gametes, but there is no evidence of brooding or planulae production in these populations (Glynn et al. 1991; Colley et al. 2006; Chavez-Romo and Reyes-Bonilla 2007; Glynn and Colley 2009). The great variation in reproductive characteristics and life history traits recorded among populations identified as *P. damicornis* in different regions indicate that these characteristics are unusually variable in this "species"; alternatively, *P. damicornis* may be a species complex containing cryptic species with different reproductive patterns (e.g., Flot et al. 2008; Souter 2010).

At least one of the two *Tubastrea* species known to brood asexually generated planulae (Ayre and Resing 1986) is also thought to spawn gametes (Table 4); therefore the other *Tubastrea* species that produces asexual planulae may also exhibit both modes of development. *O. crispata* colonies in Japan and Hong Kong produce sperm and azooxanthellate eggs that are spawned over an extended period, and later develop brooded zooxanthellate planulae during the period when gametogenesis is not occurring, hence these planulae may be produced asexually (Nakano and Yamazoto 1992; Lam 2000). Production of brooded asexual planulae by locally adapted genotypes is likely to enhance local settlement and survival leading to higher recruitment success in some species, as predicted by the "strawberry coral model" (Williams 1975), whereas sexual reproduction in these species may enhance colonization of distant reefs. In contrast, Ayre and Miller (2004) concluded that although asexual production of brooded larvae was the primary mode of reproduction in a population of *P. damicornis* from the southern GBR, juveniles and adults displayed high genotypic diversity, with little evidence of asexually derived local recruitment.

The distinction between broadcast spawning and brooding modes of development becomes blurred in some species that exhibit intermediate modes of development, such as *Madracis* species, where internal fertilization leads to initial embryo and planula development during a short and variable "pseudobrooding" period of a few hours to days (Vermeij et al. 2003, 2004; de Putron 2004). *Eusmilia fastigiata* colonies spawn gametes through the polyp tentacles in Puerto Rico (Steiner 1995), whereas eggs or early stage embryos appear to be released through tentacles at Bonaire and Venezuela, which may indicate some degree of brooding or intermediate modes of development in these corals (de Graaf et al. 1999; Bastidas et al. 2005). Female *Stephanocoenia intersepta* colonies in Curaçao exhibit intratentacular fertilization, whereby the eggs are transferred into slits extending along the tentacles and held there for up to 10 min to increase exposure to spawned sperm and enhance fertilization success before the fertilized eggs are released (Vermeij et al. 2010); which is an intermediate mode of development. *Goniastrea favulus* spawns negatively buoyant eggs in a sticky mucus matrix that initially remains on or near the parent colony and may trap sperm, and this intermediate spawning strategy can lead to very high rates of fertilization (Kojis and Quinn 1981; Babcock 1984; Miller and Mundy 2005).

Both modes of development have been recorded within 13 families and clades, while six other families and clades in which at least two species have been studied have only broadcast spawners recorded (Table 2). Broadcast spawning dominates in the families Acroporidae (150 species), faviids and related clades (76 species), Fungiidae (22 species), and the mussid and related clades XVIII–XXI (24 species), while brooding is more common than broadcast spawning in the Family Pocilloporidae (Table 1). The proportion of broadcast spawning species is about 83% in both the "complex" and "robust" clades, whereas the proportion of brooding species is higher in the "complex" clade than in the "robust" clade (Table 2). All but one of the species reported to exhibit both modes of development occur in the "robust" clade (Table 2).

Overall, the occurrence of brooding corals among so many families and clades that are dominated by broadcast spawning species suggests that brooding has evolved in many coral taxa. Therefore, the mode of development appears to be a relatively plastic and variable life history trait compared with sexuality and other reproductive characteristics (Harrison 1985). Shlesinger et al. (1998) suggested that broadcast spawning was the ancestral mode of development in scleractinians and other Hexacorallia, and viviparous brooding is a derived reproductive characteristic.

8 Summary and Conclusions

The renaissance in coral reproduction studies that began in the 1980s has provided a wealth of data on many aspects of sexual reproduction in hermatypic zooxanthellate and some other corals. Information on sexual reproduction is available for at least 444 coral species, with hermaphroditic broadcast spawning the dominant pattern, and gonochoric broadcast spawning moderately common, whereas relatively few

hermaphroditic brooding or gonochoric brooding species have been recorded. A small number of coral species have mixed or contrasting sexual patterns or both modes of development recorded, and a few species are known to produce asexual planulae. Multispecific spawning has been reported on many reefs where diverse coral assemblages have been studied; however, the degree of reproductive synchrony varies greatly within and among species at different locations. These differences in reproductive timing and synchrony result in a continuum of coral reproductive patterns ranging from temporal reproductive isolation, through various scales of multispecific spawning, to very large-scale synchronous mass spawning events involving many corals of many species from diverse families and clades.

The discovery of hybridization and genomic introgression between some morphologically different coral species that spawn synchronously, the existence of some morphologically similar but reproductively isolated cryptic species, and more recent molecular research showing that many conventionally defined scleractinian families, suborders and some genera are polyphyletic, have led to a radical reappraisal of coral taxonomy, systematics, and evolutionary processes in scleractinians. Molecular studies have also contributed to improved understanding of the extent to which coral larvae are retained on, or near, their natal reefs and contribute to localized recruitment, or are dispersed to other reefs providing connectivity over larger geographic scales, and these dispersal patterns vary among species, and over space and time. Increased knowledge of larval development and competency periods combined with data from population genetic studies have provided evidence for highly localized larval settlement and recruitment in some species, as well as varying scales of ecologically significant gene flow and connectivity among coral populations on different reefs over distances of tens to hundreds of kilometers.

Research has also clearly demonstrated that sexual reproductive processes are highly sensitive to a wide range of natural and anthropogenic stressors, which impair or block the critically important phases of reproduction and recruitment that are required to maintain and replenish coral populations. The magnitude of these stresses will be increasingly exacerbated by the rising tide of human populations using coral reef habitats, and by climate change impacts from modified thermal environments and altered seawater chemistry that can interfere with initiation of calcification in newly settled coral polyps and reef-building by hermatypic corals. Therefore, it is essential to manage reef environments to ensure that ecologically appropriate environmental conditions are maintained to enable successful reproduction by corals into the future.

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