Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7-11 July 2008
Session number 11

# Survival of Brooding and Broadcasting Reef Corals Following Large Scale Disturbances: Is There Any Hope for Broadcasting Species During Global Warming?

**P. W. Glynn[1], S. B. Colley[2]**

1) Univ. Miami, RSMAS, MBF, 4600 Rickenbacker Cswy, Miami, Florida 33149 USA
2) PBS&J, 3230 West Commercial Blvd., Suite 100, Ft. Lauderdale, Florida 33309 USA

**Abstract.** The reproductive ecology of extant equatorial eastern Pacific (EEP) zooxanthellate scleractinian corals is examined relative to projected global warming conditions. Life history characteristics and patterns of abundance and distribution of 13 recently studied species in Costa Rica, Panamá, and the Galápagos Islands are considered. Twelve of these are broadcast spawners, which are numerically abundant, widely distributed, and the principal EEP reef builders. *Porites panamensis*, the lone brooder, is a small nodular coral with a restricted distribution. The majority of the broadcasting species are highly fecund, release gametes during large parts of the year, and produce sexual recruits that appear to disperse relatively far to diverse habitats. Asexual fragmentation is also common in most EEP broadcasting species compared to *P. panamensis*. We hypothesize that diverse habitats and varying environmental conditions (e.g., upwelling/nonupwelling centers, varying thermal conditions, high/low turbidity, high/low productivity, El Niño/La Niña activity) increase the probability of survival of sexual recruits and the asexual fragments of broadcasting species. Surviving refuge populations could serve as sources to repopulate degraded coral communities. The EEP reef coral fauna, dominantly broadcasting species, possess traits (e.g., high fecundity, widely dispersed) that could help resist environmental challenges during global warming.

**Key words:** Broadcast-spawning coral survival, eastern Pacific.

## Introduction

During multiple and diverse disturbances to coral reefs since the early 1980s, the perception has gained favor that corals brooding and releasing planula larvae have higher survival rates and subsequent success in reproduction and recruitment to degraded reefs than broadcast-spawning corals. This view was especially supported by studies in the Caribbean (e.g., Aronson and Precht 2001; Knowlton 2001). Following hurricanes, coral disease outbreaks, bleaching events and other disturbances, it was found that brooding species on many reefs demonstrated higher rates of survivorship and recruitment than broadcasting species. Relatively small colonies of brooding species have replaced major frame-building species on several western Atlantic coral reefs.

The cool/turbid and elevated nutrient conditions associated with upwelling in early Miocene time was postulated to have led to the demise of about one-half of the coral genera in the Caribbean. From an analysis of the coral genera that survived these changing conditions during the Caribbean Oligocene-Miocene extinction event, Edinger and Risk (1995) concluded that brooding corals were disproportionately favored over broadcasting coral taxa. Edinger and Risk (1995) extended their analysis to the modern eastern Pacific, suggesting that the upwelling environments in the equatorial eastern Pacific (EEP) would also favor the survival of brooding corals. At the time of Edinger and Risk's (1995) study, little was known of the reproductive modes of eastern Pacific corals. Several studies are now available, providing information for a re-examination of the relative benefits of brooding and broadcasting reproductive modes in marginal reef settings. Here we examine these contrasting modes of reproduction in the EEP region, in the context of coral bleaching caused by elevated temperature stress.

## Material and Methods

This re-analysis is based on the reproductive biology and ecology of EEP zooxanthellate scleractinian corals, chiefly from study sites in Costa Rica, Panamá and the Galápagos Islands (Fig. 1). Life history information was compiled from Glynn et al (1991 1994 1996 2000); Colley et al (2002 2006); and unpublished observations. The 13 species considered, of the 23 known species constituting the EEP fauna, are the principal reef-building corals. This study examines physical environmental conditions,

reproductive traits, spatial/seasonal reproductive patterns, and geographic distributions from the published literature and unpublished sources.

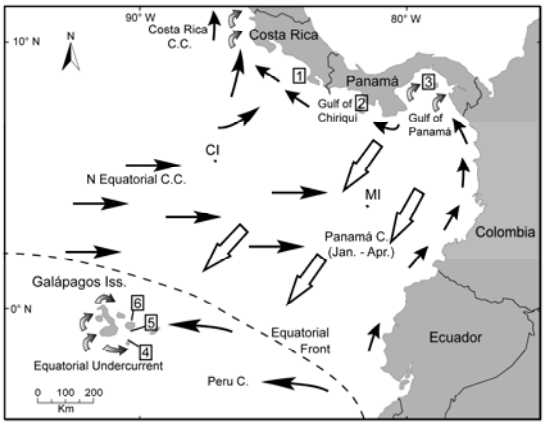


Figure 1: Coastal and offshore island sites of the equatorial eastern Pacific region. Numbered study sites: 1 – Caño Is, Costa Rica; 2 – Uva Is, Panamá; 3 – Saboga Is, Panamá; 4 – Floreana Is, 5 – Santa Cruz Is, 6 – Canal de Itabaca, Galápagos Islands. Locations of surface currents and upwelling centers (small thick arrows off NW Costa Rica, in Gulf of Panamá and W sector of Galápagos Iss) are noted. Key: Costa Rica C.C., Costa Rican Coastal Current; N Equatorial C.C., North Equatorial Counter Current; Panamá C., seasonal Panamá Current (large open arrows); Peru C., Peru Current; CI, Cocos Island; MI, Malpelo Island.

## Results

Of the 13 studied coral species, 12 spawn gametes (Table 1). These include the major frame-building species *Porites lobata*, *Pavona gigantea*, *Pavona clavus* and *Gardineroseris planulata*, which construct massive (dome-like) colonies, and *Pocillopora damicornis* and *Pocillopora elegans* that form branching colonies. Massive colonies attain 1 m in diameter and occasionally 2-3 m. Branching colonies range from 15 to 30 cm in diameter, and when growing in juxtaposition, form vertically-oriented and interlocking branches ≥ 1 m in height. Although no data exist for *Pocillopora inflata* from the majority of study sites, they spawned gametes immediately after collection in the Pearl Islands, Panamá (pers obs). *Porites panamensis* is the only brooding species. It typically forms small (5-10 cm max diam) nodular colonies, and occasionally colonies up to 30 cm in diameter that encrust basalt substrates.

Five broadcast-spawning species and the brooder *Porites panamensis* are gonochoric. Six broadcast spawning species are hermaphroditic: two pocilloporids are simultaneous hermaphrodites and four agariciids are sequential cosexual hermaphrodites. Sequential cosexual hermaphrodites are those species that display multiple cycles of gamete development during a breeding season; maturation of the sexes alternates in tissues, revealing early stage gametes of one sex with late stage gametes of the opposite sex (Policansky 1982). Asexual fragmentation occurs occasionally to commonly in all species except *Porites panamensis* and *Psammocora superficialis*.

Table 1. Life history traits of presently studied EEP zooxanthellate coral species. SG-spawns gametes, BP-broods planulae; sexuality: G-gonochoric, H-hermaphroditic, simul-simultaneous, seq, sequential cosexual; Growth form (greatest dimension): nod-nodular, mas-massive, branch-branching, encrust-encrusting, pet-petaloid, sm-small (5-10cm), med-medium (10-30cm), lg-large (0.3-2m); Asexual reproduction: rare-seldom observed, occ-occasional, sometimes observed, com-common, frequently observed. Environmental conditions: Gulf of Panamá, seasonal upwelling; Gulf of Chiriquí, nonupwelling, seasonal shoaling of thermocline; Galápagos Islands, seasonally cool. Numbers in bold indicate number of months during the calendar year when Stage IV oocytes were present in histological sections. Numbers in parentheses indicate number of non-overlapping months when Stages I-III oocytes were present. n/a, species not present, too uncommon or rare to sample, or not sampled seasonally.

| Species | Sexuality | Growth form | Asexual reprod. | No. of months with mature ovaries | | |
|---|---|---|---|---|---|---|
| | | | | Gulf of Panamá | Gulf of Chiriqui | Galápagos Islands |
| *Porites panamensis* (BP) | G | nod, encrust, sm | Rare | **8** (2) | **12** | n/a |
| *Porites lobata* (SG) | G | mas, lg | Com | **0** (1) | **5** (3) | **1** (5) |
| *Pocillopora damicornis* (SG) | H, simul | branch, md | Com | **2** (0) | **6** (4) | **1** (0) |
| *Pocillopora elegans* (SG) | H, simul | branch, md | Com | **2** (0) | **11** (0) | **3** (7) |
| *Pocillopora inflata* (SG) | ? | branch, md | Com | n/a | n/a | n/a |
| *Pavona clavus* (SG) | G | mas, lg | Occ | **4** (1) | **3** (5) | **6** (2) |
| *Pavona varians* (SG) | H, seq | encrust, md | Occ | **4** (2) | **5** (6) | **4** (7) |
| *Pavona gigantea* (SG) | H, seq | mas, lg | Occ | **3** (4) | **6** (4) | **7** (5) |
| *Pavona chiriquiensis* (SG) | H, seq | encrust, md | Occ | n/a | **5** (6) | **4** (7) |
| *Gardineroseris planulata* (SG) | H, seq | mas, lg | Com | **0** (0) | **6** (1) | n/a |
| *Psammocora stellata* (SG) | G | branch, sm | Com | **1** (3) | **8** (1) | **6** (2) |
| *Psammocora superficialis* (SG) | G | encrust, sm | Rare | n/a | **4** (0) | **3** (2) |
| *Diaseris distorta* (SG) | G | petal, sm | Com | n/a | n/a | **4** |

The temporal presence of mature ovaries in broadcast-spawners was highly variable, depending on locality, which in turn was strongly influenced by seasonal thermal conditions. In general, species in the thermally stable Gulf of Chiriquí were reproductively active from 3 to 11 months of the year. Six of the 10

broadcast-spawners in the Galápagos Islands contained mature oocytes from 4 to 7 months of the year. Zooxanthellae were present in both the oocytes of *Porites panamensis* and three broadcast-spawning species, namely *Porites lobata, Pocillopora damicornis* and *Pocillopora elegans*. In the seasonally upwelling (late December-through April) Gulf of Panamá, planulae were present in *P. panamensis* during 8 nonupwelling months, and year round in the Gulf of Chiriquí where temperature conditions were high and more stable. Where quantified, fecundity estimates were high for six broadcast-spawning species: *Porites lobata, Pavona clavus* (unpub data), *Pavona varians*, *Pavona gigantea*, *Pavona chiriquiensis* and *Gardineroseris planulata*, and the brooder *Porites panamensis*.

*Porites panamensis* has the narrowest distribution of all 13 species. Within the eastern Pacific region it is known only from mainland localities and the Revilla Gigedo Islands, Mexico (Table 2). The majority of the broadcast-spawning species are present at several eastern Pacific localities, including all major oceanic island sites (Garzón-Ferreira and Pinzón-C 1999; Glynn and Ault 2000; Guzmán and Cortés 2007). Eleven of the 12 EEP broadcast-spawners are also present in the Indo-Pacific region. *Pocillopora inflata* occurs in the Phoenix Islands (D Obura, pers comm) and *Pavona chiriquiensis* at Wallace Island (M Pichon, pers comm). While P. damicornis occurs from the eastern Pacific across the tropical Indo-Pacific, it is a broadcast-spawner in the eastern Pacific and releases brooded planulae throughout the remainder of its range (Richmond and Hunter 1990).

A global survey of the number of coral taxa that experienced major bleaching disturbances during the past few decades shows relatively high survival and recovery of broadcast-spawning species (Table 3, Baker et al in press). High proportions of the dominant recovering corals in the Indian Ocean, eastern Pacific, central W/S Pacific, and Arabian Gulf were broadcast spawning species. Even in the western Atlantic reductions in the relative abundances of broadcast-spawners were markedly less than brooding species after the 2005 coral bleaching/disease event in the U.S. Virgin Islands (Rogers et al 2008). Agariciid brooders showed the greatest declines in abundance.

Table 2. Known geographic distributions of EEP zooxanthellate corals. BP, broods planulae; SG, spawns gametes. Localities: EPM, eastern Pacific mainland; REV, Revilla Gigedo Islands; CLP, Clipperton Island, ca 1,200 km off Mexican coast; COC, Cocos Island, Costa Rica; MAL, Malpelo Island, Colombia; GAL, Galápagos Islands, Ecuador; CPC, central Pacific; WPC, western Pacific; IOC, Indian Ocean. Double lines for *P. damicornis* denote planula brooding at all studied Indo-Pacific regions.

| Species | Eastern Pacific localities | | | | | | Indo-Pacific regions | | |
|---|---|---|---|---|---|---|---|---|---|
| | EPM | REV | CLP | COC | MAL | GAL | CPC | WPC | IOC |
| *Porites panamensis* (BP) | ---------- | | | | | | | | |
| *Porites lobata* (SG) | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- |
| *Pocillopora damicornis* (SG, BP) | ---------- | | | ----- | | ----- | ========== | ========== | ========== |
| *Pocillopora elegans* (SG) | ---------- | | | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- |
| *Pocillopora inflata* (SG) | ----- | | | ----- | | ---------- | | | |
| *Pavona clavus* (SG) | ---------- | | | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- |
| *Pavona varians* (SG) | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- |
| *Pavona gigantea* (SG) | ---------- | ---------- | ---------- | ---------- | ---------- | | | | |
| *Pavona chiriquiensis* (SG) | ----- | | | ---------- | | | | ------ | |
| *Gardineroseris planulata* (SG) | ----- | | | ---------- | ---------- | ---------- | ---------- | ---------- | ---------- |
| *Psammocora stellata* (SG) | ---------- | ---------- | ---------- | | ---------- | ---------- | ---------- | ---------- | ---------- |
| *Psammocora superficialis* (SG) | ----- | | | ----- | | ---------- | ---------- | ---------- | ---------- |
| *Diaseris distorta* (SG) | ----- | | | ----- | | ---------- | ---------- | ---------- | ---------- |

Table 3. Reproductive mode of predominant recovering coral taxa following major bleaching events worldwide.

| Region | Reproductive mode (no) | | Predominant recovering taxa |
|---|---|---|---|
| | broadcasters | brooders | |
| Indian Ocean | 11 | 1 | *Montipora circumvallata, Pavona* spp., *Acropora* spp., *Porites* spp., *Galaxea fascicularis*, *Pocillopora* spp., *Fungia* spp. |
| West Atlantic | 4 | 1 | *Montastraea annularis* complex (3 spp.), *Siderastrea siderea*, *Porites porites* |
| Eastern Pacific | 8 | 0 | *Porites lobata*, *Pocillopora* spp., *Pavona* spp., *Psammocora* spp., *Gardineroseris planulata* |
| Central W/S Pacific | 10 | 2 | *Pocillopora damicornis*, *Acropora* spp., *Porites* spp., *Montipora* spp., Faviidae, *Pavona* spp., *Galaxea fascicularis* |
| Arabian Gulf | 7 | 0 | *Porites* spp., *Acropora downingi*, *Platygyra daedalea*, *Leptastrea transversa*, *Favia* spp. |

**Discussion**

Present information on the reproductive traits of EEP reef-building corals indicates that the great majority, 12 of 13 studied species, are broadcast-spawners. Szmant (1986) hypothesized that the survival and recruitment of Caribbean brooding species should be favored in habitats that are subject to frequent disturbances. Such species are typically small, short-lived, reach reproductive maturity at an early age, iteroparous (with 9-12 reproductive cycles yr-1), produce lecithotrophic larvae, host zooxanthellae, and undergo local settlement/recruitment. Some observations have purported to show that the planulae of brooders can potentially disperse over long distances, thanks to the presence of energy-rich food stores and phototrophic zooxanthellae (e.g., Richmond 1987). Even some brooders with zooxanthellate larvae, however, have been shown to have short dispersal ranges with the majority recruiting to within 100 m of their natal colony (Underwood et al 2007). The literature review of Harrison and Wallace (1990) indicates a long pelagic phase for the larvae of broadcast spawning corals compared with brooded planulae. In addition, a recent study quantifying the survival of larvae of broadcast spawners suggests a greater potential for long-distance dispersal than previously recognized (Graham et al 2008).

Some recent studies in the western Atlantic appear to support Szmant's (1986) prediction. For example, brooding poritid and agariciid species have replaced broadcasting acroporid and faviid species on reefs in Jamaica (Hughes 1994) and Belize (Aronson and Precht 2001). In Brazil, small brooding recruits of siderastreid, agariciid and faviid species were much more abundant after unknown disturbances (possibly storm waves and mechanical damage by divers) than broadcast-spawning mussid corals (Kikuchi et al 2003). However, a survey of recovering corals from a bleaching event in the US Virgin Islands revealed a higher survivorship of broadcasting over brooding species (Rogers et al 2008). In this study, it was found that broadcast-spawning species in the *Montastraea annularis* complex remained community dominants whereas brooding *Agaricia agaricites* declined dramatically in abundance.

Edinger and Risk (1995) inferred that the majority of coral genera that survived increased upwelling in the early Miocene in the Caribbean were brooding species, compared with broadcast-spawning species that suffered high rates of extinction. They assumed that the surviving genera of brooding and broadcasting corals followed the same developmental patterns observed in present-day taxa. It is necessary to exercise caution when inferring the reproductive mode of coral species within particular genera. For example, the genera *Porites*, *Acropora* and *Pocillopora* contain species that exhibit brooding and broadcast spawning. *Porites* and *Acropora* were classified as taxa exhibiting a mixed mode of reproduction. In the Caribbean, all *Porites* spp. are brooders, but in the Indo-Pacific most *Porites* spp. are broadcast spawners. Even within the morphospecies *Pocillopora damicornis*, broadcast spawning occurs in the EEP and planula release in the Indo-Pacific (Richmond 1990). Ongoing studies have revealed that the major reef-building corals in the EEP are broadcast spawners and not brooding species as suggested by Edinger and Risk (1995).

During both the 1982-83 and 1997-98 ENSO bleaching events in Costa Rica (Guzmán et al., 1987) and Panamá (Glynn, 1990; Glynn et al 2001) whole colony mortality was high in *Porites panamensis* compared with partial colony mortality in several large broadcast spawning species. *Porites panamensis* demonstrated a delayed bleaching/mortality response, 2-3 months after most other scleractinian species, and disappeared from several monitored sites as well as two entire coral reefs for 3 to 5 years (Glynn 1984). This brooding species was considered regionally endangered by Glynn et al (2001).

An important issue relating to the survival of reef corals of divergent reproductive modes is the discrepancy in time and space on evolutionary and ecological scales. In this analysis, we have considered the survival of particular reproductive groups over evolutionary time. The ecological data supporting these survival patterns, i.e. which groups recover following disturbances over periods of years to a few decades, are at variance with the long-term trends. In some cases, brooders seem to demonstrate higher survival (e.g. Jamaica, Belize, Brazil), supporting Szmant's (1986) predictions, while in other cases broadcast spawning species appear to be more successful at surviving disturbances (e.g. Virgin Islands, Indian Ocean, eastern Pacific). This difference may be due in part to disturbance type (chronic vs acute), site specificity or previous history (Hughes 1989). Over evolutionary time, however, the variability of responses may become reduced with the life history traits of some taxa promoting long-term survival.

Considering the localized settlement behavior of *Porites panamensis* and the widespread distribution of EEP broadcast spawners, we conclude that EEP species with the latter reproductive mode have a high potential for dispersal. In addition, the EEP offers a wide variety of environmental settings for colonization: upwelling/nonupwelling centers, variable temperature regimes, carbonate/basalt substrates, wet/dry season conditions, high/low

turbidity, high/low productivity, and El Niño/La Niña activity. Environmental circumstances that could enhance coral survival during stressful warming events are upwelling centers, shallow thermocline development, and high tidal amplitude with attendant strong current flow (Riegl and Piller 2003). The variety of major surface currents should also promote a relatively high degree of connectivity between EEP localities. In conclusion, the life history traits of broadcast spawning corals, in combination with an opportunity to colonize diverse EEP environments, would appear to enhance the survival of broadcast-spawning corals following large-scale disturbances in this region.

**Acknowledgements**
We thank JR Guest, AH Baird, A Heyward and K Clifton for the invitation to present this study. We also appreciate the technical help offered by I Enochs and AMS Correa in the preparation of this manuscript. The manuscript benefited from critiques by AH Baird, W Cooper and RH Richmond. Financial support was provided by the US National Science Foundation, grant OCE-0526361 and earlier awards.

## References

Aronson RB, Precht WF (2001) Evolutionary paleoecology of Caribbean coral reefs. in Allman WD, Bottjer DJ (eds) Evolutionary paleoecology: the ecological context of macroevolutionary change. Columbia University Press, New York. pp. 171-233

Baker AC, Glynn PW, Riegl B (In press) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine Coastal Shelf Sci

Colley SB, Feingold JS, Peña J, Glynn PW (2002) Reproductive ecology of *Diaseris distorta* (Michelin) (Fungiidae) in the Galápagos Islands, Ecuador. Proc 9th Int Coral Reef Sym 1:373-379

Colley SB, Glynn PW, May AS, Maté JL (2006) Species-dependent reproductive responses of eastern Pacific corals to the 1997-1998 ENSO event. Proc 10th Int Coral Reef Sym 1:61-70

Edinger EN, Risk MJ (1995) Preferential survivorship of brooding corals in a regional extinction. Paleobiol 21:200-219

Garzón-Ferreira J, Pinzón C. JH (1999) Evaluación rápida de estructura y salud de las formaciones coralinas de la Isla de Malpelo (Pacífico Colombiano). Bol Invest Mar Cost 28:137-154

Glynn PW (1984) Widespread coral mortality and the 1982-83 El Niño warming event. Environ Conserv 11:133-146

Glynn PW (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In: Glynn PW (ed.) Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier Oceanography Ser 52, Amsterdam pp 55-126

Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19:1-23

Glynn PW, Maté JL, Baker AC, Calderón MO (2001) Coral bleaching and mortality in Panamá and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-1983 event. Bull Mar Sci 69:79-109

Glynn PW, Colley SB, Ting JH, Maté JL, Guzmán HM (2000) Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá and Galápagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona* sp.a. Mar Biol 136:785-805

Glynn PW, Colley SB, Gassman NJ, Black K, Cortés J, Maté JL (1996) Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). III. Agariciidae (*Pavona gigantea* and *Gardineroseris planulata*). Mar Biol 125:579-601

Glynn PW, Gassman NJ, Eakin CM, Cortés J, Smith DB, Guzmán HM (1991) Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). I. Pocilloporidae. Mar Biol 109:355-368

Glynn PW, Colley SB, Eakin CM, Smith DB, Cortés J, Gassman NJ, Guzmán HM, Del Rosario JB, Feingold JS (1994) Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). II. Poritidae. Mar Biol 118:191-208

Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27:529-539

Guzmán HM, Cortés J (2007) Reef recovery 20 years after the 1982-1983 El Niño massive mortality. Mar Biol 151:401-411

Guzmán HM, Cortés J, Richmond RH, Glynn PW (1987) Efectos del fenómeno de "El Niño Oscilación Sureña 1982/83 en los arrecifes coralinos de la Isla del Caño, Costa Rica. Rev Biol Trop 35:325-332

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed.) Coral Reefs. Ecosystems of the World 25, Amsterdam pp 133-207

Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. Ecology 70:275-279

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551

Kikuchi RKP, Leão ZMAN, Testa V, Dutra LXC, Spanó S (2003) Rapid assessment of the Abrolhos Reefs, eastern Brazil (Part 1: Stony corals and algae). In: Lang JC (ed) Status of coral reefs in the western Atlantic: results of initial surveys, Atlantic and gulf rapid reef assessment (AGRAA) program. Atoll Res Bull 496:172-187

Knowlton N (2001) The future of coral reefs. Proc Nat Acad Sci USA 98:5419-5425

Policansky D (1982) Sex change in plants and animals. Annu Rev Ecol Syst 13:471-495

Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93:527-533

Richmond RH (1990) Relationships among reproductive mode, biogeographic distribution patterns and evolution in scleractinian corals. In: M Hoshi and O. Yamashita (eds.), pp. 317-322, Advances in Invertebrate Reproduction 5, Elsevier Science Publishers B.V. (Biomedical Division).

Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. Mar Ecol Prog Ser 60:185-203

Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. Int J Earth Sci (Geol Rundsch) 92:520-531

Rogers CS, Miller J, Muller EM, Edmunds P, Nemeth RS + 20 others (2008) Ecology of coral reefs in the US Virgin Islands. In: Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer pp. 303-373

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43-54

Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Mol Ecol 16:771-784