The effects of human-induced pollution on the replenishment of coral reefs

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Annex B2.1

The effects of human-induced pollution on the replenishment of coral reefs

Chris K. Schelten and Callum M. Roberts
Environment Department, University of York, York, YO10 5DD, UK

1.1 Abstract

Coral reefs are suffering severe declines world-wide caused by multiple anthropogenic disturbances combined with natural events such as storms. Their future depends on the resilience of replenishment processes. However, few studies exist on the effects of multiple stresses on early life history of corals. In this review, We describe coral early life history processes including reproduction, settlement and post-settlement survival. We then review the literature focusing on the effects of four major human-induced threats, sedimentation, eutrophication, fishing and rising sea water temperature on reproduction, settlement and post-settlement survival. Research shows that in many cases different stresses affect the same replenishment process. Using two simple models we show that additive and synergistic stress can harm not only the energy budget of a single coral colony, but could also drive a species to extinction. A coral confronted by a disturbance may show a decrease in its energy budget due to either a change in environmental conditions such as reduced light penetration, or increased energy use for defensive mechanisms such as increased sediment rejecting activities. Adding other disturbances may reduce growth and/or reproductive output. If the energy budget decreases even further, processes involved in basal metabolism may suffer and the coral might finally die. Multiple stresses decrease maximum per capita growth of coral populations due to, for example, lower larval survival and decreased settlement success. Coral population extinctions may occur when interacting stresses are combined with Allee effects. Reduced coral densities and reduced reproductive output can lead to decreased fertilisation success. Hence, multiple stresses threaten not only adult corals, but also impact upon replenishment of coral reefs. This is a severe concern and highlights the importance of long-term studies of coral reef recovery and stress mitigation, particularly at a time where threats to reefs are expected to increase further in number, frequency and severity.

1.2 Introduction

Coral reefs are often referred to as 'the rain forests of the ocean' due to their high biodiversity (Reaka-Kudla 1995). Primary production on coral reefs is very high with large populations of organisms living in this ecosystem (Williams and Hatcher 1983, Roberts and Polunin 1994). However, coral reefs are known to be fragile because they support a large number of delicate invertebrates that makes them susceptible to human-induced disturbances (Kühlmann 1988).

Many coastal pollution problems arise due to increasing coastal activities in both developed and under-developed countries. Consequently, coral reefs are

exposed to a great amount of human-induced disturbances that can be classed into different categories: sedimentation, sewage pollution, thermal pollution, radioactive pollution, physical disturbances, hydrodynamic impacts, extractive activity, introductions of new species and tourism (Done 1992) The problems of developing countries, where most coral reefs occur, are expected to increase due to an exponentially increasing human population (Bryant et al. 1998).

It is not easy to define the 'health' of coral reefs considering that a reef is in a state of flux due to biological (e.g. bioerosion and variations in juvenile coral abundance) and non-biological events (e.g. hydrodynamic regimes, storms, etc). For example, hard coral cover, which has been used widely as an indicator for reef health, can vary greatly among reefs not subject to anthropogenic stress (Thomason and Roberts 1992). Additionally, a big question is whether undisturbed coral reefs still exist in our world today. Hence, reef sites used as control or undisturbed samples might already be affected by human activity.

From the perspective of the reef ecosystem as a whole, a key indicator of reef degradation is when carbonate erosion exceeds carbon deposition. This can occur when there is mass mortality of corals followed by an invasion of algae on the dead coral skeleton (Done 1992). However, the progressive loss of coral species, that does not result in net carbonate loss, is also a form of reef degradation. Coral growth, including regrowth of damaged colonies, and the successful production of new corals, replaces losses of the reef framework, whereas coralline algae play an important role in cementing the reef framework together (Langer et al. 1997). The loss of coralline algae, such as by enhanced growth of filamentous and macroalgae, could have impacts on reef growth. In addition, the disappearance of any other species such as sponges, gorgonians and fish, is also a symptom of reef decline. Nevertheless, massive and long-lived scleractinian corals are the main builders of the reef framework and, consequently, "if the coral population on the reef goes into decline, so will the rest of the community" as highlighted by Richmond (1997).

Since juvenile corals replace recently degenerated (partly or wholly) adult coral colonies, coral reproduction and juvenile survival are critical factors in determining coral population dynamics and reef community ecology (Szmant 1986, Done 1992, Smith 1992, Richmond 1997). If this balance between mortality and juvenile coral survival fails, the reef will gradually decline (Szmant 1986, Done 1992, Soong and Lang 1992, Richmond 1997). This makes the early life history and replenishment of coral populations central to the vitality of coral reefs.

Coral reproductive processes are complex and susceptible to environmental changes and disturbances. Adult corals react to high levels of pollution at different scales: (1) individual corals show behavioural or physiological changes (Lasker 1980, Dallmeyer 1982, Harriott 1983, Rogers 1983, Ward 1995); and (2) through changes at the community level such as in species composition or/and diversity (Tomascik and Sander 1987a). However, there is a lack of knowledge of the effects of natural and human-induced perturbations on the early life history of corals. Levels of pollution that have little impact on adult coral colonies may be harmful to coral larvae and recruits (Richmond and Hunter 1990). For example, changes in salinity have a detrimental impact on coral gametes while adult coral colonies are more tolerant to altered

salinity levels (Richmond 1993, Richmond 1994). Wittenberg and Hunte (1992) pointed out that juvenile corals are more threatened by sedimentation than larger adult individuals because they barely rise above the substrate and can be smothered more easily by depositing sediment layers. Birkeland (1977) also reported high mortality rates of newly settled corals in eutrophic waters, whereas adult colonies could survive and grow under eutrophic conditions.

It is important to understand the early life history of corals in order to determine how reefs will respond to altered environmental conditions (Richmond 1997). The period from the production of coral gametes to the successful integration of a coral colony into the adult coral community can be split into three different phases: reproduction, settlement and post-settlement. Richmond (1997) emphasised that this distinction is important as it is possible that reproduction is successful but larvae are not able to settle or survive due to unfavourable environmental conditions.

In this review we first examine reef degradation and describe the major human-induced disturbances affecting reefs today. Then we will briefly summarise the early life history of corals before discussing the effects of human-induced disturbances on these stages. Finally, we will look at the implications for management and future prospects for coral reefs in a human-dominated world.

1.3 Reef degradation

Some claim that coral reefs are robust and able to recover after strong disturbances (Brown 1987, Done 1987, Dahl and Salvat 1988), while others describe coral reefs as fragile systems mainly due to their narrow physiological tolerances (Johannes 1975, Loya 1976b, Pearson 1981, Grigg and Dollar 1990, Hallock 1997). Brown (1997) however, pointed out that over long time-scales coral reef ecosystems are clearly robust surviving variability over periods of millions of years, but on the time-scales important for human society, coral reefs have shown susceptibility to a variety of disturbances.

Over the past two to three decades, a dramatic transition has been observed world-wide from reefs dominated by corals to algal-dominated benthic communities (Hughes 1994, McClanahan and Muthiga 1998, McClanahan et al. 1999, McCook 1999). This process, when algae come to dominate reefs, is called 'phase-shift' (Done 1992). A phase shift towards algal dominance may be triggered by several factors such as outbreaks of coral predators, coral mass mortality due to highly contagious diseases, as well as natural disturbances such as storms and hurricanes (Done 1992). Done (1992) claimed that reefs can change from a coral-dominated to an algal-dominated state either abruptly or slowly. Coral-dominated, as well as a macroalgal-dominated benthic communities are both thought to be stable sates (e.g. Knowlton 1992). However, there is insufficient knowledge of differences in population and community dynamics, ecosystem structure and function between algal-dominated and coral-dominated reefs (Done 1992). Furthermore, it seems to be easier to identify a reef that has undergone a phase shift by massive algal invasion than to distinguish the causes of this event (Done 1992).

As mentioned above, coral reefs are threatened by numerous natural and anthropogenic disturbances which we will not be able to cover equally. This

review will focus on three major human-induced causes of reef degradation: sedimentation, eutrophication and overfishing (Roberts 1993, Ginsburg 1994). However, in view of the growing number and severity of coral bleaching episodes (Souter et al. 2000, Wilkinson 2000), we will also discuss the effects of rising sea temperature on the early life-history of corals, considering that this may be also a result of human activities.

1.3.1   Sedimentation

In the Caribbean and Pacific, one of the biggest causes of reef degradation is human-induced sedimentation (Johannes 1975, Rogers 1983, Kühlmann 1988, Rogers 1990, Richmond 1993). Major sources of sediment include coastal development, land-clearance and agriculture. Sediments are primarily transported to the sea by rivers, especially following heavy rainfall (e.g. Pastorok and Bilyard 1985, Sladek Nowlis et al. 1997). Consequently, the amount of sediment runoff depends on the size and watershed structure of the river, type of soil and intensity of rainfall (Rogers 1990). Unfortunately, in some situations it is difficult to determine if the disturbance to coral reefs close to a river mouth, is due to fresh water runoff and low salinity or due to sedimentation (Rogers 1990, Sakai and Nishihira 1991). Hydrodynamic characteristics can influence the level of sedimentation. For example, strong currents and high wave exposure flush off sediment and transport it away from reefs while sediment can be trapped in bays, or at a smaller scale, behind rocks and corals where water movement is slower and particles can settle (Cortès and Risk 1985, Rogers 1990, Hodgson 1993).

While some scientists measure mud thickness on a coral reef to show the connection between reef degradation and sedimentation (e.g. Sladek Nowlis et al. 1997), the most common and also more precise way of measuring sedimentation rate is to establish sediment traps. Measured sedimentation rates in the Caribbean range from 0.3 to 37mg.cm^{-2} day^{-1} and in the Indo-Pacific from 0.1 to 228mg.cm^{-2} day^{-1} (see Pastorok and Bilyard 1985). Rogers (1990) suggested that sedimentation levels < 10mg.cm^{-2} day^{-1}, or < 10mg l^{-1} are harmless to coral reefs, while sedimentation rates above these levels, as well as chronic sediment loads, have negative impacts that affect processes of reef development and alter benthic reef substrate composition. This is supported by Tomascik and Sander's (1985) results from their study of reefs in Barbados which suggests that short-term sedimentation, or high resuspension rates of short duration, have less impact on coral growth (skeletal extension) than persistent sediment loading.

Sedimentation has several damaging effects on individual corals: (a) total burial leads to mortality (Pearson 1981, Pastorok and Bilyard 1985, Sladek Nowlis et al. 1997), (b) reduced coral growth by abrasion, smothering and reduced light availability (Allert 1974, Tomascik and Sander 1985, Colgan 1987), and (c) modification in growth form towards more sediment-tolerant forms (Allert 1974). At the level of coral communities, a decreased coral abundance and density as well as reduced coral diversity are observed on reefs with high sedimentation (e.g. Tomascik and Sander 1985, McClanahan and Obura 1997, Nemeth and Nowlis 2001). Pastorok and Bilyard (1985) found that reefs with intermediate levels of sedimentation have the greatest variance in coral community structure. At low levels of sedimentation, biological factors such as competition and

predation lead to low variability of diversity, whereas at high sediment levels, only a few species can cope due to physical stress. Consequently, at intermediate sedimentation rates, moderate stress (biological and physical) allows several alternative community structures and compositions to develop. Many studies (e.g. Rogers et al. 1984, Chou 1988, Sladek Nowlis et al. 1997) agree that sedimentation has a more serious impact on corals in deeper water because this is where the sediment particles are mainly deposited through lower wave exposure. Deeper water corals could also suffer more from sedimentation because of reduced light availability from sediment particles in the water column (Rogers, 1984). Sedimentation is a serious threat to coral reefs because even after elimination of the source, the sediment particles can remain on the reef, continuing to affect the benthic reef community through resuspension (Pastorok and Bilyard 1985).

However, it is important to understand that different results of sedimentation studies may be caused by different types of sediment (e.g. sewage, industrial sediment or sand) and laboratory or field observations. Even particle size may have important impacts on the reaction of different coral species. Additionally, the type and size of sediment may influence the effects on the individual coral and coral communities (Babcock and Davies 1991).

1.3.2 Eutrophication

The main sources of eutrophication on coral reefs are agricultural run-off, land clearing and sewage outlets (Pastorok and Bilyard 1985, Roberts 1993). These impacts result in problems such as sedimentation, raised turbidity, increased nutrients mainly due to fertilisers, as well as pesticides, chemicals and bacterial activity (Walker and Ormond 1982, Pastorok and Bilyard 1985, Tomascik and Sander 1987b). Pastorok and Bilyard (1985) reported that PCBs, metals, chlorine, phosphate, pesticides and petroleum are often found in sewage discharges. Therefore, it is difficult to separate among detrimental factors affecting the coral reef system and its organisms (Tomascik 1991, Rice and Hunter 1992). Connell and Miller (1984) explained that pesticides and toxic substances change over space and time. Sometimes the original chemical substance breaks down into more toxic and resistant products (Connell and Miller 1984, Pastorok and Bilyard 1985). There are concerns that chemicals are more active in tropical waters due to the higher temperature of the water (Connell and Miller 1984). However, data-collection on metals, chemicals and other toxins in sea water is costly and difficult. The products are swiftly diluted, so even if symptoms are still detectable, information and field investigations are rare.

Nutrient enrichment on coral reefs can lead to a proliferation of algae, stressing or killing corals by shading and smothering them (Pastorok and Bilyard 1985, Lapointe et al. 1987, Lapointe 1997, Schaffelke 2001, Stimson et al. 2001, McClanahan et al. 2002). In Kaneohe Bay, Hawaii, increases in the green algae *Dictyosphaeria cavernosa* were observed due to sewage pollution (Evans et al. 1986, Smith et al. 2001). Guzman et al. (1990) in the Eastern Pacific (Costa Rica and Panama) reported greater biomass of phytoplankton due to nutrients, affecting light penetration and increasing the biochemical oxygen demand to the point that corals may be impacted. In addition, decreased life-expectancy of individual

corals has been linked to toxic substances diluted in the sea water (Pastorok and Bilyard 1985). Kinsey and Davies (1979) conducted a large scale experiment on a reef patch at One Tree Island, Great Barrier Reef. They enriched the surrounding water with phosphate and nitrogen for 3hours each day over a period of 8 months. They observed that reef calcification decreased by half and suggested that this reduction in carbonate deposition was due to phosphate rather than nitrate enrichment. Nutrient enrichment from sewage decreases photosynthetic efficiency of the symbiotic zooxanthellae of corals because the zooxanthellae increase in size to the point of becoming self-shading (Dubinsky et al. 1990). A large-scale experiment (ENCORE = Enrichment of Nutrients On a Coral Reef Experiment) with controlled nutrient enrichment was conducted in 1997 for a two year period on twelve patch reefs on the Great Barrier Reef, Australia (Koop et al. 2001). Coral mortality increased with nutrient addition, which also decreased coral growth (Koop et al. 2001). Added phosphorus reduced coral skeletal density causing increased susceptibility to breakages (Koop et al. 2001).

Eutrophication has also been reported to decrease the abundance and especially the diversity of adult corals (Tomascik and Sander 1987a, Wittenberg and Hunte 1992). Few studies have assessed the impacts of eutrophication on the settlement process and the post-settlement survival of juvenile corals.

1.3.3 Overfishing

Tropical reefs are often situated close to densely populated coastlines, of mostly developing countries that depend heavily on reef fisheries for their food (Bryant et al. 1998). Globally, coral reefs only cover 0.09% of the ocean (Spalding et al. 2001), yet around 15% of all fish catches come from this ecosystem (Munro 1996). Consequently, there is high exploitation pressure on fish stocks.

Herbivorous fish and sea urchins play a key role in determining the amount of algae on coral reefs. High fishing pressure can reduce herbivorous fish stocks to levels where the control on algal growth through grazing disappears (Rogers et al. 1984). Where there are no other major herbivores this can lead to a phase shift from coral to algal dominance due to uncontrolled growth of algae (Done 1992). In the Caribbean, phase shifts occurred on a large scale after the mass mortality of the urchin *Diadema antillarum* in 1983-84 due to a disease epidemic that destroyed 99% of them (Lessios et al. 1984). This was followed by an increase in algal biomass and a change in algal composition, killing corals by shading, smothering and direct overgrowth (Lessios 1995).

Eutrophication and sedimentation can have compounding effects. High nutrient loads enhance algal growth and make them superior competitors for space compared to corals that are specialised for living in oligotrophic water (Loya 1976b, Lapointe 1997). Excessive algal growth enhanced by increased nutrients might exceed capacity of herbivores to keep it under control. In addition, sediment particles get trapped in the filamentous algae and so could provide an unsuitable substrate for coral larval settlement, post-settlement survival and coral growth (Walker and Ormond 1982).

1.3.4   Rising sea temperature

When corals bleach, they can lose 60-90% of their symbiotic zooxanthellae, a dinoflagellate that normally lives in the tissue of the coral host, and the remaining zooxanthellae may lose 50-80% of their pigments (Glynn 1996). Due to the lack of the zooxanthellae in the coral tissue, the coral appears bleached white because the lime skeleton becomes visible. Corals receive photosynthetic products (sugars and amino acids) from the zooxanthellae (Trench 1987) and suffer death due to starving without the additional supply of these products produced by the zooxanthellae. However, after short-term bleaching events bleaching does not necessarily induce coral death and the coral may be able to recover by regaining zooxanthellae in their tissue. Glynn (1984) drew attention to the first large-scale coral bleaching event with subsequent high mortality rates observed in 1982-83 in the Eastern Pacific. It became clear later that other tropical areas had suffered similar effects over the same period (see Table 1 in Brown 1987).

A decade ago, there were still ongoing discussions about the link between bleaching events and high sea water temperatures. Some argued that there was a lack of long-term, high-quality temperature data to support ecological observations combined with the uncertainty as to whether or not there has been an increase in the frequency and intensity of coral bleaching, or just an increase in the frequency and extent of observations (e.g. Atwood et al. 1992). However, now long-term data have been put together and there is no doubt about the connection between increasing sea temperatures and coral bleaching events (Sheppard and Rayner 2002, Sheppard et al. 2002). In addition, laboratory experiments have shown that high temperatures alone can induce bleaching, conforming observations in the field (Glynn 1990). It appears that bleaching is a response to predominant mean temperatures and not induced by thermal shock of rapidly fluctuating temperatures (Jokiel and Coles 1990). Now scientists suggest that high solar irradiance and ultraviolet radiation in particular have induced bleaching and have the potential to increase adverse impacts dramatically by acting synergistically with increased temperatures (Jokiel and Coles 1990, Drollet et al. 1994, Glynn 1996, Brown 1997, Dunne and Brown 2001). Bleaching on a small-scale has also been observed after stress disturbances to corals such as sediment and sand burial (Riegl 1995, Sladek Nowlis et al. 1997, Nemeth and Nowlis 2001).

The most severe global coral bleaching event documented so far was in 1998 causing near complete mortality on 16% of the world's coral reefs (Wilkinson 2000). Models predict that even under moderate global warming rates (a doubling of current greenhouse gas concentrations by 2100) bleaching events like the one in 1998 are likely to become common within 20-30 years (Hoegh-Guldberg 1999). By the end of 2040, most reefs will experience a 1998-like bleaching event annually (Hoegh-Guldberg 1999). Adaptations as well as acclimatisation of coral and zooxanthellae to increasing water temperatures have been reported (Rowan et al. 1997, Brown et al. 2000). However, it seems unlikely that these processes can keep pace with the present rapid rate of increasing water temperatures (Hoegh-Guldberg 1999).

1.4 Coral early life history

1.4.1 Reproduction

1.4.1.1 Sexual reproduction

Corals have two major modes of sexual reproduction: broadcast spawning and brooding (Sammarco and Andrews 1988, Richmond 1997). Broadcast spawners are the most fecund. Their colony size is generally larger than brooder colonies and broadcasters spawn for shorter periods each year (Fadlallah 1983, Szmant 1986). They predominate in stable environments where detrimental disturbances are rare (Szmant 1986). Brooders have multiple planulating cycles each year and produce fewer but larger larvae (Szmant 1986). They tend to predominate in environments with more frequent perturbations (Richmond and Jokiel 1984, Szmant 1986). Of the species studied so far, around 15% are brooders and 85% broadcast spawners (Richmond 1997). Occasionally, species can perform both broadcast spawning and brooding, but which occurs will depend on where the coral is located. For example, *Acropora humilis* is a brooder in the Central Pacific and Red Sea whereas on the Great Barrier Reef it reproduces by spawning (Richmond and Hunter 1990). Nevertheless, this situation is rare.

Corals are either hermaphroditic or gonochoric. Hermaphrodites produce both sperm and eggs whereas gonochoric corals produce either sperm or eggs (Szmant 1986). A hermaphroditic species may be either a brooder or a broadcast spawner, likewise for a gonochoric species. Szmant (1986) described that Caribbean *Porites* are brooders with small adult colony size, whereas the Pacific *Porites* are gonochoric spawners which are large and long-lived. Hermaphroditism is particularly favourable in small and isolated populations where members of the opposite sex may be too far apart to reproduce successfully, except by self-fertilisation (Richmond and Hunter 1990, Harriott 1992, Richmond 1997).

Broadcast spawners release sperm and eggs into the water column where fertilisation takes place and the planula larvae develop. Fertilisation of brooders occurs inside the parental colony and this is also where the larvae develops. Larvae are supplied with zooxanthellae by the brooding adult before release (Babcock 1985, Babcock 1988, Fitzhardinge 1988, Richmond 1988). After release, larvae of brooders can settle out immediately and may do this close to the parental colony (Smith 1992). This is advantageous because it reduces risky time spent in the plankton and ensures larvae settle in a habitat where parental colonies have been successful. This strategy results locally in high abundance of new settlers (Szmant 1986). It may be advantageous in areas of high physical disturbance where subsequent high adult mortality can be offset by low mortality rates of juvenile corals. However, since brooded larvae are equipped with zooxanthellae and greater lipid stores than the larvae of broadcast spawners, they can also undertake long-distance dispersal in search of new favourable habitat (Sammarco and Andrews 1988, Harriott 1992, Richmond 1997). Species with long dispersal abilities may be widely distributed and this decreases their risk of extinction from local events (Richmond 1997). Brooders also produce larvae that have faster growth rates than the larvae of broadcast spawners (Rylaarsdam 1983, Babcock 1985, Fitzhardinge 1988). This results in higher juvenile survival for

brooders. Szmant (1986) suggested that brooding in corals is a means of increasing both reproductive success and reproductive efficiency.

1.4.1.2   Asexual reproduction

Asexual reproduction of scleractinian corals is either through fragmentation or budding. Fragmentation is when a coral colony breaks into smaller pieces and one or more of them reattach to the substratum to form an independent colony. Coral species in the Caribbean that primarily use this form of reproduction are mainly fast growing, branching species such as *Madracis mirabilis, Acropora cervicornis* and *Porites porites* (Hughes 1985). By virtue of their growth form branches can break in conditions that do not kill the whole colony. This may be in a strong current or during a period of high wave activity. Some fish and sea turtles also break corals by bumping into them. After fragmentation, the resulting pieces initially lose their capacity to reproduce either sexually or asexually. This may seem disadvantageous but because the fragments divert their resources to growth, they are able to reach a 'safe size' more quickly. Being bigger helps corals to avoid mortality from predation, overgrowth or smothering by sediment (see Szmant 1986). When a 'safe size' is reached, the colony can divert resources back to reproduction.

Budding is a process during which new coral polyps are built and 'pinched off' by an adult colony (Richmond 1997). The newly budded polyp may disperse considerable distances. All corals can reproduce in this way, but it is never their main mode of reproduction (Richmond 1997). Clearly, asexual reproduction results in little genetic variability and fragmentation limits dispersal (Richmond 1997).

1.4.2   Settlement

Settlement is the process when a coral larva leaves the water column and settles into a sessile benthic lifestyle (Richmond 1997). At this point, the larva undergoes metamorphosis and begins to produce its exoskeleton. This involves a series of morphological and biochemical changes.

The larvae of brooding and spawning corals have cilia that are equipped with chemoreceptors. These are important in guiding the larvae by chemical cues whilst they crawl along the benthos in search of a suitable place to attach (Pawlik 1992). Settlement is a complex process. For example, specific chemical inducers may be necessary to activate metamorphosis (Hadfield 1986). In corals of the genus *Agaricia*, species-specific chemical signals from particular types of crustose coralline algae are needed by the larvae in order for them to settle (Morse and Morse 1992). More generally, there are specific short-chain peptides or diatomaceous films which may trigger settlement (Van Moorsel 1988, Pawlik and Hadfield 1990, Morse and Morse 1991).

Factors thought to influence coral settlement and post-settlement survival patterns are sedimentation (e.g. Hodgson 1990a, Chiappone 1996), grazing (e.g. Birkeland 1977, Fitzhardinge 1988), spatial competition (e.g. Chiappone 1996), hydrodynamic regimes (e.g. Black 1993), physical and biological suitability of the substrate (Morse and Morse 1992) and light intensity, (e.g. Maida et al. 1994). In

addition, Rylaarsdam (1983) discovered that larvae which settle at a larger size are competitively stronger than smaller-sized settlers.

If conditions seem to be unsuitable for a newly settled coral to grow and survive, it can undergo reverse metamorphosis. Te (1992) exposed coral larvae to different levels of sedimentation. He found that settled larvae were able to return to the water column. By doing this they can select a new site where their chances of survival may be improved. This process is called 'bail out' and could modify patterns of larval settlement on polluted reefs.

Settlement is also influenced by the topography of the benthos. Studies have shown that the abundance and diversity of newly settled larvae increases as the surface becomes more irregular (Carleton and Sammarco 1987). It is possible that cracks, crevices and concavities promote larval settlement by reducing predation pressure (Russ 1980). In the field, where several factors such as grazing, overgrowth by algal or other benthic organisms and smothering by sediment are acting together, mortality rates of around 6% per month of coral recruits smaller than 5mm are commonly observed (Bak and Engel 1979, Rylaarsdam 1983).

1.4.3   Post-settlement

In this review we use the term post-settlement to describe the period after larval settlement up until the juvenile coral reproduces for the first time. The term recruitment is widely used by others but with many different definitions (e.g. Wallace 1983, Sammarco 1986, Wallace et al. 1986, Harriott and Fisk 1987, Hodgson 1990a). In natural biological systems, long-term settlement rate is always higher than the number of juvenile corals found on a reef (Richmond 1997). This is because newly settled corals have high mortality rates due to factors such as predation, competition for food and space, sedimentation and overgrowth (Babcock 1985). Consequently, post-settlement survival to the age of first reproduction is important because it describes the real replenishment of coral communities (Richmond and Hunter 1990).

Like abundance of settlers, higher juvenile coral abundances are found on rougher substrata (Chiappone 1996, Connell 1997). High complexity could offer protection from grazing and water turbulence. Different juvenile species compositions are found on different types of reefs (Rylaarsdam 1983, Chiappone 1996) probably showing the existence of specific settlement preferences.

Studies show a range of relationships between juvenile and adult densities, species composition and diversity. Some studies show a positive relationship between juvenile and adult coral populations, and this is especially the case amongst brooders (Rylaarsdam 1983, Harriott 1985, Chiappone 1996, Hughes et al. 1999). Chiappone and Sullivan (1996) suggested that this relationship may reflect a relatively constant supply of juvenile corals and post-settlement survival rate. This is supported by Hughes et al. (1999) who observed low variation in the settlement rate of brooders onto settlement plates over a period of two years on the Great Barrier Reef. However, other studies have reported that the composition of juvenile corals is independent of the structure of the adult population (Bak and Engel 1979, Fitzhardinge 1985, Harriott 1985). If there is a mismatch between the juvenile and adult community structure, the population may be in a state of flux. Alternatively, other biotic and abiotic factors may affect post-settlement survival

and determine composition of the adult coral population (Harriott 1985). This was confirmed by Hughes et al. (1999) who discovered that on the Great Barrier Reef broadcast spawners showed up to five times more annual variation in larval settlement rate and mortality of settlers compared to brooders. In contrast to the juvenile coral population, the total abundance of adult broadcast spawners on a large scale was relatively homogenous despite considerable variation in post-settlement survival. Consequently, Hughes et al. (1999) suggested that on reefs with lower densities of juvenile corals, post-settlement mortality is less than that on reefs with high juvenile densities.

However, it is well known that number and density of new settlers of marine organisms, including scleractinian corals, varies in space and time (e.g. Gaines and Roughgarden 1985, Wallace 1985b, Gaines and Bertness 1992). Hence, all factors (biotic and abiotic) affecting coral community structure are compounded by variability in production of new juvenile corals. For example, in years of high successful larval settlement natural and anthropogenic disturbances that decrease post-settlement survival could fail to be detected and, hence, would be ignored (Wallace 1985b).

1.5   Effects of human disturbances on early life history of corals

Natural and human disturbances can affect corals at any stage of their life cycle (Richmond 1997). Perturbations that inhibit successful replenishment of coral reef communities by reducing or even preventing reproduction, settlement and post-settlement survival, could be highly detrimental. Recovery from mass mortality events is dependent on these processes.

There are practical difficulties in separating the effects of stresses that occur on reefs. Monitoring studies of settlement patterns and juvenile coral distribution fail to separate factors such as predation and sedimentation due to the long time period the newly settled corals are exposed to the surrounding environment (Hodgson 1990a, Te 1992). Consequently, there has been much deliberation as to whether sediment reduces settlement or increases post-settlement mortality or whether changes in juvenile coral abundance are due to predation (Babcock and Davies 1991). In addition, eutrophication is also associated with high turbidity due to particles in the water column. This can lead to sedimentation effects. In this review, we discuss effects of high turbidity and sedimentation on reproduction, settlement and post-settlement survival only in the section 'sedimentation' to prevent repetition.

Contaminants are found mixed with and/or bind to sediment particles (e.g. Budzinski et al. 1997, Puig et al. 1999, Venkatesan et al. 1999, Zhang et al. 2002). However, we keep the 'sediment' section focused on the effects of sediment particles. The harm of contaminants on the early life history of corals will be described in the section on the effects of eutrophication. This is because eutrophication is often associated with discharge of other chemicals and pollutants such as oil washed from urban areas.

Finally, the effects of harmful human-induced disturbances on the early life history of corals can effect processes of settlement and post-settlement survival which may be different to separate because some processes are linked with each other. Hence, these two processes will be treated together.

1.5.1 Sedimentation
1.5.1.1 Reproduction

In areas with high sedimentation, corals show different tactics for freeing themselves from depositing sediments: (1) increased production of mucus to collect the sediment particles and transport them to the edge of the coral colony or enable them to be removed by water movement, (2) increased activity of tentacular and ciliar movement, and (3) tissue distension through uptake of water by the polyp (see Rogers 1990). All these mechanisms use energy, reducing the amount available for metabolic functions, reproduction and growth (Allert 1974, Dodge and J.R. 1977, Dallmeyer et al. 1982, Bak 1983, Van Veghel and Bak 1994). This is supported by Meester et al. (1992) and Meesters and Bak (1993) who show that sedimentation caused by construction of an artificial beach in Curaçao, Netherlands Antilles, decreased tissue regeneration potential of corals.

However, under conditions of physiological stress and energetic costs like sedimentation, stressed corals will predominantly use their available energy to secure survival. The first energy consuming activity of the coral that will be cut off from further energy input is reproductive activity (Kojis and Quinn 1984, Tomascik and Sander 1985, Tomascik and Sander 1987a, Van Veghel and Bak 1994). Kojis and Quinn (1984) compared fecundity of *Acropora palifera* on reefs in Papua New Guinea with different sedimentation levels and found a negative relationship between fecundity and sedimentation. On the reef with the highest sedimentation rate, fecundity of *A. palifera* was depressed by more than half compared with the reefs with lowest sediment input (Kojis and Quinn 1984). Due to the large size of the eggs and the high numbers of sperm that corals produce, Szmant (1986) concluded that a great amount of energy is used for reproduction.

The coral polyp receives most of its energy from the symbiotic zooxanthellae (Muller-Parker and D'Elia 1997). Dallmeyer et al. (1982) conducted an experimental study which showed that the primary production and the chlorophyll content of *Montastrea annularis* was decreased by the addition of peat particles to the water which raised turbidity. This may indicate the loss of symbiotic zooxanthellae (Pastorok and Bilyard 1985). Different results were obtained by Edmunds and Davies (1986, 1989) who measured the photosynthetic energy production of *Porites porites* in high and low sediment stress areas. Their results indicated that corals living under stressful environmental conditions had a higher photosynthetic productivity and a lower respiration rate resulting in higher loss of energy and reduced growth rate. Higher productivity, despite lower light availability under sediment conditions, arises due to photoadaptation in the coral (Edmunds and Davies 1989). However, the results of the lower respiration values and the high energy losses should be taken cautiously because Edmunds and Spencer (1989) assumed that dark respiration is the same as respiration in light. This may be questionable because they did not assess under which light intensity metabolism increases for example due to growth and reproduction. However, from their results it can be concluded that under high sediment conditions that reduces growth rate, reproduction is probably also reduced as a consequence of the energy costs of sedimentation.

Scleractinian corals depend on light for skeletal growth (Goreau 1961). On reefs with high sedimentation and associated high turbidity, light conditions are decreased and a reduction in coral growth occurs (Dodge 1973, Allert 1974, Bak 1978, Bak and Engel 1979, Cortès and Risk 1985, Tomascik and Sander 1985, Hodgson 1990a). This is compounded with lower energy supply for growth due to sediment rejecting mechanisms (Hubbard and Pocock 1972, Dodge 1973, Loya 1976b, Burns et al. 1984). Older and larger corals have been found to be most fecund (Fadlallah 1983, Kojis and Quinn 1983, Szmant-Fröhlich 1985, Szmant 1986) and it takes several years for a coral to become reproductively active (Szmant-Fröhlich 1985, Babcock 1988). Consequently, Richmond (1997) proposed that if the growth rate of a coral is negatively influenced by stress, e.g. sedimentation, decreased reproduction may also be a result of reduced growth.

Sediment particles can damage corals by abrasion (Johannes 1975, Loya 1976b, Rogers 1983). Van Veghel and Bak (1994) showed that there are trade-offs between reproduction and the regeneration of small lesions of coral tissue. They removed areas (size 160mm², depth 4mm) of tissue and skeleton of several *Montastrea annularis* colonies on reefs in Curaçao. After regeneration of the damaged areas, no gonads were found in the new polyps. Also the polyps around the regenerated area showed a reduced amount of gonads and the number of fertile polyps (i.e. polyps with gonads) of previously harmed corals was lower compared to control colonies. All treated colonies showed decreased fecundity. The experiment was carried out in the breeding season and, hence, tissue regeneration was slow because energy was diverted to reproduction. Rinkevich and Loya (1989) reported that the regeneration of broken branches of *Stylophora pistillata* also resulted in a significant decrease in fecundity, lasting at least 19 months after regeneration started.

1.5.1.2 Settlement and post-settlement

Sediment particles in the water decreasing light penetration may add a physiological stress through reduced photosynthesis in coral larvae. It is also possible that sediment particles have direct negative impacts on coral larvae by physical abrasion, and in this way delay or even inhibit larval settlement by damaging or killing it (Tomascik 1991, Te 1992).

Maida et al. (1994) conducted an experiment using artificial settlement plates on the Great Barrier Reef and showed that light intensity was the most important factor determining the settlement position of coral larvae. The settlement stacks they used were created so that the light intensity decreased asymptotically from the edge to the centre of the settlement plates. Maida et al. (1994) concluded that the coral settlement pattern was determined by active larval choice of a site with a suitable light regime for attachment, rather than to avoidance of predation. Such site selection would only be possible when light is present and it thus appears likely that scleractinian larvae attach to the substrate during day time (Maida et al. 1994). Consequently, Maida et al. (1994) suggest that a decrease in overall light penetration on a coral reef, caused for example by increased sedimentation, would make many cryptic reef microhabitats unsuitable for coral settlement, due to suboptimal light regimes. This would then restrict coral settlement to upper surfaces, exposing settlers to higher levels of

sedimentation and grazing activity, resulting in a substantial reduction in the settlement, and subsequent growth and survivorship of settlers (Maida et al. 1994). This is supported by many other studies that show a change in the preference of the larval settlement position from vertical to horizontal angles with increasing depth, claiming that this is the result of decreasing light and increasing sedimentation levels with increasing depths (Birkeland 1977, Bak and Engel 1979, Birkeland et al. 1981, Wallace and Bull 1981, Rogers et al. 1982, Hodgson 1990a).

Coral planulae, like other larvae of sessile organisms, are unable to attach or anchor firmly enough to loose, fine sediment to begin growing (Roye and Smith 1971, Hodgson 1990a). Consequently, levels of sedimentation that have no harmful impact on adult coral colonies may inhibit settlement (Hodgson 1990a). On sediment stressed reefs the number of corals that settle successfully increases on vertical compared to horizontal settlement plates (Cortès and Risk 1985, Fisk and Harriott 1989, Babcock and Davies 1991, Tomascik 1991, Maida et al. 1994). Also Babcock and Davies (1991) who conducted a controlled laboratory experiment reported a highly significant effect of sediment on the number of settling larvae moving from the upper- to the undersurfaces of settlement plates, but densities of settlers per plate were not significantly different. However, these results have to be interpreted cautiously because in experimental aquaria other factors that may induce changes in settlers density are excluded (Babcock and Davies 1991).

At Lord Howe Island, Australia, Maida et al. (1994) observed that not only coral settlement was reduced but also most other invertebrate settlement, and even algal growth was not substantial after 4 months on the upper surfaces of artificial settlement plates. This, they claimed, was linked to a sediment layer that accumulated onto the plates and prevented every form of colonization. Hence, coral reefs with shallow slope angles would suffer more from high sediment conditions due to reduced areas of suitable substrate (i.e. vertical walls) for coral settlement post-settlement survival. In addition, it is reported that on the upper surface of artificial settlement plates, newly settled larvae have the fastest growth rates (Birkeland 1977). In high sediment situations, coral settlers may be restricted to areas where they will grow more slowly and this may result in lower survival as it will take them longer to reach a size where they are less susceptible to factors such as predation and overgrowth. On natural substrata sediment particles can get trapped in algal fronds preventing larval settlement (Walker and Ormond 1982).

Sedimentation impacts can be increased further through resuspension. Artificial settlement plates established in high sediment sites, but raised above the substrate (ca. 50cm) where turbidity due to resuspension is lower, showed a higher abundance of settled coral larvae than plates which were located closer to the substrate (Risk 1981, Cortès and Risk 1985). This type of experiment shows that even if coral larvae are present in the water column, settlement of the coral planulae and post-settlement survival are reduced.

Finally, chemical cues that are important for larval attachment (Pawlik 1992) may be obscured by sediment or altered by chemical contaminants in the sediment and in this way prevent successful larval settlement (Richmond 1997). However, studies are still lacking to test this prediction.

Smaller–sized corals have been argued to be at an advantageous in high sediment conditions because they do not have to transport the sediment layer so far to reach the edge of the colony (see Rogers 1990). On the other hand, survival of a coral colony is positively correlated with size (Bak and Engel 1979, Rylaarsdam 1983, Werner and Gilliam 1984, Hughes and Jackson 1985, Van Moorsel 1985, Fitzhardinge 1988). Connell (1973) suggested that this is due to the greater regeneration ability larger corals have. A disturbance may kill a whole small coral compared to the killing of a few polyps leading to partial mortality of larger coral colonies (Lewis 1997). This may make juvenile corals more susceptible to burial and smothering by depositing sediments than bigger coral colonies. Faster growing coral species may therefore have a lower juvenile mortality rate in sediment conditions than coral species that grow slowly.

The growth form of a coral colony may also affect survival rate on reefs with sedimentation stress (Hubbard and Pocock 1972, Riegl 1995). Van Morsel (1988) highlighted the importance of the growth form of *Agaricia agaricites*. All colonies which did not show any sign of stress such as overgrowth and partial mortality, had a typical colony edge which was raised above the substrate. In this way, submergence in shifting sediments and overgrowth by other competitive benthic organisms could be avoided. Hence, Van Morsel (1988) suggested that encrusting species (e.g. *Agaricia humilis*) are more susceptible to burial by sediment and stress by overgrowth.

Asexual reproduction by fragmentation dominates in areas with high wave energy and unstable benthic substrata probably due to the fragments' large size preventing predation and burial by sediment and thus reducing high larval and juvenile mortality rates (Highsmith 1982, Gilmour 1999). However, Hughes (1985) reported that comparing asexual and sexual produced recruits of different species the mortality rate of coral fragments was actually higher than the mortality rate of sexually produced recruits in Rio Bueno, Jamaica. The contradictory nature of these statements could perhaps be explained by differences in the form, intensity and type of disturbance present in the sites studied. Highsmith (1980) argued that in areas where sexual reproduction dominates under favourable conditions, asexual reproduction may dominate during altered environmental circumstances and disturbances. This is because asexual reproduction is favoured by not requiring a partner of the opposite sex, spreading locally adapted genotypes (Richmond and Hunter 1990).

Juvenile corals have adapted phenotypic characteristics of their parental colony. Some of these characteristics may also determine the capability of juvenile corals to withstand disturbances. For example, large corallites and high extension ability of polyps are favoured in sedimented conditions, while small corallites, low polyp extensibility and ramose coral growth form have less ability to reject sediment (Hodgson 1990a, Riegl 1995). Tomascik and Sander (1987a) counted a higher density of polyps on *P. porites* in eutrophic areas which may be an adaption to the turbid conditions. But confusion can arise when coral species show a combination of sediment benign and disadvantageous phenotypic characteristics (Hodgson 1993). Hence, some coral species are more or less capable of rejecting sediment than others, but contrary observations about different species exist (e.g. insufficient: *Porites astreoides, Porites porites* (Bak

1978), *Siderastrea sidera* (Kolehmainen 1973), sufficient: *S. radians*, *S. siderea*, *Diploria strigosa*, and *Meandrina meandrites* (Loya 1976a), *D. strigosa* (Kolehmainen 1973)). Fragmentation may offer an advantage over sexually produced coral settlers because, being larger, they prevent themselves from getting buried by sediment or smothered by algae (Wittenberg and Hunte 1992).

Bacteria are responsible for coral tissue necrosis and subsequent coral mortality when buried by sediment (Hodgson 1990b, Riegl 1995). Sediment layers may stimulate rapid population growth of pathogenic bacteria (Mitchell and Chet 1975, Egan 1987). However, some corals seem to produce mucus that is resistant to bacterial invasion (Lewis 1973, Ducklow and Mitchell 1979). This could already give juvenile corals that produce antibacterial mucus a survival advantage (Tomascik and Sander 1987a).

1.5.2 Eutrophication and toxic chemicals
1.5.2.1 Reproduction
The timing of reproduction depends on various abiotic factors such as water temperature, water level, nocturnal illumination and chemical signals (e.g. Harriott 1983, Jokiel et al. 1985, Shlesinger and Loya 1985, Babcock et al. 1986, Hunter 1988, Oliver et al. 1988, Coll et al. 1989, Atkinson and Atkinson 1992). Factors such as petroleum products, pesticides, herbicides and heavy metals may alter water quality significantly. Consequently, changes in water quality can have an impact on the transmission and admission of chemical signals in corals, upsetting the timing of the gametogenesis and the synchronisation of the release of gametes (Richmond 1994, Richmond 1997). Concentrations of many pollutants and contaminants are highest at the ocean surface and it is also at the surface where fertilisation of braodcast spawned coral eggs takes place because eggs have positive buoyancy due to stored lipids (Richmond 1997). Pollutants and contaminants introduced to the sea with nutrient run-off from the land, could therefore affect successful fertilisation of gametes.

Eutrophication has been shown to shift coral sex ratios. Tomascik and Sander (1987a) observed a skewed sex ratio of *P. porites* by 2:1 in favour of males on eutrophic reefs compared to a 1:1 sex ratio on control reefs in Barbados. They also reported that on reefs with lower nutrient levels gonochoric brooders were dominant, while on eutrophic reefs hermaphroditism dominated. Hermaphroditism may be more advantageous in polluted areas since fertilisation may be less successful, as partners of the opposite sex may be rare or gamete production may be reduced (Richmond and Hunter 1990). On the other hand, hermaphroditism may lead to coral populations with low genetic variability on eutrophic reefs, rendering them more susceptible to environmental changes.

Tomascik and Sander (1987a) also found that timing and mode of reproduction in *P. porites* varied with eutrophication intensity. Populations in eutrophic locations started reproducing one to two months earlier than populations on less polluted reefs and showed depressed gamete production. This may be a response to eutrophication since energy may be diverted to metabolic functions essential for the coral's survival and by extending the breeding season they increase the chance of successful release of larvae (Tomascik and Sander 1987a). However, Tomascik and Sander (1987a) did not find differences in fecundity of *P.*

porites on reefs with high eutrophication compared to reefs with lower levels of nutrients.

By contrast, pollution from oil spills has been shown to negatively affect reproductive organs of corals in the polluted area even years following the spills (Guzman and Holst 1993). Guzman and Holst (1993) investigated reproduction of the Caribbean coral *S. siderea* on reefs of Panama five years after a major oil spill. Reefs were still affected chronically by oil and the sediment was characterised by high levels of toxic hydrocarbons (Guzman and Holst 1993). They found significantly smaller gonads in the impacted areas compared to those in control areas. Additionally, injured coral colonies showed smaller gonads on the part where the injury occurred compared to the uninjured part of the same colony (Guzman and Holst 1993). In the impacted areas, colony size was also reduced compared to control areas (Guzman and Holst 1993). Hence, Guzman (1993) suggested that due to a combination of these negative effects, oil pollution can reduce population survival by decreasing number of reproductively viable colonies and gamete production.

Epstein et al. (2000) investigated in an laboratory experiment using different oil dispersants (used by for example Israel to treat oil spills in the sea) in different concentrations the effects of these dispersants on coral larvae. They found a reduction in settlement attempts, decreased settlement rates, and high toxicity causing larval mortality, larval morphology deformations, loss of normal swimming behaviour and rapid tissue degeneration when exposed to the dispersants.

Copper is found in sewage discharge (Pastorok and Bilyard 1985), used in herbicides and fungicides for agriculture (Cremlyn 1979) and is a main component in anti-foulant paints for boats (Selinger 1989, Claisse and Alzieu 1993). In an experimental study, Reichel-Brushett and Harrison (2000) showed that relatively low concentrations of copper impair or inhibit larval settlement of *Acropora tenuis*, a spawning coral species common on the Great Barrier Reef, Australia. Negri et al. (2002) also found detrimental impacts of anti-foulant paint on coral larvae and settlement. They tested the effects on larval settlement of sediment contaminated by anti-foulant paint after a cargo ship collided with a reef, part of the Great Barrier Reef, and remained there for close to two weeks. The results showed this sediment, containing tributylin (TBT), copper and zinc significantly inhibited larval settlement and metamorphosis (Negri et al. 2002). Hence, recovery of reefs after collisions of boats using anti-foulant paints may be reduced (Negri et al. 2002). Overall, these studies provide evidence that toxins are harmful to coral larvae, reduce their viability and successful settlement or even have detrimental impacts on their genes.

1.5.2.2   Settlement and post-settlement
Coral larvae compete with other sessile organisms such as algae, sponges, tunicates and other invertebrates for space to settle on. In studies using artificial settlement plates, biomass on settlement plates (which consists mainly of filamentous algae) is greater in eutrophic sites than on reefs with low nutrient inputs, including a thicker layer of sediment on the upperside of horizontal settlement plates (Tomascik 1991, Wittenberg and Hunte 1992). On less eutrophic

reefs, settling plates tend to be covered by an invertebrate community that consists mostly of hydroids, colonial tunicates, bryozoans and sponges (Tomascik 1991). Algae and other fast-growing fouling organisms are able to take advantage of high nutrient conditions on polluted reefs (Birkeland 1977, Birkeland 1988). These organisms occupy important benthic substrate for larval settlement and can smother newly settled coral larvae reducing settlement success and subsequent survival (Hatcher 1984, Tomascik 1991, Done 1992, Hughes 1994).

Ward and Harrison (1997) investigated effects of elevated nutrients on coral larval settlement as part of the ENCORE experiment on the Great Barrier Reef in Australia (see 1.3.4). They found that on reefs treated with different levels of phosphorus, settlement was lower compared to control reefs (Ward and Harrison 1997). Larvae that had been raised in elevated nutrients and then transported onto untreated reefs, did not show any significant difference in settlement rates compared to control reefs (Ward and Harrison 1997). In an additional experiment, larvae that developed from gametes produced by corals from nutrient-treated reefs, showed enhanced settlement when transported to untreated reefs (Ward and Harrison 1997). Hence, these experiments show that part of the settlement process or the larvae themselves are negatively affected by (Ward and Harrison 1997). An experiment on One Tree Reef, Great Barrier Reef, conducted by Kinsey and Davies (1979) using both added nitrogen and phosphorus showed that reef calcification decreased by around 50%. It may be possible that nutrient enrichment prevents the initial calcification process of the larvae as suggested by Ward and Harrison (1997). Bell and Gabrice (1990) found increased toxic cyanobacteria with increasing eutrophication and suggested that they may also be able to negatively affect settlement of coral larvae.

A lower abundance of coral settlers is found in eutrophic sites and, in addition, increasing settlement rates on the undersurfaces of horizontal artificial settlement plates with increasing eutrophication (Tomascik 1991, Wittenberg and Hunte 1992). Since no or low algal cover is observed on the lower side of horizontal settlement plates as well as on vertical plates, highest settlement rates are observed on these surfaces due to lower spatial competition with algae (Rogers et al. 1984, Oren and Benayahu 1997). Consequently, the undersurfaces of overhangs may be the only available spaces for successful settlement on eutrophic reefs. However, such places will have less light intensity which, while limiting colonization and growth of algae, could also reduce coral growth (Wittenberg and Hunte 1992).

Nutrient enrichment may enhance coral growth up to a certain point but, beyond this, growth declines due to smothering by sediment, overgrowth by algae, and reduced light penetration. This is supported by Tomascik and Sander (1985) who found higher growth rates of adult *Monatstrea annularis* colonies on eutrophic reefs compared to less eutrophic reefs in Barbados. On the same reefs, Wittenberg and Hunte (1992) observed a greater mean diameter of juvenile corals on the reefs with high levels of nutrients than on low eutrophic reefs. They also suggested either: (1) faster growth stimulated by nutrient enrichment, (2) lower settlement rates on eutrophic reefs, or (3) higher mortality of smaller individuals.

Conversely, it has been suggested that high levels of nutrients may shift the size structure towards smaller coral colonies that are more susceptible to

smothering by sediments, overgrowth or predation (Bak and Engel 1979). Bak and Engel (1979) found smaller recruits on a highly eutrophic reef compared to reefs with low nutrient input in Curaçao and Bonaire. They suggested that competition for space can also limit coral growth. *Pocillopora damicornis* shows a suppressed growth rate when competing with dense filamentous algae for space (Harriott 1983, Sato 1985). In addition, abnormal growth forms have been reported for corals competing with dense algae (Dustan 1975, Hubbard and Scaturo 1985, Rinkevich and Loya 1985). Nutrients in the water stimulate increasing biomass of algae (Wittenberg and Hunte 1992). This may not only result in reduced growth rate but may also increase the mortality rate of juvenile corals (Wittenberg and Hunte 1992).

Bioerosion could also be harmful to juvenile corals exposed to high eutrophication. Corallivorous and herbivorous fish (parrotfishes being the most important by scraping algae from dead coral skeletons) together with boring organisms, e.g. polychaetes, sponges and endolithic algae, are all agents of calcium carbonate erosion. However, on eutrophic reefs, bioerosion may be increased due to a higher activity of bioeroders e.g. filter feeders (Hallock and Schlager 1986). Van Morsel (Van Moorsel 1985) proposed that boring sponges in combination with endolithic algae are responsible for high juvenile coral mortality by weakening the substrate the coral is attached to. In Fanning Lagoon, Roye and Smith (1971) found $1.0 mg.l^{-1}$ calcium carbonate in clear waters while turbid waters in the same area contained $3.5 mgl^{-1}$ calcium carbonate. Most coral colonies in the area with high turbidity showed increased boring activity (see also Le Bris et al. 1998, Holmes 2000, Holmes et al. 2000, Zubia and Peyrot-Clausade 2001).

1.5.3   Overfishing

Herbivorous organisms, mainly sea urchins and herbivorous fish, are key organisms on coral reefs. High grazing activity can reduce the algal standing crop to very low levels over large areas (Carpenter 1986). Corals benefit from reduced algal biomass because algae and corals compete for space and light. Rogers et al. (1984) found highest juvenile coral abundances in areas of low algal cover and high herbivore activity. Filamentous algae can smother corals and reduce light needed for photosynthesis by symbiotic zooxanthellae. On reefs with high fishing pressure, herbivorous fish biomass is significantly reduced (McClanahan 1994, McClanahan and KaundaArara 1996, Williams and Polunin 2001) and algae proliferate, occupying important substrata for coral settlement (Sala and Boudouresque 1997, McClanahan and Muthiga 1998).

The most detrimental algae for corals are macroalgae. They form canopies that shade corals, thereby reducing the photosynthetic output of symbiotic zooxanthellae (Duggins et al. 1990). Barnes and Chalker (1990) reported that shading reduces coral growth. Macroalgae have also been observed to actively overgrow corals (Van Steveninck and Bak 1986, Hughes 1989). Leathery macroalgal thalli can also damage coral tissue when swept around by water motion (Coyer et al. 1993) and increase energy demand for tissue regeneration, reducing energy for reproduction (Tanner 1995). Tanner (1995) observed decreased fecundity in corals that were in contact with macroalgae. In plots

cleared of macroalgae, fecundity in coral colonies doubled compared to control plots (Tanner 1995).

Herbivorous fish, sea urchins and other grazers may also negatively affect abundance of juvenile corals because they scrape or bite small recruits off the substrate (Bak and Engel 1979, Rogers et al. 1984). Fish grazing is an indirect factor increasing post-settlement mortality of coral larvae on horizontal, open surfaces (Sammarco 1980, Harriott 1985, Fisk and Harriott 1990, Sammarco 1991). Corals which are not killed directly may still be damaged, affecting their development and making them more susceptible to other environmental changes. Bak and Engel (1979) monitored juvenile corals smaller than 40mm in permanent quadrats in Curaçao and observed that one-third of them disappeared completely after a six months time interval. They claimed that fish scraped them off the substrate when grazing rather than died due to overgrowth by algae or smothering by sediment. However, Birkeland (1977) observed herbivorous fish (surgeonfish and the parrotfish *Scarus croicensis*) grazing algae from artificial settlement plates but avoiding corals as small as 3 mm in diameter. However, under laboratory conditions, Rylaarsdam (1983) found size-dependent mortality of juvenile corals due to grazing activity by the sea urchin *Diadema antillarum*. Juvenile corals smaller than 3mm had only a 20% chance of surviving longer than 2-3 months compared to a 95% chance of survival for larger colonies. Field studies in Kenya have shown that a decrease of fish stocks due to overfishing increases the population of sea urchins (McClanahan 1994). This is mainly due to the removal of the triggerfish *Balistapus undulatus* that is a 'keystone predator' on sea urchins (McClanahan 1995). Consequently, it can be suggested that increased fishing pressure of sea urchin predators would decrease post-settlement survival of corals.

1.5.4 Rising sea temperature

Observations have shown that high water temperatures reduce the fecundity of corals. Kojis (1984) studied fecundity of *A. palifera* on different reefs in Papua New Guinea for a period of two years. Fecundity on both reefs was least when temperatures were highest (Kojis and Quinn 1984). This scenario might be made even worse when assuming that sperm production and mobility is also reduced following bleaching events after a mass bleaching event. This was observed by Omori (2001) who collected coral fragments of several mass-spawning acroporid corals of Okinawa, Japan. Each coral colony was kept separately in a container to spawn (Omori et al. 2001). After spawning, gamete bundles were collected and percentage fertilisation of artificially mixed eggs and sperm estimated. Omori (2001) found a drop from the usual 94% fertilisation success or more to an average of 42%, combined with reduced sperm motility. A hundred times more sperm were needed to reach more than 80% fertilisation which shows that dilution plays an important role in limiting the fertilisation success of eggs (Omori et al. 2001). Hence, Omori (2001) concluded that settlement rates following bleaching events are likely to be low probably decreasing recovery rate.

Reduced gamete production and coral densities after mass mortality of corals caused by a severe bleaching event will also decrease fertilisation success, reducing reef recovery by larval settlement (this Allee effect will be discussed in more detail in the next section). Glynn et al. (2000) reported that he did not find

any new settlers of the coral *Pavona varians* on reefs of the Galapagos Islands after the 1982/83 bleaching caused 97% coral mortality on these reefs. He also observed settlement failure during bleaching events in 1982/83 and 1997/98 when sea surface temperature anomalies exceeded 1.6 to 1.9 C° (annual mean sea surface temperatures are 24 to 25 C°, see Podesta and Glynn 1997). Edwards (2001) reported similar observations from artificial and natural reefs in the Maldives. Due to a large-scale bleaching event in 1998, live coral cover decreased from 42% to 2% (Edwards et al. 2001). This caused a shift in the coral community from dominance of branching over massive corals before the bleaching event (95% compared to 5%), to dominance of massive over branching corals after the bleaching event (97% compared to 3%). Settlement rates reflect the same trend and showed more settlers of branching (6%) than of massive corals (33%) before 1998, whereas after 1998, more massive coral settlers (94%) than settlers of branching corals (6%) were found. McClanahan (2000) found 29 settlers.m^2 on Maldivian coral reefs were massive coral species, whereas only 0.65 settlers.m^2 were branching coral species. In total, Edwards et al. (2001) found a decrease in the number of settlers after the bleaching event (before 1998: n = 3136, after 1998: n = 202). Even if these settlement rates seem to be very low, settlement has not failed completely as proposed by Hoegh-Guldberg (1999). However, Sheppard et al. (2002) who studied erosion and recovery of coral reefs after the bleaching event in 1998 on Chagos reefs in the Indian Ocean, observed an average of 78 juvenile corals m^{-2}, but they were found mostly on eroding or unstable substrate and the species mainly occurring were less robust. Hence, they concluded that recovery of the reefs by new coral settlers will be first possible when all unsteady rubble erodes into finer particles and are transported from the reefs, opening stable and solid substrate for coral larval settlement.

As mentioned earlier, ultraviolet radiation (UVR) is linked to increasing water temperatures (e.g. Brown 1997). However, Kuffner (2001a) conducted a field study using specially designed coral larval settlement chambers on the Great Barrier Reef to investigate the effects of UVR on coral larvae. Larvae were obtained from coral colonies from different depths (< 0.5m and 2-3m) from the reef and acclimated under UV-transparent (UVT) and UV-opaque (UVO) filters, before being placed back on the reef in the settlement chambers at 0.5m depth exposed to UVT and UVO conditions. He failed to find increased mortality rates of coral larvae, but showed that settlement was reduced significantly. Hence, Kuffner (2001a) suggested that these results indicate that larvae may delay settling to the substrate when UVR is high. Under increasing UVR conditions, corals increase the amount of compounds (mycosporine-like amino acids, MAAs) used to absorb UVR and stored in their tissue (Kuffner 2001b). In a further study, Kuffner (2001b) used *Porites compressa* branches from a single male colony and exposed them to different UVR levels including samples with no UVR, to measure MAAs production, chlorophyll-a concentration in the tissue and growth rate. Whereas no difference was found in MAAs production and in chlorophyll-a concentration between the treatments, Kuffner (Kuffner 2001b) found that calcification rate was negatively affected, although not significantly (Kuffner 2001b). Therefore, it may be speculated that since production of MAAs reduces growth, reproduction may also be limited. Reduced energy for reproduction may

also occur when bleaching causes partial mortality of corals (Wesseling et al. 1999) and regeneration of coral tissues is ongoing (Rinkevich 1996).

Generally, increasing sea water temperatures are stressful for corals. This was clearly shown by an experiment conducted by Meesters and Bak (1993) who made lesions on bleached and non-bleached corals during a mass bleaching event on reefs in Curaçao, Netherlands Antilles, in 1990. Regeneration was much slower in corals that bleached and mortality rate of these corals was higher compared to corals that did not show signs of bleaching (Meesters and Bak 1993).

Bleaching has also been observed in new coral settlers, but they show higher resilience compared to adult coral colonies (Mumby 1999). On reefs of Glovers Atoll, Belize, during the 1998 bleaching event, 70 to 90% of the adult coral colonies showed bleaching, whereas only 25% of the juvenile population showed signs of bleaching (Mumby 1999). Since coral bleaching can cause partial mortality (Wesseling et al. 1999), we expect smaller coral colonies such as coral recruits to suffer higher mortality rates. However, the only study looking into this was done by Mumby (1999) and his results did not support my hypothesis.

Bleaching might have long-term effects on coral reproduction. Michalek-Wagner and Willis (2001) studied fecundity, egg size and fertilisation of the soft coral *Lobophytum compactum* in the Red Sea. The most heavily bleached coral colonies showed lowest fecundity, mean egg size and complete failure of fertilisation. After 20 months, egg size and fecundity were still significantly reduced (Michalek-Wagner and Willis 2001). However, there is still a lack of long-term studies investigating reproductive output of scleractinian corals following bleaching events.

Finally, Glynn and Colgan (1992) reported that survival of predators and bioeroders on reefs in the eastern Pacific can increase post-settlement mortality and decrease coral settlement rates. Grazing sea urchin populations increased after the 1982/83 bleaching event on many reefs in Panama and Galapagos that suffered high coral mortality (Glynn and Colgan 1992). *Diadema mexcianum* densities increased from 3 to 80 indiviuals.m^2 on reefs in Panama (Glynn and Colgan 1992) and on reefs of the Galapagos Islands, *Eucidaros thouarsii* increased from 5 to 50 individuals.m^2 (Glynn 1990). Both species erode the reef framework increasing erosion of carbonate (Glynn 1983, Glynn and Colgan 1992).

1.6 Additive and synergistic multiple stresses

Often several stresses affect a coral reef simultaneously. A disturbance, which may have only a minimal or short-lived impact on corals in pristine environments, may be detrimental for corals already exposed to stress (Rogers 1990). This makes investigations into aspects of coral biology or the effects of environmental impacts difficult (Done 1992). Separating an individual impact of one stress when combined with other stressors is problematic. For example, a coral on a reef near a river mouth may be subjected to stress from low salinity, sedimentation, eutrophication, and reduced light penetration (Tomascik and Sander 1985, Tomascik and Sander 1987a, Van Katwijk et al. 1993).

A further problem of multiple stresses is that even if the types of stressors are different, they can affect the same processes. This is shown in Table 1, which

summarises the impacts of the three main human-induced stresses (sedimentation, eutrophication and overfishing) and increasing water temperature on reproduction, settlement and post-settlement processes. The impacts of these disturbances on the early life history of corals have been discussed in detail before (section 1.5).

For example, sediment particles can reduce settlement success for coral larvae (Walker and Ormond 1982). Also eutrophication negatively affects larval settlement by enhancing algal growth (Wittenberg and Hunte 1992). In addition, intensive fishing has reduced herbivorous fish stocks, resulting in increased algal growth, and further decreases in suitable substrate for settlement (Done 1992). On Jamaican reefs, algal growth took off after two hurricanes cleared large areas of space but was exacerbated by overfishing of herbivorous fish populations and mass mortality of the grazing sea urchin *Diadema antillarum* due to an epidemic disease (Liddell and Ohlhorst 1986, Rogers 1993, Steneck 1993, Hughes 1994)

Extensive 'bleaching' followed by mass mortalities of corals have been reported globally (Wilkinson 2000). Glynn (1984) observed extensive death of reef corals on the Pacific Coast of Panama after a bleaching event in 1983, with

Early life history	Sedimentation	Eutrophication	Overfishing	↑ Sea temperature
Reproduction		↓ synchronised spawning		
		↓ fertilisation success		↓ fertilisation success
				↓ reproductive output
	↓ energy availability (due to ↑ increased sediment rejecting mechanisms)	↓ energy availability (due to ↑ algal growth)	↓ energy availability (due to ↑ algal growth)	
	↓ growth		↓ growth (due to ↑ algal growth)	
	↓ photosynthetic output (due to ↓ light penetration)	changed reproductive periods	↓ photosynthetic output (due to ↑ algal growth)	
	↑ asexual reproduction	altered sex ratio		↓ asexual reproduction
Settlement and Post-settlement	sediment particles damage or kill larvae			↑ mortality
		↓ growth rate (due to ↑ algal growth)	↓ growth rate (due to ↑ algal growth)	
	↓ photosynthetic output (due to ↓ light penetration)			
	↓ substrata availability to settle (due to depositing sediment particles)	↑ spatial competition (due to ↑ algal and invertebrate growth) reduces settlement rate	↑ spatial competition (due to ↑ algal growth)	↓ settlement rates
		↑ bioeroders (e.g. filterfeeders, worms) weaken skeleton and substrate		↑ bioeroders (e.g. sea urchins) reduce quality of settlement substrate
	↓ diversity			

Table 1: Summary of the effects caused by the main human-induced stresses on the early life history of corals.

subsequent invasion by macroalgae (Glynn 1984). Herbivorous fish are thought to be able to control macroalgal growth before it becomes a large-scale problem provided fish populations are large enough (reviews by Hatcher 1983, Carpenter 1996, McCook 1999). Thus, in places where herbivorous grazer populations have been depleted, the invasive effect of macroalgae may be stronger. In addition, the reduction in adult coral populations, the source of reproduction, leads to lower gamete production.

Multiple stresses can have detrimental impacts on the energy budget of the coral (Brown and Howard 1985). A 'healthy' coral, like other organisms, produces enough energy to support growth, reproduction and basal metabolism (Peters 1983). In the case of a high demand for energy due to a disturbance, growth and reproduction, processes not essential for survival, will be shut off (Tanner 1997). However, it is not clear which process is the most likely to be cut off first. Corals that have physically damaged tissue show decreased fecundity and decreased gonads per polyp due to energy being allocated for the regeneration of the tissue (Van Veghel and Bak 1994). Mendes and Woodley (2002) looked at the effects of the 1995-96 bleaching event on polyp tissue depth, growth, reproduction and skeletal band formation in the Caribbean coral *Montastrea annularis*. They found that tissue depth recovered fastest while reproduction took the longest to recover (Mendes and Woodley 2002). Reproductive output of the most severely bleached coral colonies remained reduced even two years after the bleaching events when compared to previously unbleached colonies (Mendes and Woodley 2002). However, Guzman et al. (1994) found lower growth rates of corals on reefs affected by a major oil spill in Panama compared to corals on unpolluted reefs. Similarly, disturbance by sediment particles was found to increase the energy investment in growth of the tissue by stressed corals (Edmunds and Davies 1989). Tanner (1995) found that corals in plots with reduced macroalgae grew faster and their fecundity was twice as high as corals in plots with macroalgae present (Tanner 1995). However, studies have shown that if a coral colony decreases in growth, reproductive output also decreases because, being colonial organisms, the number of reproductive actively polyps also decreases (e.g. Hughes 1984, Hall and Hughes 1996).

In Figure 1, scenario (a), we show the energy budget of a coral over time when additive stresses affect the colony. If a coral is confronted by a single stress, e.g. reduced light penetration caused by sedimentation that decreases the photosynthetic output of the zooxanthellae, the coral's energy budget is decreased without necessarily having a significant effect on fitness. The coral may at this point have enough energy resources to cope with a second stress. This stress might be, for example, sediment particles that deposit onto the coral under sedimentation conditions. The coral will then need to activate its sediment rejecting mechanisms such as increased tentacular activity or mucus production. However, if a third stress confronts the coral, for example, increased growth of algae prompted by nutrient input, the coral might be forced to reduce reproductive output and/or growth. This is because the additive stresses push the colony beyond the first threshold below which the energy budget is not sufficient enough to support all processes. Adding a further stress, e.g. overfishing that depletes the herbivorous fish stocks and boosts algal growth, might push the energy budget

under a second threshold which for the coral means that there is a lack of energy to support its basal metabolism and the coral might finally die.

A further scenario is possible, which is shown in Figure 1, scenario (b). In the background to all these stresses, the environmental conditions a coral has to live in might already have deteriorated by, for example, increased water temperature. Under these circumstances, decreased vitality of the coral means that each stress has a larger impact on the coral's fitness. In this situation, stresses act synergistically rather than additively, and the coral would succumb more quickly to further stresses.
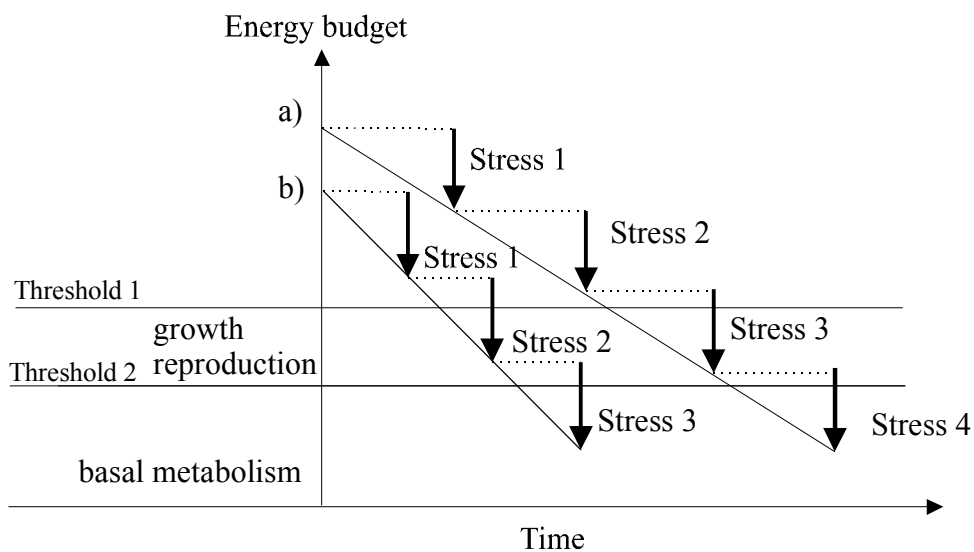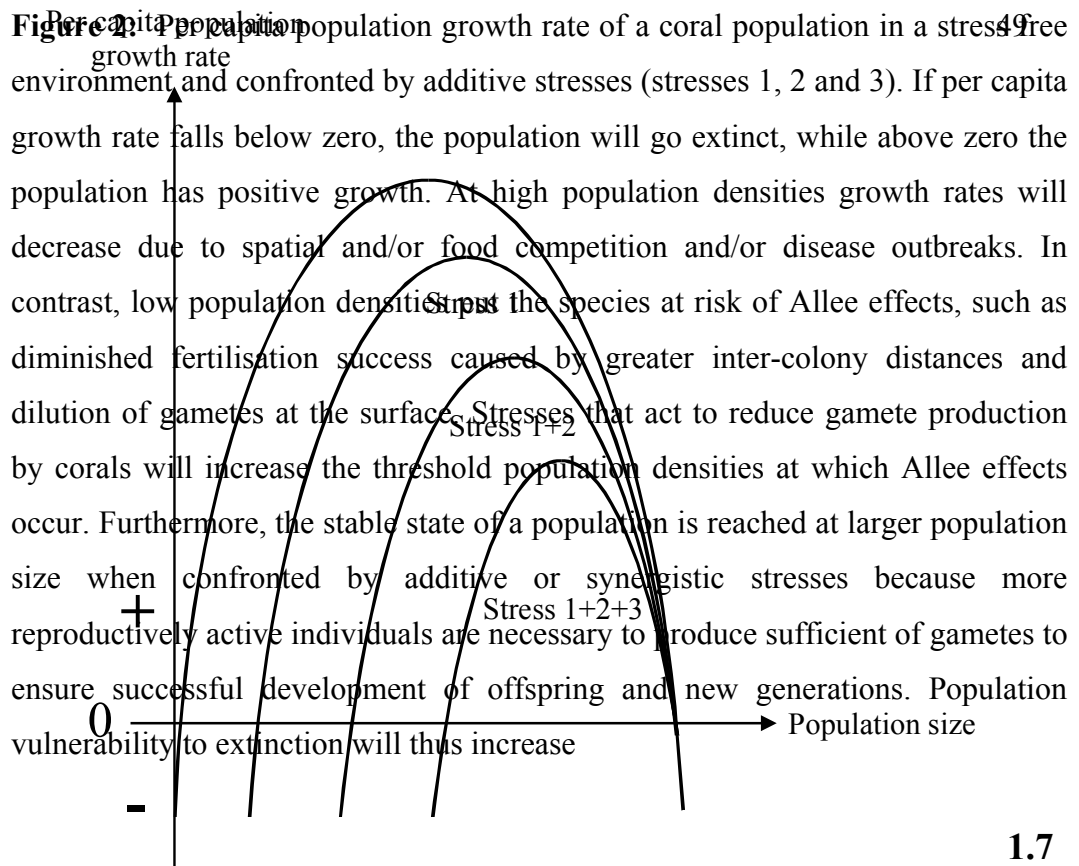

Figure 1: Energy budget of an individual coral colony confronted by multiple stresses. Under the conditions shown in (a), stresses act additively. However, in (b) another background stress, e.g. seawater warming, acts synergistically to increase the impact of each stress.

Allee effects can compound problems for coral populations. This is the situation when a population suffers falling reproductive success or survival as population densities decline and was first described in 1949 (Allee 1949). Coral densities can fall due to factors such as mortality caused by bleaching due to rising water temperatures, disease or predators outbreak. This can lead to fertilisation failure due to reduced colony density (Levitan et al. 1992). If sources of mortality go unchecked, densities could fall beneath a critical threshold under which sexual reproduction fails completely.

Multiple stresses affecting colony vitality, in combination with Allee effects, could threaten the persistence of some coral species and/or populations. This is presented in a simple model in Figure 2. For example, bleaching can cause extensive reductions in coral cover, pushing the density of some coral species so low that fertilisation success may be significantly decreased leading to low settlement rates (McClanahan 2000). In combination with further disturbances, such as sedimentation, fertilisation success may further decline, due to reduced

reproductive output of adult colonies caused by allocation of energy to sediment rejecting mechanisms, regeneration of tissue and active water uptake of the polyp (see Rogers 1990, Van Veghel and Bak 1994). Furthermore, sediment particles in the water can reduce the light penetration leading to lower photosynthetic output of corals which causes reduced energy supply for gamete reproduction of coral colonies (Tomascik and Sander 1987b). In Figure 2 it also becomes clear that per capita growth rate decreases with increasing numbers of stress factors. This is because larvae that are produced might fail to settle or suffer higher post-settlement mortality due to these factors.

The model in Figure 2 also shows that a population affected by additive or synergistic stresses moves its stable state equilibrium towards larger population sizes. More reproductively active individuals are needed to produce enough larvae to ensure new coral settlers balance mortality.

Figure 2. Per capita population growth rate of a coral population in a stress-free environment and confronted by additive stresses (stresses 1, 2 and 3). If per capita growth rate falls below zero, the population will go extinct, while above zero the population has positive growth. At high population densities growth rates will decrease due to spatial and/or food competition and/or disease outbreaks. In contrast, low population densities put the species at risk of Allee effects, such as diminished fertilisation success caused by greater inter-colony distances and dilution of gametes at the surface. Stresses that act to reduce gamete production by corals will increase the threshold population densities at which Allee effects occur. Furthermore, the stable state of a population is reached at larger population size when confronted by additive or synergistic stresses because more reproductively active individuals are necessary to produce sufficient of gametes to ensure successful development of offspring and new generations. Population vulnerability to extinction will thus increase

Graph labels: Per capita population growth rate · Stress free growth rate · Stress 1+2 · Stress 1+2+3 · Population size · 0 · + · −

1.7 Implications of coral early life history for manage

ment

The early life history processes of corals are a critical stage because they are very sensitive to disturbances (Richmond 1997). Larval supply, settlement success and post-settlement survival rates determine the relative amount and pace of recovery after coral cover reduction from a disturbance. The type of perturbation, species composition of the reef community, location of the damaged reef, extent of damage and subsequent modification of the benthic substrate, intensity and frequency of the perturbation, availability of coral larvae, current patterns, and the availability of substrate for larval settlement are only some of the factors which determine the amount of successful settlement, survival and rates of reef recovery from disturbances. Hence, reef managers have to pay more attention to these processes. Although some disturbances may be uncontrollable, like storms, other perturbations could be reduced and prevented by managers using controls and regulations. It is important to consider early life history processes to ensure reef growth and recovery.

Richmond and Hunter (1990) suggested that reef management may be improved by using data on reproductive patterns, larval settlement and post-settlement survival. For example, in peak reproductive seasons discharges of chemical pollution to coral reefs should be minimised. Additionally, coral transplantation, construction of artificial settlement substrate, and reseeding could support replenishment of degraded coral communities (Richmond and Hunter 1990, Oren and Benayahu 1997, Richmond 1997).

There is a need to rehabilitate degraded reefs (Richmond and Hunter 1990). This could be done, for example, by transplanting living coral fragments (e.g. broken branches). The type of reseeding might be beneficial in areas with high sedimentation or high density of predators because the fragments are already large enough to reduce their susceptibility to stress. Reseeding of sexually reproduced settlers may be successful in areas that have suffered coral loss, but are now free of disturbances or stress. This process could be supported by transplanting fertile adult coral colonies, installing artificial substrate that is already settled by coral larvae bred in laboratories, or release of artificially bred coral larvae. Coral larvae produced in mass spawning events have been collected and successfully introduced into areas of the Great Barrier Reef which have been previously damaged by *Acanthaster planci* (see Richmond 1997). This example shows that reseeding of reefs is possible if the reef is suitable for recovery. In addition, recolonisation of corals could be stimulated with the help of chemical cues of coralline algae, the preferred settlement substrate (Morse et al. 1994, Morse and Morse 1996). Research on captive breeding of coral larvae is still in its infancy. Even if some projects have been successful (see Borneman and Lowrie 2001, Petersen and Tollrian 2001), this restoration strategy is very time-consuming and expensive (Petersen and Tollrian 2001). However, successful recolonization as well as reseeding depends on prevention of pollution and human damage to the substratum. For example, careful planning and implementation of protective measures during coastal construction projects can reduce damage to the marine ecosystem (Dubois and Towle 1985, White 1987).

Large-scale variation in settlement and juvenile coral survival rates have profound implications for reef management (Hughes et al. 1999). For example,

replenishment of degraded coral reef communities on Caribbean reefs is slower than on the Great Barrier (Kojis and Quinn 1994, Connell 1997). Smith (1992) suggested that higher densities of acroporids that are spawning coral genera, on Pacific reefs than on Caribbean results in greater reproductive effort per unit area and, consequently, higher settlement success. Spawning corals are the most abundant settlers on reefs in the Pacific, whereas brooders dominate in the Caribbean (Smith 1992). However, settlement rates of brooding species are around the same on Atlantic and Pacific reefs (Wallace 1985a, Wallace 1985b, Babcock 1988, Fitzhardinge 1988). Coral cover and numbers of adult corals differ little between reefs in the Caribbean and the Great Barrier Reef (Rogers et al. 1984, Richmond and Hunter 1990, Smith 1992) implying that post-settlement mortality is lower in the Caribbean (Hughes et al. 1999). This is supported by Connell et al. (1997) who over a 30-year period followed coral larval settlement and juvenile survival on Heron Island, Australia. He found juvenile coral mortality to be higher than rates reported from the Caribbean. Differences in mortality rates of juvenile corals from different regions may be due to different biotic and abiotic factors such as hurricane events and predation (Sammarco 1985, Richmond and Hunter 1990).

Some reefs appear to be self-seeding (Baggett and Bright 1985, Sammarco and Andrews 1988, Andrews and Clegg 1989, Sammarco and Andrews 1989) while others may depend on distant coral communities for their supply of larvae (Richmond 1987, Babcock 1988). Consequently, a coral community can be either a 'source' or a 'sink' for motile propagules or it could be both. Roberts (1997) suggested that because of the current patterns in the Caribbean that transport larvae, management of the Caribbean reefs should be interconnected and work together. He recommended the implementation of marine reserve networks to secure the production of larvae into areas that depends on them and to protect populations of upstream reefs (Roberts 1997). Nevertheless, local protection of 'sink' areas is at least as important as the protection of 'source' populations, to ensure that conditions are suitable for larval settlement and post-settlement survival. However, knowledge of 'sink' and 'source' areas is still very poor due to the long distances larvae can be transported and their different dispersal abilities.

The establishment of marine reserves can be combined with monitoring programs to detect disturbances at an early stage to prevent collapse of populations and communities. For example, Brown and Howard (1985) suggested that monitoring of the energy budget of corals may give early indications of environmental stress. Peters and Pilson (1985) proposed several other physiological and histopathological methods to monitor stress effects on corals. Nevertheless, these are not useful tools for managers because they are too difficult and still too costly to measure. We suggest the monitoring of settlement and juvenile coral survival. These methods have been shown to be sensitive to human-induced pollution. Methods to monitor these processes can be done very easily and inexpensive by using artificial settlement constructions and permanent photo quadrats in which the fate of individual juvenile corals can be followed over time (e.g. Rogers et al. 2001).

Marine reserves might also help to reduce human-induced stress. Increases of depleted fish stocks, have been observed following the establishment of marine

reserves (Roberts et al. 2001) and this may increase grazing pressure on algae, reducing algal cover and opening space for coral larval settlement. Hence, marine reserves might play an important role in reversing phase shifts from algal dominated to coral dominated reefs. Reefs that suffer high nutrient inputs will probably be better off with high herbivore populations than reefs with high eutrophication and low herbivory. However, marine reserves are not able to protect from disturbances like hurricanes or increased water temperature. They also may be less effective in combination with disturbances such as sediment pollution. We studied the interaction between marine reserves and sedimentation stress on coral cover in St. Lucia from 1995 to 2001. On reefs with high sedimentation at 15m depth, there was a steady decrease in coral cover in both marine reserves, where all types of fishing are forbidden, and fishing grounds over these years. Sedimentation is believed to be the cause of the decline in coral cover because no major disease outbreak, bleaching event or physical destruction e.g. storm impact has been observed in these locations over this period. In 1994, Tropical Storm Debbie brought a lot of sediment onto St. Lucia's reefs (Sladek Nowlis et al. 1997). The resuspension effects of the deposited sediment combined with new sediment input have negatively affected coral cover despite protection from fishing (Nugues 2002).

Stresses on modern coral reefs are more numerous, more intense and more frequent than before (Hoegh-Guldberg 1999, Hughes and Connell 1999, Scavia et al. 2002). Coral reefs that already suffer chronic pollution like sedimentation and eutrophication will show slower recovery after disturbances or recovery might even fail altogether (Rogers 1990). Hence, it is important that reef managers focus on managing stresses rather than the effects they cause. Sources of chronic stress such as sedimentation or eutrophication need to be reduced or eliminated. This also includes actions to mitigate global climate change (Goreau and Hayes 1994, Reaser et al. 2000), although they lie beyond the power of local reef managers.

1.8 Conclusions

This literature review indicates that there is a crucial need for investigations into the effects of disturbances (natural and human-induced) on coral larvae and juvenile corals. Impacts which have no detectable effects on adult corals may still decrease coral larvae viability and, consequently, settlement and post-settlement survival. Hence, living coral cover alone (abundance and diversity) does not reliably reflect the health of a reef. Such values only describe the state of the reef at a moment in time. Settlement patterns and post-settlement survival hold the key to what the future of a reef may be. Adult corals may be able to survive in areas where reproduction is failing and larvae are unable to settle (Richmond 1997).

A lot of research exists on the impacts of disturbances, however, there is still a lack of research on the recovery of reefs following these disturbances. This is mainly because coral growth is slow and most studies cover periods not longer than three years. Hence, there is a profound need for long-term and large scale studies investigating dynamics of early life history processes.

1.9 References

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