

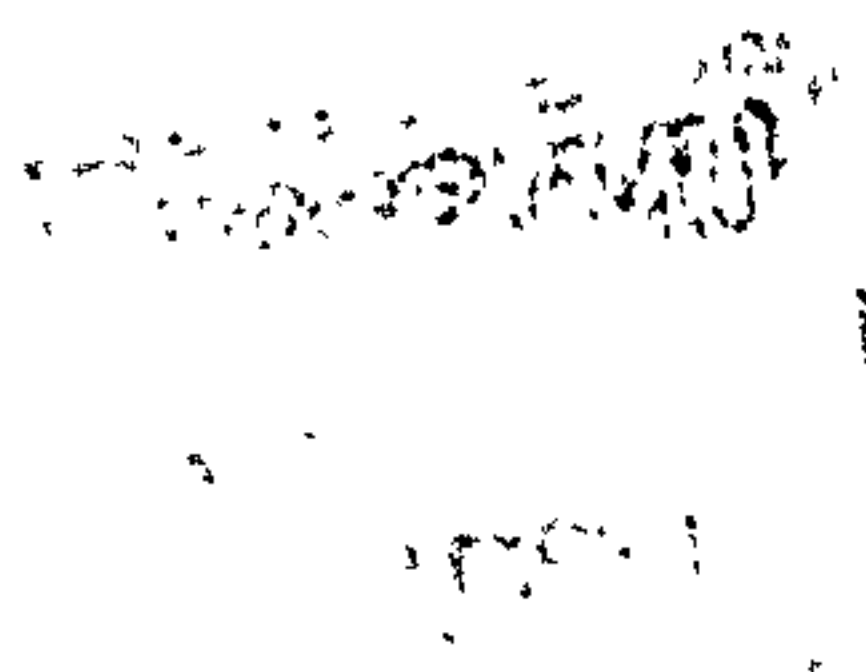
The impacts of multiple stresses
on the replenishment of coral communities

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Abstract

Coral reefs are threatened by multiple stresses and have been suffering severe degradation world-wide. Replenishment processes are thus important to the resilience of coral reefs and their ability to recover from human and natural disturbances. However, there is a lack of knowledge on the effects of multiple stresses on the replenishment of coral communities. This thesis focuses on the impacts of fishing, sedimentation and hurricanes on coral communities, juvenile coral assemblages, their growth and mortality, and coral larval settlement. The study was conducted on reefs on the west coast of St. Lucia, West Indies. Several no-take marine reserves in the study area provided sites with exposure to different levels of fishing. Rivers caused sediment input along two coastal stretches. A tropical storm and hurricane caused sediment runoff and reef destruction prior to and during my research. Although chronic sediment input was continuous throughout the study period, the greatest coral mortality occurred after the storm and hurricane events. However, especially in deeper water on reefs close to the river mouths, sedimentation was responsible for a steady decline in coral cover and inhibited reef recovery. Generally, coral losses were immediately replaced by algal cover. Juvenile coral numbers, diversity and growth rates were negatively affected by sedimentation. Also juvenile species composition was modified by sediment input. Coral larval settlement increased with decreasing sedimentation on both natural and artificial substrata. Juvenile coral mortality was lowest on reefs with intermediate levels of sediment input. Herbivorous fish may increase coral settlement and post-settlement survival by grazing on algae, but their role on these reefs remains unclear. Even in marine reserves, where herbivorous fish stocks tripled in biomass over the study period, macroalgal cover was not affected. Longer-term studies are needed to investigate whether marine reserves are successful management tools in reversing phase shifts between coral and algal dominated states. In addition, land-based management is required to reduce sources of sediment which as this study shows are detrimental to the replenishment of coral populations.

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Declaration

The benthic substrate monitoring was initiated by Joshua Sladek Nowlis in 1995 and extended monitoring was conducted by Maggy Nugues from 1996 to 1998. I continued the monitoring project in 2000 and 2001. Data on fish biomass were collected by Prof. Callum Roberts and Julie Hawkins. Allan Smith from the Caribbean Natural Resource Institute developed the design of the sediment traps. Most of the sediment traps were installed by Maggy Nugues. After Hurricane Lenny in 1999, I rebuilt several traps that had been destroyed by waves and also extended the sedimentation trap measurements at 5m depth in the low sedimentation sites in 2000. Sara Svensson was my field assistant on my second and third field trip and took over collection of sedimentation data when I was lying sick in bed. In July and August 1998, Tessa McGarry, Rachel Miller and Annalie Morris carried out the sedimentation measurements. Paula Low helped to collect sedimentation data in 2001. I collected all other data and interpreted them. The writing of the thesis is solely my own work. Prof. Callum Roberts offered editorial comments on all chapters.

General Introduction

Coral reefs are unique formations. Reef organisms build massive limestone constructions, but the living organic material is only a thin coating on the surface of the limestone. And this coat is incredibly productive: in the open ocean productivity is around $0.01\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, whereas on coral reefs it is estimated as $40\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Hatcher 1988). This makes a coral reef an 'oasis' surrounded by a low nutrient desert. Moreover, coral reefs are often referred to as the rainforests of the ocean (Connell 1978, Reaka-Kudla 1995). This is because like rainforests, reefs are inhabited by large numbers of species for which they provide food, shelter and protection from predation (Nixon 1982, Sheppard 1998, Lugo et al. 2000). Furthermore, coral reefs protect coastal areas and islands from waves and storms (Birkeland 1997). Global warming might increase frequency and severity of storms (Emanuel 1987, Goldenberg et al. 2001), hence, this service reefs provide, will become even more important to prevent land loss by erosion.

Although coral reefs cover barely 0.09% of the ocean (Spalding et al. 2001), around 15% of the world's population (0.5 billion people) are estimated to depend at least partly on coral reefs for their livelihood (Bryant et al. 1998). Apart from being a source of food and coastal protection, pearls and shells that serve as jewellery, many biochemicals produced by diverse reef organisms have been now discovered as extremely valuable for pharmaceuticals (Carte 1996, Birkeland 1997, Moberg and Folke 1999). However, with expanding human population, threats to coral reefs are increasing and there are serious concerns that marine species living on coral reefs could become extinct, taking with them all their potential values for medicine.

Tourism is the fastest growing economic sector associated with coral reefs and for many developing countries the most important source of income (Birkeland 1997, Bryant et al. 1998, Hodgson and Dixon 2000). However, uncontrolled development of hotels and resorts including direct sewage discharge into the ocean and careless behaviour of tourists (e.g. reef trampling) have caused severe damage to coral reefs (Hawkins and Roberts 1993, Bryant et al. 1998). In

addition, fishing is the main source of protein for many people in developing countries (Parsons 1992, Jennings and Lock 1996). An estimated 15% of the global fishery is estimated to take place on coral reefs (Munro 1996). Due to continuing global coral decline, scientists and reef managers met in 1993 to discuss threats to coral reefs (Roberts 1993, Ginsburg 1994). The three major threats they identified were overfishing, sedimentation and nutrient pollution.

Sedimentation and nutrient pollution are the result of deforestation, agriculture and coastal construction and development (Linden 1990, Bryant et al. 1998). Corals exposed to sediment and nutrient input suffer lower photosynthetic output of the symbiotic zooxanthellae due to reduced light penetration and they show increased energy use for sediment rejecting activities (see Rogers 1990). In contrast, algae that compete with corals for space are less susceptible to sediment (Cortès and Risk 1985, Tomascik and Sander 1987, McClanahan 1997, McCook 1997, Purcell 2000). Nutrients fertilise and enhance algal growth (Bell 1992, Bell and Elmetri 1995, Lapointe 1997). Due to such influences coral reefs are changing into algal dominated reefs world-wide, and Caribbean reefs in particular have experienced such a phase-shift (Done 1992, Hughes 1994, McClanahan and Muthiga 1998, Williams and Polunin 2001).

Coral reefs have been described as robust and resistant to natural impacts at least over geological time scales (Brown 1987, Done 1987, Dahl and Salvat 1988). This may not hold true for today's coral reefs. This is because stresses, acting additively and synergistically, are reducing the resilience of reefs (Brown 1996, Connell 1997, Nyström et al. 2001). One well studied and often cited example is the fate of coral reefs in Jamaica. Hurricane Allen hit Jamaican reefs in 1981 causing severe damage (Woodley et al. 1981). Hughes et al. (1987) reported recovery of these reefs due to new coral settlers, supported also by effective grazing of the Caribbean sea urchin *Diadema antillarum*. However, an epidemic disease in 1983 caused mass mortality of this herbivore and soon after this event, algal cover increased dramatically (reviewed by Lessios 1988). Herbivorous fish were at that time already so heavily depleted due to direct and indirect effects of fishing, that they failed to control algal growth (Hughes 1994).

A further more recent threat to coral reefs is rising sea water temperature. In 1998, coral populations on an estimated 16% of coral reefs world-wide were destroyed or severely damaged due to the most intense and geographically widespread bleaching event seen to date (Wilkinson 2000). Hoegh-Guldberg (1999) predicts that mass bleaching events on coral reefs will occur more frequently in the future, for example in the Caribbean, bleaching can be expected annually by the year 2020.

Establishment of new coral colonies is a crucial process for sustaining coral reef communities (Pearson 1981). This ecological function becomes even more vital considering the coral decline we see today. However, successful recovery of reefs might depend on several factors including the presence of other disturbances (Souter et al. 2000, Nyström et al. 2001). For example, if herbivores on reefs occur only in low numbers, algae will out-compete corals by preventing coral larval settlement (Hunte and Wittenberg 1992, McCook et al. 2001). In addition, new settlers might be more vulnerable to stresses than adult coral colonies because their mortality is greater compared to larger corals (Bak and Meesters 1999). Stresses often alter the benthic substrate of reefs and this might affect settlement success of coral larvae (Bak and Meesters 1999). Recovery may be rapid under 'stress free' conditions (e.g. Connell 1997). However, studies have also shown long-term failure of recovery due to multiple stresses of natural and human-induced origin (Kinsey 1988, Hughes 1994, Lapointe 1997).

In this thesis I have investigated early life history processes of corals on reefs that suffer chronic disturbances and acute impacts. I also examine whether a phase-shift from coral to algal dominance can be reversed. I conducted my study in St. Lucia, West Indies, where I took advantage of a large-scale and long-term monitoring project carried out mostly on reefs of the Soufrière Marine Management Area (SMMA), a network of no-take marine reserves and fishing zones. This area provides a range of different conditions of sedimentation and wave exposure levels. I also looked at a further stretch of coast to the north of the SMMA to increase replicate locations affected by the same stresses. In 1994, Tropical Storm Debbie brought torrential rain to St. Lucia which caused land slides and severe erosion on land (Sladek Nowlis et al. 1997). Soil and sediment

were washed onto the reefs where they smothered corals (Sladek Nowlis et al. 1997). In 1999, Hurricane Lenny caused high waves on the west coast of St. Lucia damaging coral reefs. Hence, I was able to undertake research on the impacts of sedimentation, fishing and hurricanes and their interacting effects.

The main aims of this thesis were to study the effects of these disturbances individually and in combination on:

- 1) the benthic substrate components such as coral and algal cover,
- 2) juvenile coral assemblages,
- 3) coral larval settlement on natural and artificial substrata,
- 4) juvenile coral mortality rates,
- 5) juvenile coral growth.

In Chapter 1, I present a literature review on the effects of sedimentation, eutrophication, fishing and rising sea temperature on reproduction, larval settlement and post-settlement processes. Since virtually all studies focus on the effects of only one stress, I then summarise the findings to look at impacts of additive and synergistic stresses on the early life history process of corals. I present two simple models that describe (1) the impacts of additive and synergistic effects on the energy budget of a coral colony, and (2) per capita growth and population size in a stress free environment and when confronted by additive stresses.

Data collected in the field in St. Lucia were used in Chapters 2 to 5. Chapter 2 describes changes in the status of the coral reefs of St. Lucia's west coast from 1995 to 2001. I investigate changes in the benthic substrate in relation to sedimentation, fishing and hurricanes. In Chapter 3 I describe juvenile coral abundance and diversity in relation to sedimentation stress, adult coral cover and cover of different functional algal groups. I also described their size distribution and the general health status of juvenile corals. In Chapter 4, I use artificial settlement plate constructions to study coral larval settlement rates along the reefs under different sedimentation levels. I also look at differences in settlement rates in relation to herbivorous fish populations and adult coral cover. Chapter 5 examines coral larval settlement rates on natural substrata in permanent photo quadrats that I installed on the reefs. In these photo quadrats, I also followed

juvenile corals over time to estimate their mortality and growth rates. Additionally, I studied the impacts of sedimentation and fishing on these processes.

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Chapter 1

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

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 chapter, I describe coral early life history processes including reproduction, settlement and post-settlement survival. I 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 I 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 I first examine reef degradation and describe the major human-induced disturbances affecting reefs today. Then I will briefly summarise the early life history of corals before discussing the effects of human-induced disturbances on these stages. Finally, I 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 states (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 I 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), I 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 3 hours 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 develop.

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

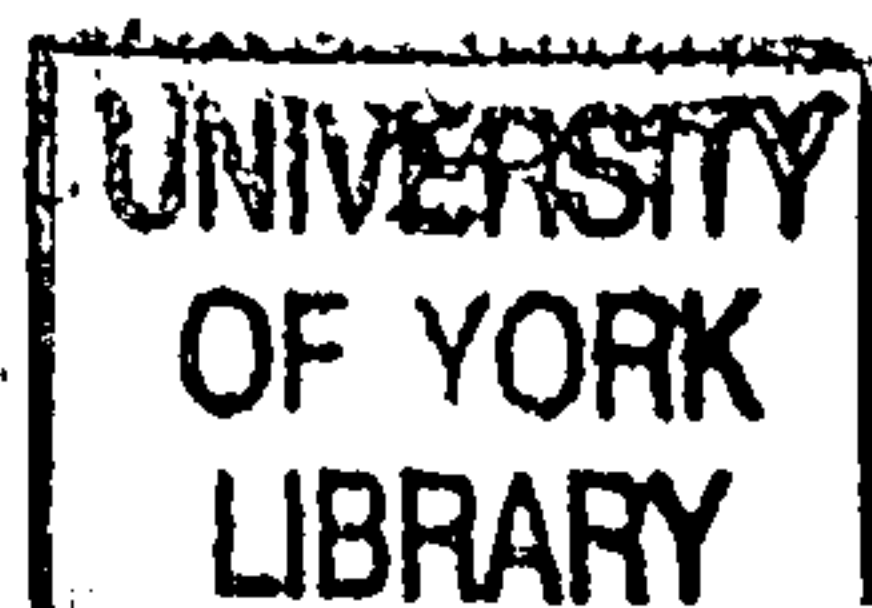
In this chapter I use the term post-settlement to describe the period after larval settlement up until the juvenile coral reproduces for the first time. The term recruitment is widely used by others but with many different definitions (e.g. Wallace 1983, Sammarco 1986, Wallace et al. 1986, Harriott and 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, I 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, I 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 adaptation 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 broadcast 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 (Cremllyn 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 tributyltin (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 1.0mg.l^{-1} calcium carbonate in clear waters while turbid waters in the same area contained 3.5mg.l^{-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.m² on Maldivian coral reefs were massive coral species, whereas only 0.65 settlers.m² 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), I 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 individuals.m² on reefs in Panama (Glynn and Colgan 1992) and on reefs of the Galapagos Islands, *Eucidaros thouarsii* increased from 5 to 50 individuals.m² (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
	sediment particles damage or kill larvae			↑ mortality
			↓ growth rate (due to ↑ algal growth)	
		↓ photosynthetic output (due to ↓ light penetration)		
Settlement and Post-settlement	↓ 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), I 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.

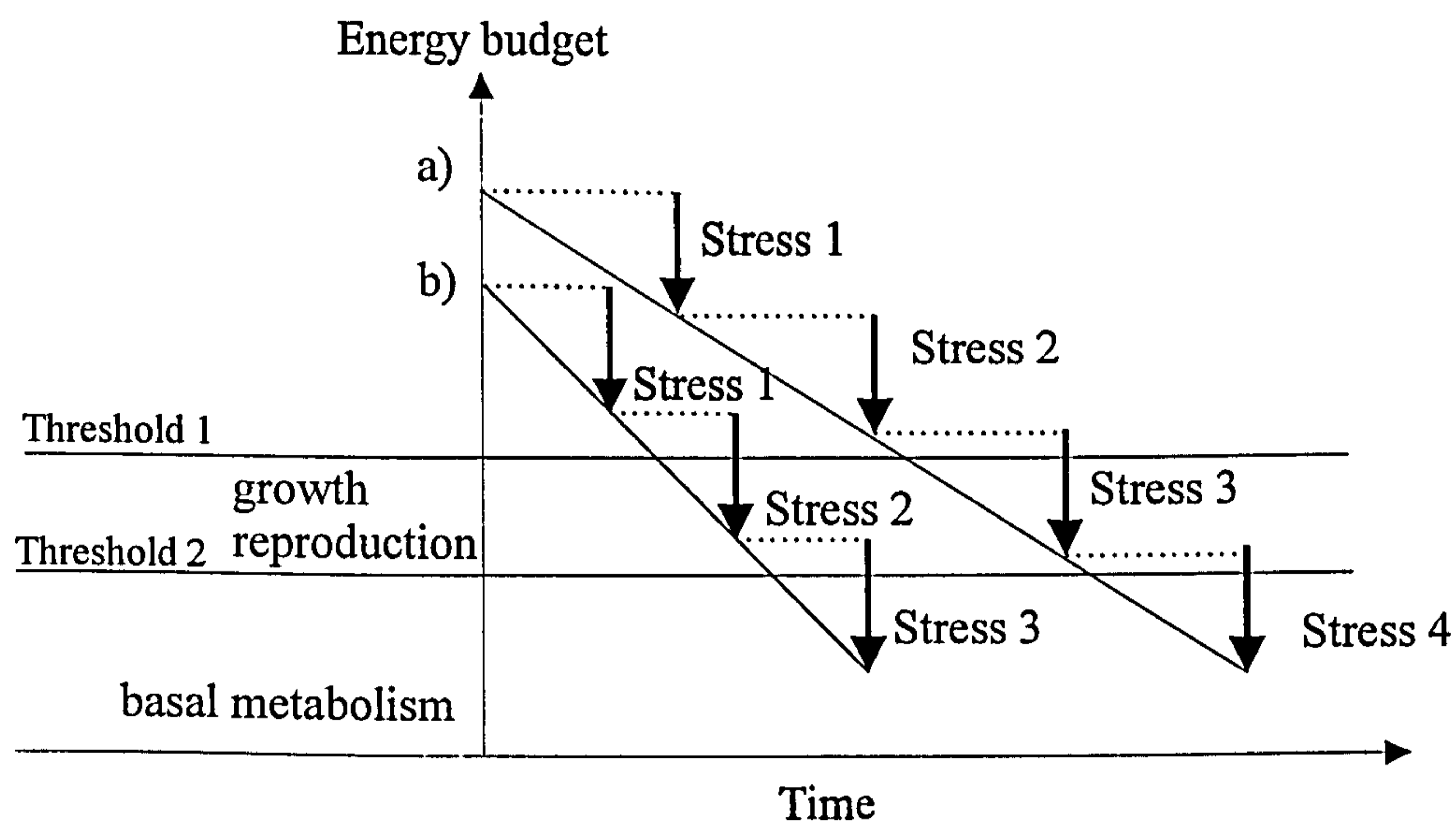


Figure 1: Energy budget of an individual coral colony confronted by multiple stresses. Under the conditions shown in (a), stresses act additively. However, in (b) another background stress, e.g. seawater warming, acts synergistically to increase the impact of each stress.

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.

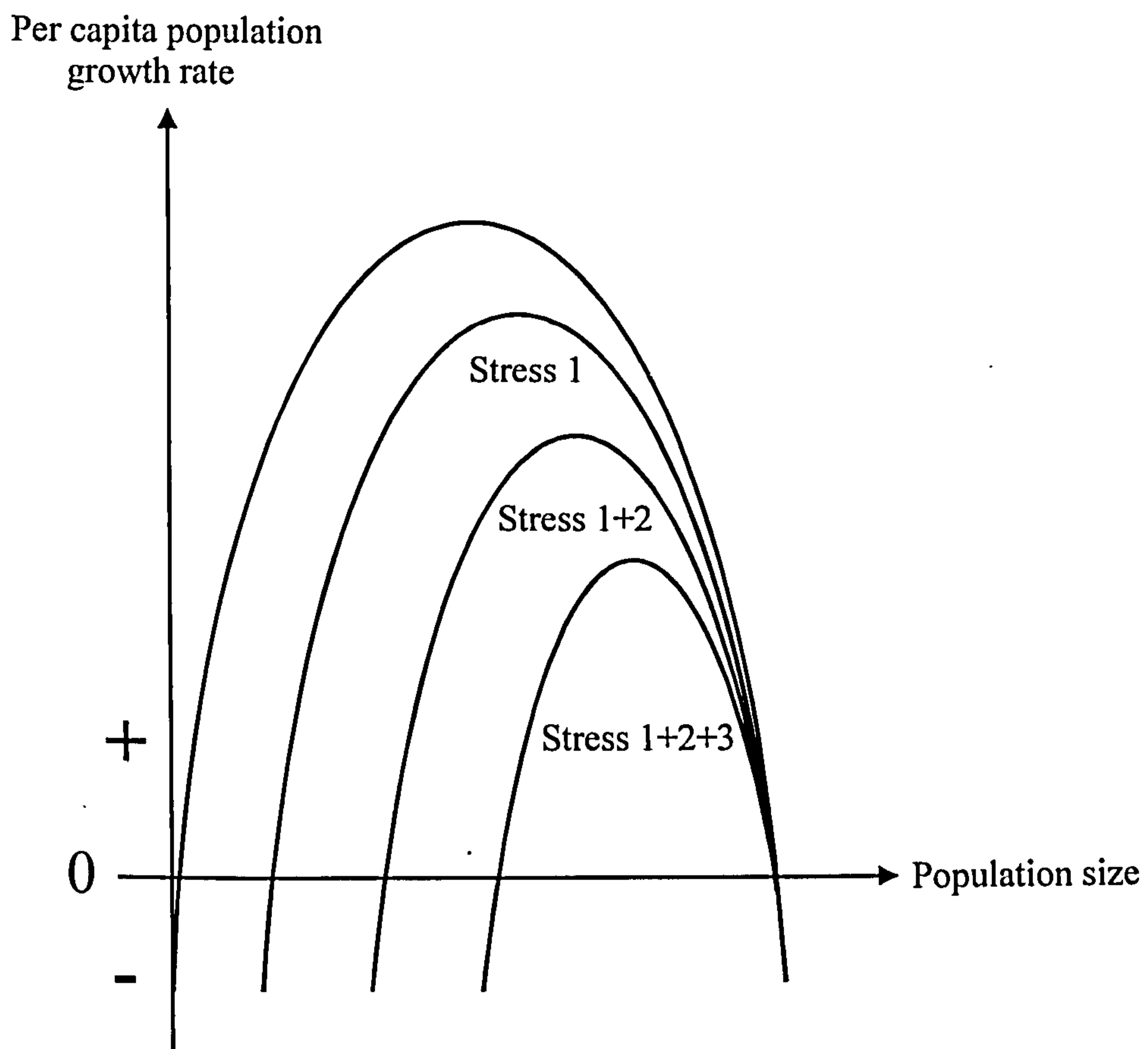


Figure 2: Per capita population growth rate of a coral population in a stress free environment and confronted by additive stresses (stresses 1, 2 and 3). If per capita growth rate falls below zero, the population will go extinct, while above zero the population has positive growth. At high population 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

1.7 Implications of coral early life history for management

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 reseedling 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 reseedling 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. Reseedling 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 reseeded 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 reseeded 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. I suggest the monitoring of settlement and juvenile coral survival. These methods have been shown to be sensitive to human-induced pollution (reviewed in this chapter). 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. I studied the interaction between marine reserves and sedimentation stress on coral cover in St. Lucia from 1995 to 2001 (see Chapter 2). 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 (Chapter 2, 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.

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Chapter 2

The interacting effects of sedimentation, fishing and hurricanes on coral reefs: A long-term study in St. Lucia, West Indies

2.1 Abstract

Coral reefs around the world suffer from interacting additive and synergistic stresses that cause reef degradation. Over the last two decades, Caribbean reefs in particular, have been observed to undergo shifts from coral to algal dominated substrate. The causes are complex and separating the effects of different disturbances, be they natural or human-induced, is often difficult. In this study, I investigate the individual and combined effects of fishing, sedimentation and hurricanes on reefs on the west coast of St. Lucia, West Indies. Benthic reef components, including coral and algal cover were monitored from 1995 to 2001. The study area includes a network of no-take marine reserves interspersed with fishing grounds. This provided the opportunity to examine the effectiveness of marine reserves in reversing phase-shifts. Over the six year monitoring period, there were major changes in benthic communities. In 1999, waves created by Hurricane Lenny hit St. Lucia's west coast causing destruction of corals mainly on reefs with low sediment input. Compared to damage caused by chronic sedimentation from 1995 to 2001, coral mortality following Hurricane Lenny was

around 15 times higher at 5m depth (44% coral mortality caused by Hurricane Lenny, 3% caused by sedimentation), but only 1.5 times higher at 15m depth (29% mortality due to hurricane impact, 19% caused by sediment pollution). Overall, coral loss was replaced directly by algal cover. In the years without severe natural impacts, coral cover in marine reserves was stable or slightly increased. This was not the case in fishing grounds or in deeper water on reefs with high sediment input, where coral cover declined over this period. Generally, changes in algal cover does not differ between marine reserves and fishing grounds. Establishment of marine reserves led to increased herbivorous fish stocks, but over the period of the study this increase appears to be insufficient to control algal growth. Although marine reserves are useful management tools to rebuild depleted fish stocks, they cannot protect reefs from natural impacts such as storms and hurricanes, nor from sedimentation.

2.2 Introduction

Corals reefs are one of the most productive marine ecosystems and they are known for their high diversity (Paulay 1997, Reaka-Kudla 1997). Over the last few decades, however, many reefs have shown signs of serious degradation related to increased anthropogenic stress (Bryant et al. 1998). Globally, sedimentation and overfishing are major threats that are steadily increasing with the growing human population (Roberts 1993, Ginsburg 1994, Bryant et al. 1998). In the Caribbean, two-thirds of the reefs are considered at risk and about one-third at high risk (Bryant et al. 1998).

Sedimentation is caused by deforestation, agriculture and development projects both on the coast and further inland (Cortès and Risk 1985, Ginsburg 1994, Bryant et al. 1998). Heavy rain causes land erosion and rivers transport sediment to the ocean where it is deposited on coral reefs (Sakai and Nishihira 1991, Sladek Nowlis et al. 1997). Here, corals can be smothered, the light penetration in the water decreases and replenishment of coral communities is inhibited due to sediment particles that cover substrate necessary for coral larval

settlement (Chapters 1 and 4, see also review by Rogers 1990). Most sediment run-off is linked with nutrient pollution (Wittenberg and Hunte 1992, Hunter and Evans 1995, Rosenfeld et al. 1999) which has been reported to enhance algal growth (Lapointe 1997). Algae can increase the effects of sedimentation when particles get trapped between their fronds (Walker and Ormond 1982). Once sediment is deposited onto reefs, it stays there until wave activity or currents transport it to other areas. Disturbance events such as hurricanes could play a significant role in such movement.

On many Caribbean reefs, phase-shifts from coral to algal dominance have been observed (Steneck 1993, Hughes 1994). A phase-shift occurs when a community moves from one stable state to another. In the case of coral reefs, this may be due to increased nutrient input into the ocean (Gabric and Bell 1993, Lapointe 1997). Another explanation is that overfishing has led to severe reductions of herbivorous fish (see Russ 1991, Roberts 1993, Hay 1997, McCook 1999). Together with the mass mortality of the grazing sea urchin *Diadema antillarum* in 1983/84 due to an epidemic disease outbreak that killed more than 97% of these animals in the Caribbean (Lessios 1995) and there also is a lack of control of algal growth by grazers (Hughes et al. 1999, Miller et al. 1999). The problem with phase-shifts is that they may be difficult to reverse (Scheffer et al. 1993, Nyström et al. 2000), even though theoretical models have predicted reversal is possible (Holling 1973, May 1977). To return a coral reef from an algal- to a coral-dominated state, high larval settlement and survivorship rates of recruits with subsequent undisturbed growth are required (Done 1992). However, this may only be possible if there is a prior or simultaneous reduction in algal cover, since algae can negatively affect corals (e.g Hughes 1989, Coyer et al. 1993, Miller and Hay 1996, see also Chapter 3 and Chapter 5). In this case, marine reserves, where all fishing is forbidden, may play an important role. Marine reserves have been shown to rebuild overexploited fish stocks (Roberts et al. 2001). An increase in herbivorous fish in numbers and/or biomass theoretically would decrease algal cover (Miller et al. 1999). However, there is a lack of long-term studies testing the effectiveness of marine reserves as a management tool to reduce algae and in turn increase coral cover. This is mainly because of a

deficiency of baseline data from the period before restrictions are imposed in an area. Additionally, many marine reserves have not existed long enough to show increases in herbivorous fish stocks that are sufficient enough to cause a significant reduction in algal growth. Furthermore, studies of reserves where data have been collected on both benthic communities and fish stocks are rare (Roberts 1995). Hence, the hypothesis that marine reserves prevent or even reverse phase-shifts has never been tested.

A further threat to coral reefs are natural disturbances, the most detrimental being hurricanes and cyclones (Woodley et al. 1981). Many studies and reports of storm impacts indicate severe wave damage to reefs with extreme declines in scleractinian coral cover (Bythell et al. 1993, Brown 1997, Connell et al. 1997). After days to weeks following a storm event, most damaged corals and new space opened by turned over coral blocks and boulders, has been found to then be heavily overgrown by algae (Woodley 1989, Littler and Littler 1999). The frequency and intensity of hurricanes and cyclones are predicted to increase due to global climate change (Karl and Knight 1998, Goldenberg et al. 2001).

Global climate change also threatens coral reefs by increasing the sea temperature (Hoegh-Guldberg 1999, Wilkinson 2000). Increased water temperature stresses corals leading to loss of their symbiotic zooxanthellae, a process called bleaching (Brown 1996). One of the most severe bleaching events reported so far occurred in 1998 when more than 16% of the coral reefs worldwide were adversely affected (Wilkinson 2000). Additionally, corals are also increasingly threatened by outbreaks of new coral diseases linked to expanding human populations causing increased pressure on reefs (Harvell et al. 1999, Porter 2001, Patterson et al. 2002). Porter et al. (2001) undertook an extensive survey of reefs from Key Largo to Key West, Florida, over a period of 2 years and found that 82% of the sites they visited were affected by coral diseases. This represented an increase of 404%. They also observed that 85% of all coral species showed signs of disease, an increase of 218% from 1996 to 1998, and that living coral cover fell by 60% during the survey.

Studies have shown that coral reefs are now threatened by multiple stresses that are difficult to isolate (Hughes et al. 1999, Nyström et al. 2001). However, only a handful of studies looked at interacting disturbances on reefs on a large scale (Kinsey 1988, Hughes 1994, Hughes and Connell 1999). Natural and human-induced disturbances act together to decrease coral cover (Hughes 1994, Brown 1996). Many threats are chronic such as nutrient and sedimentation input by rivers, others such as hurricanes are episodic (Done 1992). However, frequent storms can also be classified as a chronic disturbance (Connell et al. 1997). Cornell (1997) surveyed the literature for quantitative studies of coral abundance, in an effort to measure trends in the health of coral reefs globally, focusing on disturbances and the recovery of coral assemblages. He concluded that the principal reason for differences in coral recovery between sites is related to the type of the disturbance that caused the reduction in coral cover. Coral cover increased after 69% of acute, short-term disturbances, but after only 27% of chronic, long-term ones. Hence, the capacity of coral reefs to withstand interacting stresses and recover from coral loss is of major concern now that impacts from human activities are escalating (Bryant et al. 1998).

This study takes advantage of a long-term and large-scale project that has been conducted since 1994 on the west coast of St. Lucia, West Indies. Benthic substrate components have been monitored annually at a series of sites in parallel with fish censuses (Roberts et al. 2001). Sedimentation rates measured since 1997 give us a clear understanding about magnitude and distribution of chronic sediment inputs from two major river systems. This study was conducted in two areas that suffered from high sediment input and two areas with low sediment input. Within the study area, the Soufrière Marine Management Area, a system of four marine reserves established in 1995, where fishing of all kinds is forbidden, allowed me to study the effects of overfishing and of rebuilding fish stocks. It also makes it possible to find out if marine reserves may help in preventing or reversing increases in algal cover. The area allowed me to test the combined effects of sedimentation and release from fishing pressure by comparing changes over time in the benthic substrate composition in areas with high and low sedimentation, with and without reserves. The efficacy of reserves with high

sedimentation are compared to those with low sedimentation. Additionally, destructive waves created by Hurricane Lenny that hit these coral reefs in 1999, provided an opportunity to study the combined impacts of natural and human-induced sources of stress.

2.3 Materials and methods

2.3.1 Study sites

This study was conducted on the west coast of St. Lucia, West Indies, in the Soufrière Marine Management Area (SMMA) and, approximately 7km further north, in the Anse La Raye area (Fig. 1). Both areas, the SMMA and Anse La Raye, are composed of narrow fringing reefs interspersed by patch reefs and sandy areas. In some sites, the reef drops quickly down to a maximum of 50m whereas at other sites the reef slopes gently for the first 20m after which it finally drops off. The SMMA covers 11km of coastline and consists of four marine reserves established in 1995, where all kinds of fishing are prohibited (Fig.1). The total area of fishing restriction covers around 35% of reef habitat in the SMMA (Roberts et al. 2001). The reefs at 'Monitoring site 3' were designated as marine reserves in 1995, but, due to conflicts between fishermen and the park authority, the area was reopened for fishing a year later. In this study, this site is referred to as a fishing area. The marine reserve called Jalousie Reserve (part of the Petit Piton Marine Reserve; see Figure 1 and Table 1b) was opened for fishing in 1996 after the hotel that managed this reef went bankrupt. However, protection was reintroduced in 1998 and it has been closed to fishing since then. Hence, I refer to this site as a marine reserve. The marine reserve called Anse Chastanet was closed to fishing in 1992 and managed until 1995 by another hotel (Fig.1, Table 1b). No data on fish and benthic substrate for this marine reserve exists prior to 1995.

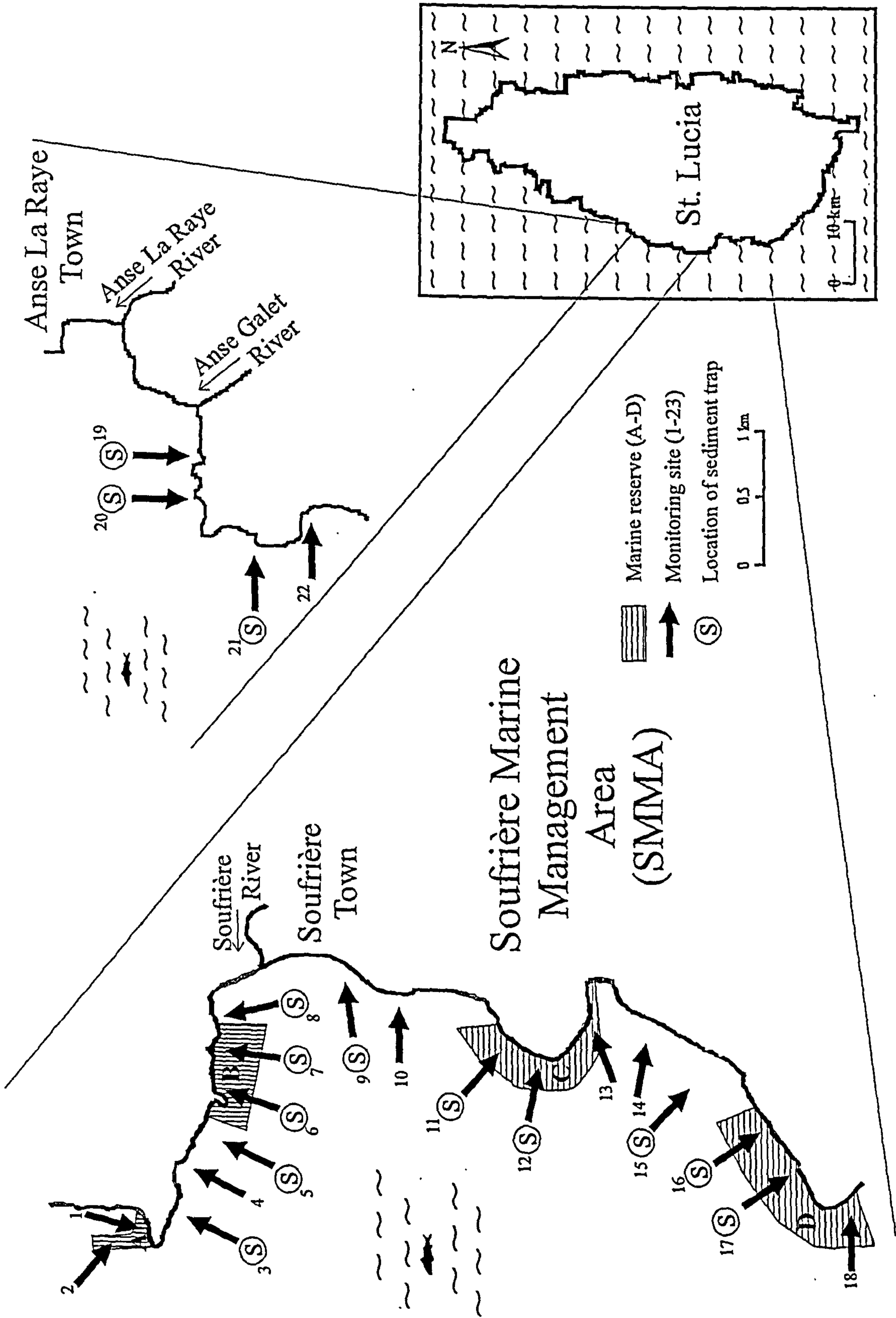


Fig. 1: Map of St. Lucia showing the study areas with the sedimentation trap sites, monitoring sites, marine reserves and the river systems. For description of monitoring sites and marine reserves see Table 1.

Table 1: For each site that was monitored from 1995 to 2001 and that is presented in Figure 1, protection level (marine reserve or fishing ground), sedimentation level (low or high) and depth the monitoring was conducted at (5m and/or 15m) is shown in Table 1(a). The names of the marine reserves of the Soufrière Marine Management Area (SMMA, see Figure 1) are shown in Table 1(b).

(a)

Site no.	Protection level		Sedimentation level		Depth	
	Marine reserve	Fishing ground	low	high	5m	15m
1	X	-	X	-	X	X
2	X	-	X	-	-	X
3	-	X	-	X	X	X
4	-	X	-	X	X	X
5	-	X	-	X	X	X
6	X	-	-	X	X	X
7	X	-	-	X	X	X
8	-	X	X	-	X	X
9	-	X	X	-	X	X
10	-	X	X	-	X	X
11	X	-	X	-	X	X
12	X	-	X	-	X	X
13	X	-	X	-	X	X
14	-	X	X	-	X	X
15	-	X	X	-	X	X
16	X	-	X	-	X	X
17	X	-	X	-	X	X
18	X	-	X	-	X	X
19	-	X	-	X	X	X
20	-	X	-	X	X	X
21	-	X	-	X	X	X
22	-	X	-	X	X	-

(b)

Marine Reserve	Name
A	Anse Chastanet
B	Grand Caille
C	Petit Piton
D	Gros Piton

2.3.2 Sedimentation rates and rainfall

The study areas, SMMA and Anse La Raye, are characterised by two major river systems (Fig. 1). The Soufrière river containing 44.1hm^3 of water empties into the Soufrière bay which is part of the SMMA area. The Anse La Raye/Anse Galet rivers containing 12.7 and 37.2hm^3 of water respectively, open into the Anse La Raye area (Sladek Nowlis et al. 1997). The sediment input from the Soufrière river is generally transported by currents along the coast northwards, whereas currents and waves transport the sediment runoff from the Anse La Raye/Anse Galet rivers southwards. Hence, the study sites established along both sedimentation gradients are referred to as high sedimentation sites, whereas the sites south of the Soufrière river and the sites at Anse Chastanet, which is situated furthest north in the SMMA area, are much less affected by the Soufrière river and referred to as low sedimentation sites.

Along the 11km coastline of the SMMA we installed sediment traps at 11 sites covering both fishing grounds and marine reserves (Fig. 1). In the Anse La Raye area, sediment traps were installed at 3 sites (Fig. 1). The traps consisted of foundations (10cm and 50cm long PVC pipes) that were cemented to the reef and to which replaceable traps could be fixed (15cm long PVC pipes, 4cm in diameter). The traps were closed at one end with a plastic disk and were slotted onto the foundations with the help of plastic cups. The replaceable traps collected depositing sediment particles. For estimating vertical fluxes of sediment, the replaceable traps had a height to diameter ratio of approximately 4 as recommended by Gardner (1980) and Blomqvist and Kofoed (1981). At each site, two pairs of sediment traps (each pair consisted of traps with mouth openings at 25 and 65cm above the reef) were installed at a depth of 5m and 15m. The taller traps measured mainly the new sediment input, whereas the shorter traps collected the new sediment input and sediment resuspended by water motion.

The replaceable traps were left in the water for around 14 days after which they were retrieved. Their contents were suction filtered on Whatman's No.1 filter paper ($0.45\mu\text{m}$) and the filter with the sediment weighed after being sun-dried for at least 24 hours. Using this method, sedimentation rates were measured for 25

Table 2: Chronology of events (including management decisions and natural impacts such as storms and hurricanes) that affected coral reefs of the SMMA and Anse La Raye area. Also listed are the dates of monitoring of the benthic substrate and fish surveys.

Date	Event
9/10 th Sept 1994	Tropical Storm Debbie hit St. Lucia <ul style="list-style-type: none"> • Amongst the wettest storms ever recorded • Large quantities of sediment runoff onto reefs on the west coast (Sladek Nowlis et al. 1997)
Nov 1994 - Feb 1995	1 st benthic substrate monitoring 1 st fish census
1 st July 1995	Establishment of Soufrière Marine Management Area (SMMA) <ul style="list-style-type: none"> • Implementation of four new marine reserves • Two previously established marine reserves (Anse Chastanet and Jalousie Reserve) incorporated into the new reserves
Sept 1995	Coral damage due to waves from Hurricanes Luis, Iris and Marilyn
July - Aug 1996	2 nd benthic substrate monitoring 2 nd fish census
26 th Oct 1996	Heavy rainfall causes severe sedimentation runoff on reefs on the west coast
July 1997	Coral disease outbreak <ul style="list-style-type: none"> • Important massive coral species in SMMA are seriously affected leading to partial mortality of many coral colonies (Nugues 2002)
July-Aug 1997	3 rd benthic substrate monitoring 3 rd fish census <ul style="list-style-type: none"> • Implementation of sedimentation rate measurements
July - Aug 1998	4 th fish census
Oct - Dec 1998	Bleaching of many coral species due to warm water
Nov - Dec 1998	4 th benthic substrate monitoring
17 th Nov 1999	Hurricane Lenny brings high swells and destructive waves to St. Lucia <ul style="list-style-type: none"> • Serious impacts on coral reefs, mainly in the SMMA
Nov 1999 – Feb 2001	<ul style="list-style-type: none"> • Extensive coastal construction work in study area
Jan - Feb 2000	<ul style="list-style-type: none"> • Rebuilding of broken sediment traps • Installation of new sedimentation traps in low sedimentation sites (5m depth)
Aug - Sept 2000	5 th benthic substrate monitoring 5 th fish census
Aug - Sept 2001	6 th benthic substrate monitoring 6 th fish census

Table 3: Functional algal groups and the characteristics used to distinguish them (adapted from Steneck and Dethier 1994).

Functional groups	Characteristics	Size ranges
Filamentous algae	Multispecies assemblages of diminutive green filaments.	0.1 - 1cm
Macroalgae	Thick algal species with few ramifications and corticated, leathery macrophytes, articulated calcareous algae; anatomically complex.	> 1cm
Encrusting algae	Thin, hard, calcified, encrusting, overgrowing rocky and limestone substrate; take on surface texture of substrate.	no size-restrictions
Blue-green algae	Long blue-green to red-brown filaments; superficially attached to the substrate; forming mats over substrate.	0.1 - 10cm
Coralline algae	Same characteristics as encrusting algae, but highly calcified.	no size-restrictions

different two-week periods on 7 fieldtrips that were carried out between 1997 and 2001, except for sediment traps employed at 5m depth in the low sedimentation sites (south of the Soufrière river) that were first established in 2000 (Table 2). On fieldtrip 6, coastal construction work took place causing high short-term sediment pulses at the monitoring 'Site 16' (see Fig. 1, Table 2). Since I am interested in the effects of chronic sediment stress only, I exclude this sedimentation measurement period from all analyses. An additional reason not to include this sedimentation pulse event is that it occurred at the end of this six year long monitoring study and I suggest that the effects will be delayed and probably not detectable during my study. Rainfall was measured by the SMMA with a weather station situated in Soufrière town. The weather station was not established until 2000, so the only rainfall measurements that could be used for analysis were from 2001 and they only cover 6 periods of sedimentation rate measurements.

2.3.3 Benthic substrate monitoring

The monitoring of benthic substrata was conducted at 5m and 15m depth once each year from 1995 to 2001, except for 1999 (Table 2). In the SMMA area, eight sites (of which one was only monitored at 15m depth) were selected that were in marine reserves and received low sedimentation input, two sites were in marine reserves with high sedimentation input, five sites were fishing grounds and received low sedimentation input, and three sites were in fishing grounds and had high sedimentation input (Fig. 1). In the Anse La Raye area, all three sites (four sites at 5m depth) monitored were in fishing grounds and had high sedimentation input. (Fig. 1). These 23 sites include the 14 sites used for sedimentation rates measurements (see Fig. 1).

The percentage composition of the benthic substrate was estimated annually at 5m and 15m depth at each site. A 1m²-quadrat was randomly placed (with computer generated intervals of 1m to 5m between the quadrats) along the reef in one direction from the point of entry on the dive. Using this method, the same reef stretch of each site was covered every year. The components of the benthic substrate monitored included coral cover (massive, branching and

Millepora spp.), functional algal groups (Table 3), sponges, gorgonians, rubble, sand and 'other' (combining e.g. ascidians, hydrozoans and anemones). From 1996 algae were classified into functional algal groups (Table 3). Data for massive coral and *Millepora* spp. were not collected separately in 1996. The percentage of recently dead and bleached corals was also noted. In each quadrat, the numbers of coral breakages, loose fragments of living coral and diseased corals were counted. The numbers of coral breakages and loose fragments of living coral were estimated in relation to branching coral cover in the quadrat (number of coral breakages / % branching coral cover). The numbers of the sea urchin *Diadema antillarum* present were also counted in each quadrat.

2.3.4 Herbivorous fish biomass

Fish populations were censused using a modification of the stationary point count method developed by Bohnsack and Bannerot (1986). A 10m long tape measure was placed across the reef and all diurnal and non-cryptic fishes observed within or passing through a 5m radius from the centre of the tape, extending 5m upwards in a cylinder above the reef, were counted during a 15min period. The lengths of individuals observed were estimated visually to the nearest centimetre. Polunin and Roberts (1993) showed that visual estimation of fish lengths can be accurate to within 3% of the actual length. Six counts were carried out at each depth at each site each year.

The fish censuses were performed by the same observers (C.M. Roberts and J.P. Hawkins) each year to minimise interannual variability in estimation methods (Bohnsack and Bannerot 1986, Polunin and Roberts 1993). Using Bohnsack and Harper's (1988) length-weight relationships, fish biomass estimates were calculated from fish length estimates.

2.3.5 Biomass of benthic overgrowth

Plastic brushes consisting of approximately fifty 20cm long plastic strings were used as markers for permanent photo quadrats for another project (see Chapter 5).

They were submerged from August/September 2000 until September 2001. Each was nailed into dead coral skeleton. They were removed and placed in plastic zip-lock bags and transported onto land in September 2001. There they were carefully put on trays of aluminium foil and sun-dried for at least four days. When they were totally dried out, the brushes were weighed and the dry weight of the benthic components that grew on them calculated.

These data were used to address the question of whether benthic biomass differs on reefs with high and low sedimentation conditions. It has been reported that macroalgal recruitment is prevented when sediment is present (Umar et al. 1998). Hence, it might be that biomass is higher when sedimentation input is low. In this study, the biomass of benthic components also includes organisms such as sponges and ascidians. However, not much is known about the effects of sedimentation on these organisms. Increased growth of algae and other organisms may stress scleractinian corals causing, for example, spatial competition (Bak and Engel 1979, Van Moorsel 1985, Oren and Benayahu 1997).

2.3.6 Statistical analyses

To investigate spatial variation in 'Sedimentation Level' (low, high), and the effects of 'Depth' and 'Trap Height' on sediment input, I used a three-way analysis of variance (ANOVA). The relationship between rainfall and sedimentation rate was estimated using linear regression analysis. The effects of 'Depth' (5m and 15m), 'Sedimentation Level' (low and high), 'Protection Level' (marine reserves and fishing grounds) and 'Year' (1995 or 1996 to 2001) on the different monitored reef factors (see above) were tested using a fractional factorial four-way ANOVA (see also Table 1 for grouping of monitoring sites). This was done to reduce the number of interaction terms in the model (there would have been 16 of these in a fully factorial four-way ANOVA). The assumption of this model is that most of the important effects are main effects or two-way interactions and complex interactions are relatively unimportant (Quinn and Keough 2002). The factor 'Year' was calculated using all years from 1995 or

1996 to 2001. The two years with the biggest difference between them are shown in Table 4.

For some analyses and Figures, changes in substrate are calculated as absolute (the 1998 value was subtracted from the 1995 value) and relative changes (the 1995 value represents 100% and the percentage difference of the 2001 value was then calculated). Total algal cover was used and estimated by adding up all functional algal groups except coralline algae. Coralline algae are known as a suitable substrate for coral larval settlement (Morse and Morse 1992) and as an important calcareous plants for reef accumulation (Hubbard et al. 1990).

Data were tested for normality and heterogeneity of variance. All percentage data were arcsin square root-transformed prior to analyses as recommended by Sokal and Rohlf (1995). The statistical significance level for all analysis is set at $P \leq 0.05$. The SPSS/PC package was used to analyse the data.

2.4 Results

2.4.1 Sedimentation rates

The ANOVA results show a significant difference between the low and high sedimentation bays in sedimentation rates measured from 1997 to 2001 (Table 4). Figure 2 reveals that the high sedimentation bays into which the Soufrière and Anse Galet/Anse La Raye rivers empty had greater frequencies of high sediment inputs compared to the low sedimentation bays at both depths. Hence, the sites south of the Soufrière River are evidently not affected by sediment runoff from the Soufrière River. Sedimentation input was significantly different between both depths (Table 4). Higher frequencies of greater sedimentation rates were found at 5m than 15m depth (Figure 2). Sedimentation rates were significantly different between the 25cm and 65cm sediment traps (Table 4). Figure 2 shows greater frequencies of high sedimentation rates collected in the 25cm than the 65cm sediment traps. This is due to resuspension effects of deposited sediment on the reef caused by wave and current action. The correlation analyses show that sedimentation was highest closest to the river mouths in high sediment sites,

Table 4: Results of three way ANOVA with sedimentation level (low, high), depth (5m, 15m) and trap height (25cm, 65cm) as independent factors and sedimentation rate ($\text{mg.cm}^{-2}.\text{d}^{-1}$) as dependent variable. Sed = sedimentation level, Trap = trap height, ns = non-significant.

Factors	df	F	P
Sed	1	78.626	< 0.001
Depth	1	7.353	< 0.01
Trap	1	6.623	= 0.01
Sed*Depth	1	1.055	ns
Sed*Trap	1	0.870	ns
Depth*Trap	1	0.826	ns
Sed*Depth*Trap	1	0.206	ns
error	2396		
total	2404		

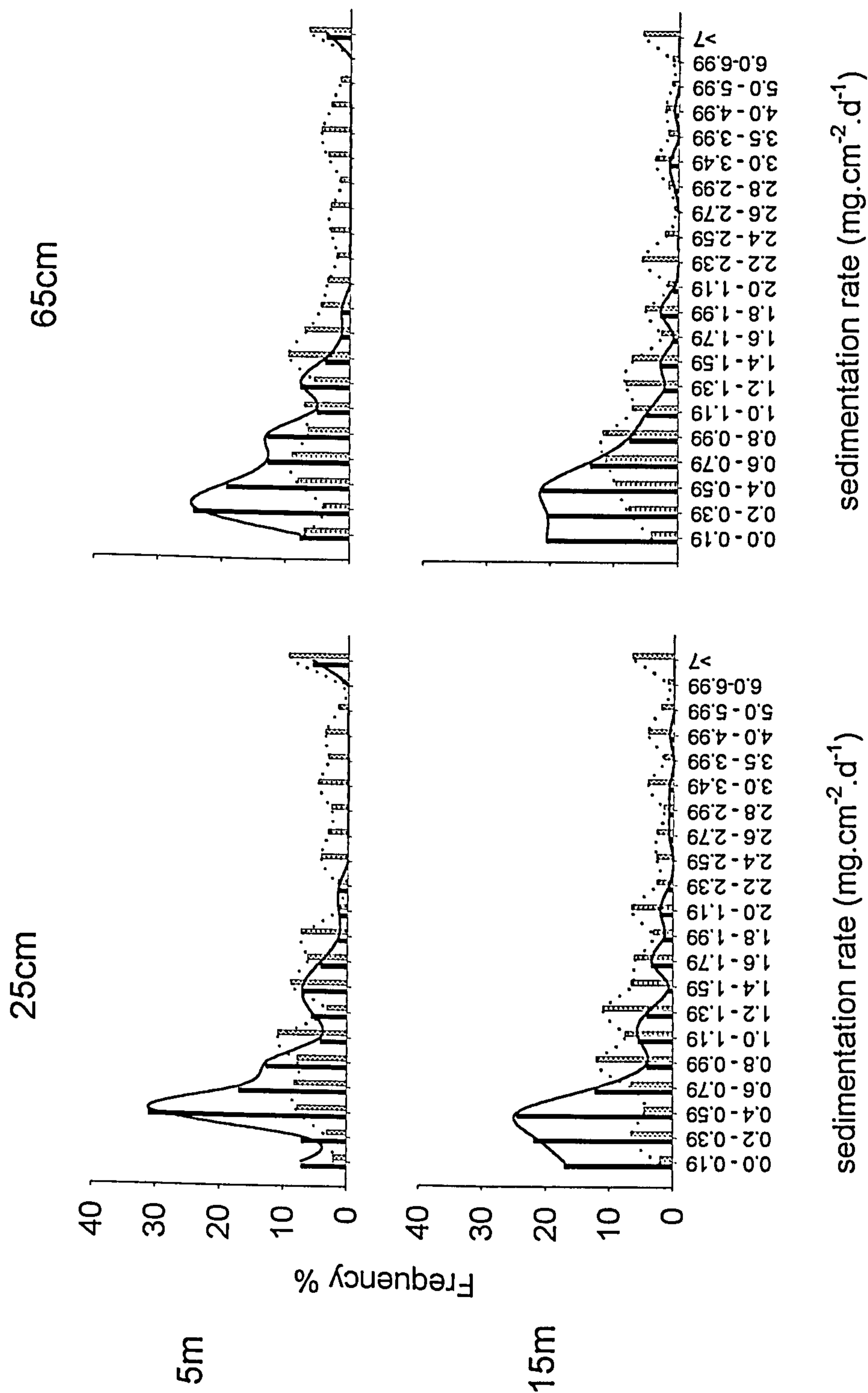


Fig. 2: Patterns of variation in measured sedimentation rates (mg.cm⁻².d⁻¹) from the 25cm and 65cm traps at 5m and 15m depth over the period 1997 to 2001. ▨ = high sediment sites, ▩ = low sediment sites, ---- = high sedimentation sites, ---- = low sedimentation sites.

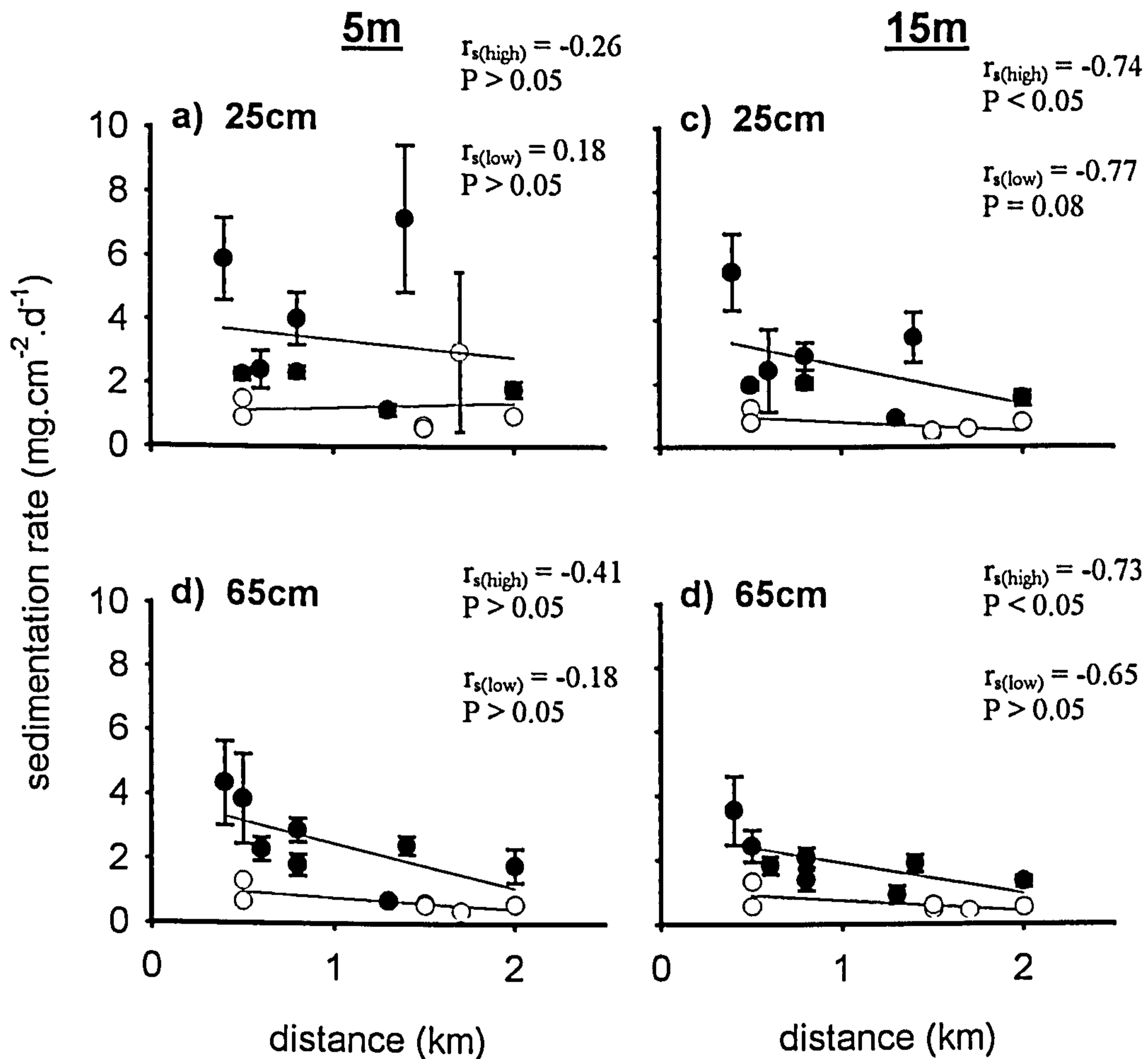


Fig. 3: Relationship between distance to the potential source of sedimentation (river mouth) and sedimentation rates ($\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) of a) 25cm traps at 5m depth, b) 65cm traps at 5m depth, c) 25cm traps at 15m depth and d) 65cm traps at 15m depth measured between 1997 and 2001 in low (\circ) and high sedimentation (\bullet) sites. Error bars represent one standard error. Spearman's rank-order correlation coefficient is based on mean values per site ($n = 14$).

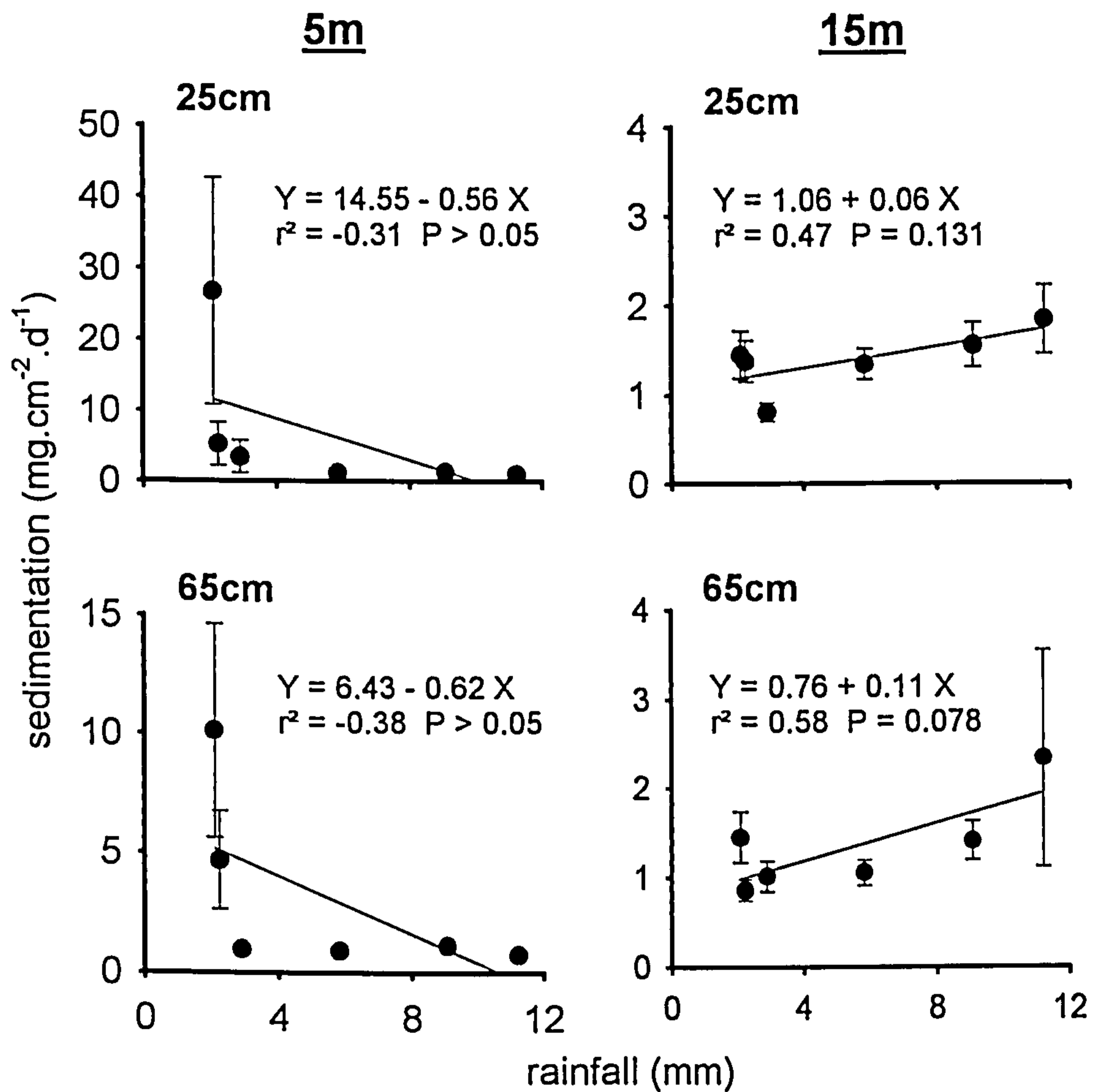


Fig. 4: Relationship between rainfall (mm) measured in Soufrière town under six different two week intervals in 2001 and corresponding sedimentation rates (mg.cm⁻².d⁻¹) at 5m and 15m depth for 25cm and 65cm traps. Sedimentation rate is calculated by pooling all sites (n = 14 sites). Error bars represent one standard error. Regression coefficients are based on mean values of sedimentation rates collected at all sites for each interval (n = 6).

decreasing with increasing distance from the river mouths (Fig. 3). However, only the correlation analyses at 15m depth are significant. The lack of a significant correlation for 5m sedimentation rates is probably due to increased sediment resuspension in shallower water (Fig. 3). There was no trend in sedimentation rate with distance for low sediment sites (Fig. 3).

Rainfall measurements were available only for six periods in 2001. The correlation analyses of the relationship between rainfall and sedimentation rates at 5m depth of both the 25cm and the 65cm sediment traps were not significant (Fig. 4). This is because wave activity causes resuspension of sediments that are then caught in the traps independent of rainfall level.

However, the results of the traps installed at 15m depth support the view that the main source of sediment is rainfall run-off although regressions were not statistically significant due to small sample sizes. With increasing rainfall, sedimentation rates increase in both 25cm and 65cm traps at 15m depth (Fig. 4). The relationship between rainfall and sedimentation is less strong for the measurements of the 25cm sediment traps, probably due to masking by the resuspension effect.

2.4.2 Benthic substrate monitoring

Changes in total coral cover and total algal cover

After an initial drop in coral cover due to waves from several hurricanes hitting the west coast of St. Lucia between 1995 and 1996, total coral cover decreased steadily from 1996 to 2001 at both 5m and 15m depths on reefs in marine reserves and fishing grounds with both low and high sedimentation inputs, while total algal cover increased reciprocally (Table 5, Fig. 5). Total algal cover could not be calculated for 1996 because coralline algal data were not collected separately in 1995. When pooling all sites and both depths, coral cover decreased from 1995 to 1996 from 40% (± 1.2 SE) to 31% (± 1.0 SE), which is a relative loss of 23%. Coral loss was higher in the high (where relative loss was 27%) than in the low sedimentation sites (where relative loss was 19%) (Table 5). In the years

Table 5: Changes in total coral cover and total algal cover from 1995 (1996 for total algal cover) to 2001 for high and low sedimentation sites at 5m and 15m depth. For sample sizes see Appendix 1.

Depth	Sedimentation Level	Year	% Total Coral Cover	% Total Algal Cover
5m	Low	1995	36 (± 2.6 SE)	-
		1996	28 (± 2.2 SE)	47 (± 2.3 SE)
		1997	27 (± 2.1 SE)	50 (± 2.2 SE)
		1998	26 (± 1.9 SE)	52 (± 1.7 SE)
		1999	-	-
		2000	7 (± 0.8 SE)	76 (± 1.3 SE)
		2001	8 (± 0.7 SE)	67 (± 1.4 SE)
	High	1995	47 (± 2.1 SE)	-
		1996	29 (± 1.9 SE)	43 (± 2.1 SE)
		1997	30 (± 1.6 SE)	44 (± 1.4 SE)
		1998	28 (± 1.3 SE)	46 (± 1.5 SE)
		1999	-	-
		2000	24 (± 1.5 SE)	56 (± 1.7 SE)
		2001	28 (± 1.5 SE)	50 (± 0.8 SE)
15m	Low	1995	39 (± 2.1 SE)	-
		1996	33 (± 1.7 SE)	40 (± 1.3 SE)
		1997	36 (± 2.0 SE)	41 (± 1.4 SE)
		1998	34 (± 1.7 SE)	39 (± 1.1 SE)
		1999	-	-
		2000	21 (± 1.4 SE)	58 (± 1.3 SE)
		2001	21 (± 1.2 SE)	51 (± 1.1 SE)
	High	1995	40 (± 2.4 SE)	-
		1996	36 (± 2.3 SE)	38 (± 1.8 SE)
		1997	33 (± 2.2 SE)	37 (± 1.7 SE)
		1998	29 (± 1.7 SE)	36 (± 1.2 SE)
		1999	-	-
		2000	24 (± 1.6 SE)	49 (± 1.4 SE)
		2001	21 (± 1.5 SE)	43 (± 1.4 SE)

following these events, coral and algal cover averaged across all sites remained quite stable. But this changed dramatically after Hurricane Lenny hit St. Lucia in 1999. Coral cover declined further while algae expanded (Fig. 5). Table 4 shows that total coral cover was much higher in 1995 than 2001, whereas total algal cover was lower in 1996 and much higher in 2001. This is also shown in the significance of the factor 'Year' for total coral and algal cover in Table 5. In 2000 coral cover averaged 18%, a relative loss of 53% since 1995 and algal cover averaged 55%, an increase of 31% relative to the 1996 value (Table 5). Values remained similar in 2001 (Table 5, Fig. 5).

In general, total coral cover was greater at 15m depth compared to 5m, greater in the high sedimentation compared to the low sedimentation areas and higher in the marine reserves than in the fishing grounds (Table 6, Fig. 6). The significance of the main factor 'Protection Level' has to be viewed with caution. At the time of the establishment of the marine reserves, total coral cover in the low sedimentation sites was much greater in the marine reserves than in the fishing grounds. Hence, although higher total coral cover is found in the marine reserves, it does not necessarily mean that there has been a positive effect of marine reserves. This statement applies throughout the results of the ANOVA analysis and might also apply to the other main factors.

However, focusing on the effects of marine reserves and fishing grounds on total coral cover in more detail, some interesting results appear. Prior to Hurricane Lenny in 1999, there was a steep drop in total coral cover between 1995 and 1996 especially at 5m, attributable to hurricane wave damage (Figs. 6). Then cover remained stable or increased in the reserves, but continued to decline in fishing grounds (where algal cover increased) (Fig. 6). The only exception was in the marine reserves at 15m depth in high sedimentation areas where coral declined continuously in both reserves and fishing grounds probably due to chronic sediment pollution by rivers and the large amount of sediment input into these sites by tropical storm Debbie in 1994 (Sladek Nowlis et al. 1997, see Table 2, Figs. 5 and 6).

All interactions describing total coral cover are statistically significant (Table 6). The interaction between 'Depth' and 'Sedimentation Level' is

Table 6: Results of the four-way ANOVA analysis testing the effects of the factors 'Depth' (5m, 15m), 'Sedimentation Level' (low, high), 'Protection Level' (reserve, fishing ground), 'Year' (from 1994/5 or 1996 to 2001) and their two-way interactions on two independent reef factors.

Reef factors	Depth	Sed	Prot	Year	SxP	DxS	DxP	DxY	SxY	PxY
% total coral cover	5<15***	L<H***	FG<R***	95>00***	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001	p=0.001
% total algae	5>15***	L>H***	FG>R***	95<00***	p<0.001	p<0.001	p<0.01	p<0.001	p<0.001	ns

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns=non-significant. For samples sizes see Appendix 1.

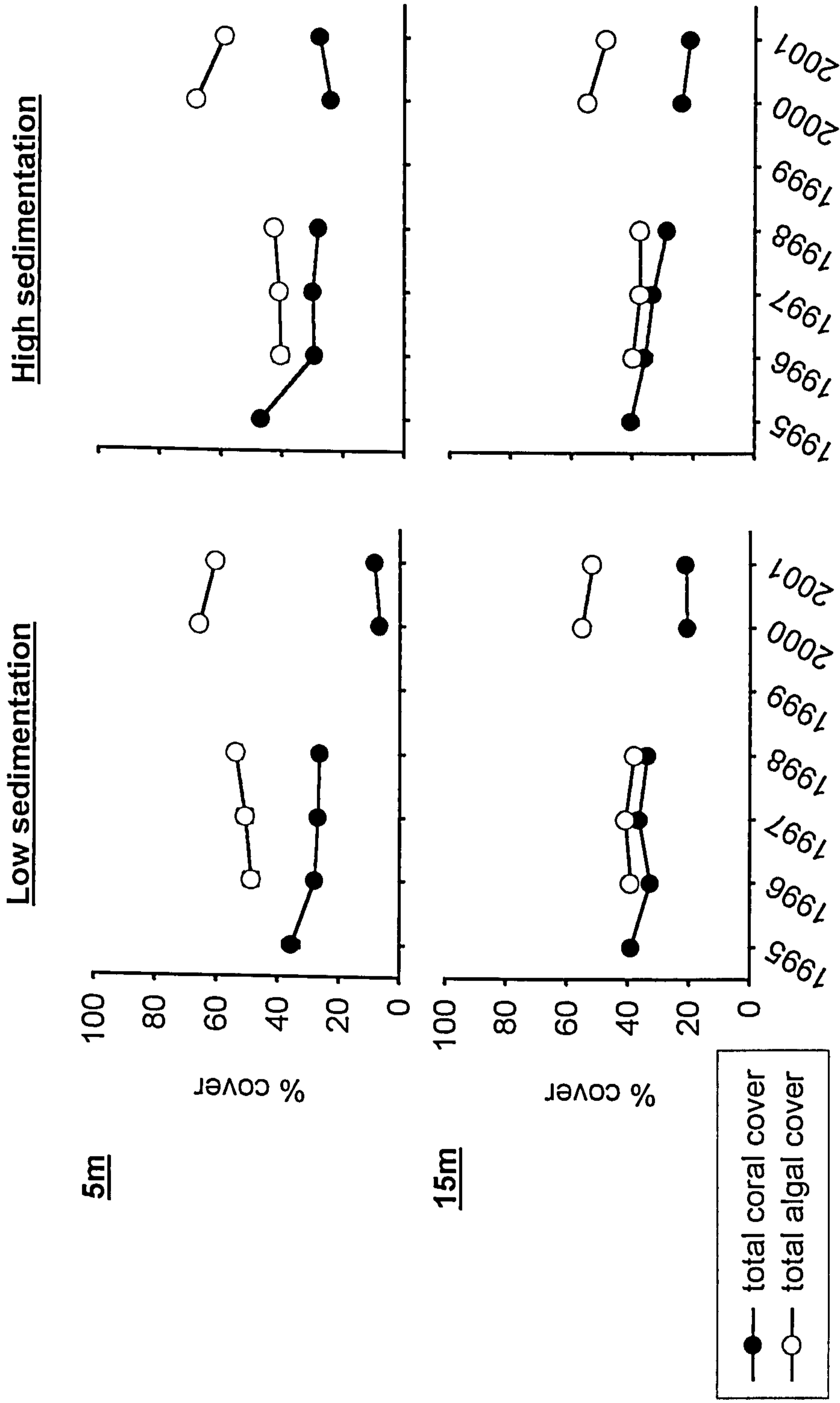


Fig. 5: Patterns of variation in percentage total coral cover (including massive corals, branching corals and *Millepora* spp.) and total algal cover (in 1995 with coralline algae, after 1995 without) under low and high sedimentation conditions at 5m and 15m depth from 1995 to 2001. Standard error bars are plotted, but they are too small to be seen on the graphs.

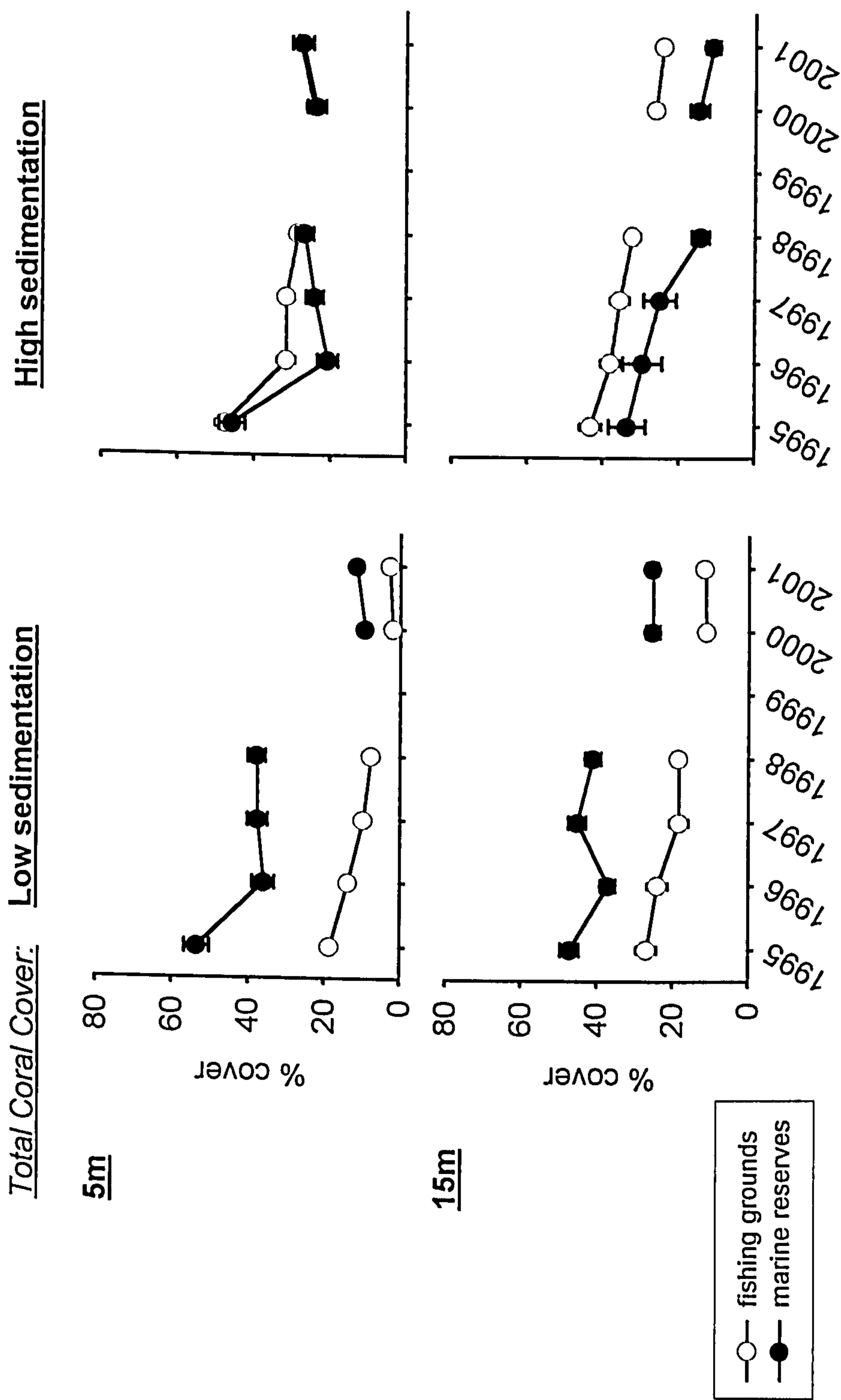


Fig. 6: Percentage total coral cover (including massive and branching coral and *Millepora* spp.) in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

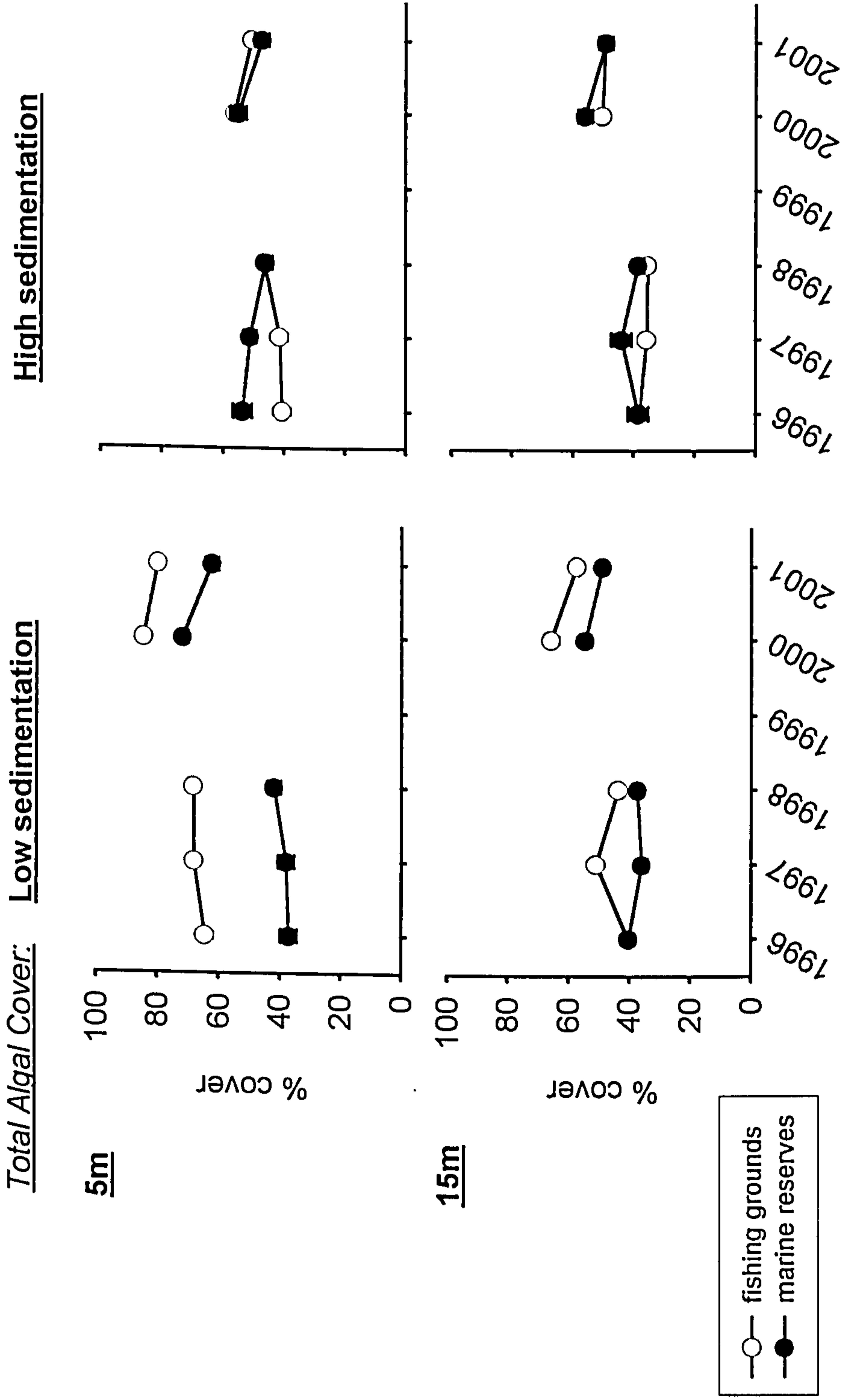


Fig. 7: Percentage total algal cover (excluding coralline algae) in low and high sedimentation areas in fishing grounds and marine reserves and at 5 and 15m depth from 1996 to 2001. Error bars represent one standard error.

significant, because the high sedimentation areas show equal amount of total coral cover at both depths, whereas the low sedimentation areas have lower total cover at 5m than 15m depth (Fig. 6). This is mainly due to the distribution of coral damage caused by Hurricane Lenny in 1999 particularly in shallow water which is further reflected in the significant interaction between 'Year' and 'Depth' and 'Year' and 'Sedimentation Level', since most damage occurred in the low sedimentation areas.

Total algal cover consists of different functional algal groups excluding coralline algae (Table 4). Total algal cover is higher in 5m compared to 15m depth (Table 5, Fig. 7). In low sedimentation areas total algal cover is higher than on reefs with high sedimentation and higher in marine reserves than in fishing grounds (Table 6, Fig. 7).

All interactions are significant. The interaction between 'Protection Level' and 'Sedimentation Level' is significant because total algal cover is higher in the fishing grounds of the low sedimentation areas and lower in the fishing grounds of the high sedimentation areas, whereas the marine reserves do not show a difference in total algal cover between high and low sedimentation areas (Table 6, Fig. 7). The interactions 'Year' and 'Sedimentation Level' and 'Years' and 'Depth' are significant due to the steep increase in algal cover after Hurricane Lenny hit the reefs in 1999 causing more damage to reefs in the low sedimentation areas in more shallow water (Table 6, Fig. 7).

Massive coral cover, branching coral cover and Millepora spp. cover

To investigate the decline of coral cover in more detail, total coral cover was split into massive, branching and fire coral (*Millepora* spp.) cover. At both depths, massive coral is the largest group followed by branching coral and *Millepora* spp. (Figs. 8-9). Massive and branching coral had higher coverage at 15m than at 5m depth, and *Millepora* spp. cover was highest at 5m than at 15m depth (Table 7, Figs. 8-12). Massive coral and *Millepora* spp. cover are lower on reefs with low sedimentation compared to high sedimentation reefs, whereas coverage of branching corals is higher on low sedimentation reefs (Table 7, Figs. 8-12). In marine reserves massive and branching coral cover is higher than in fishing

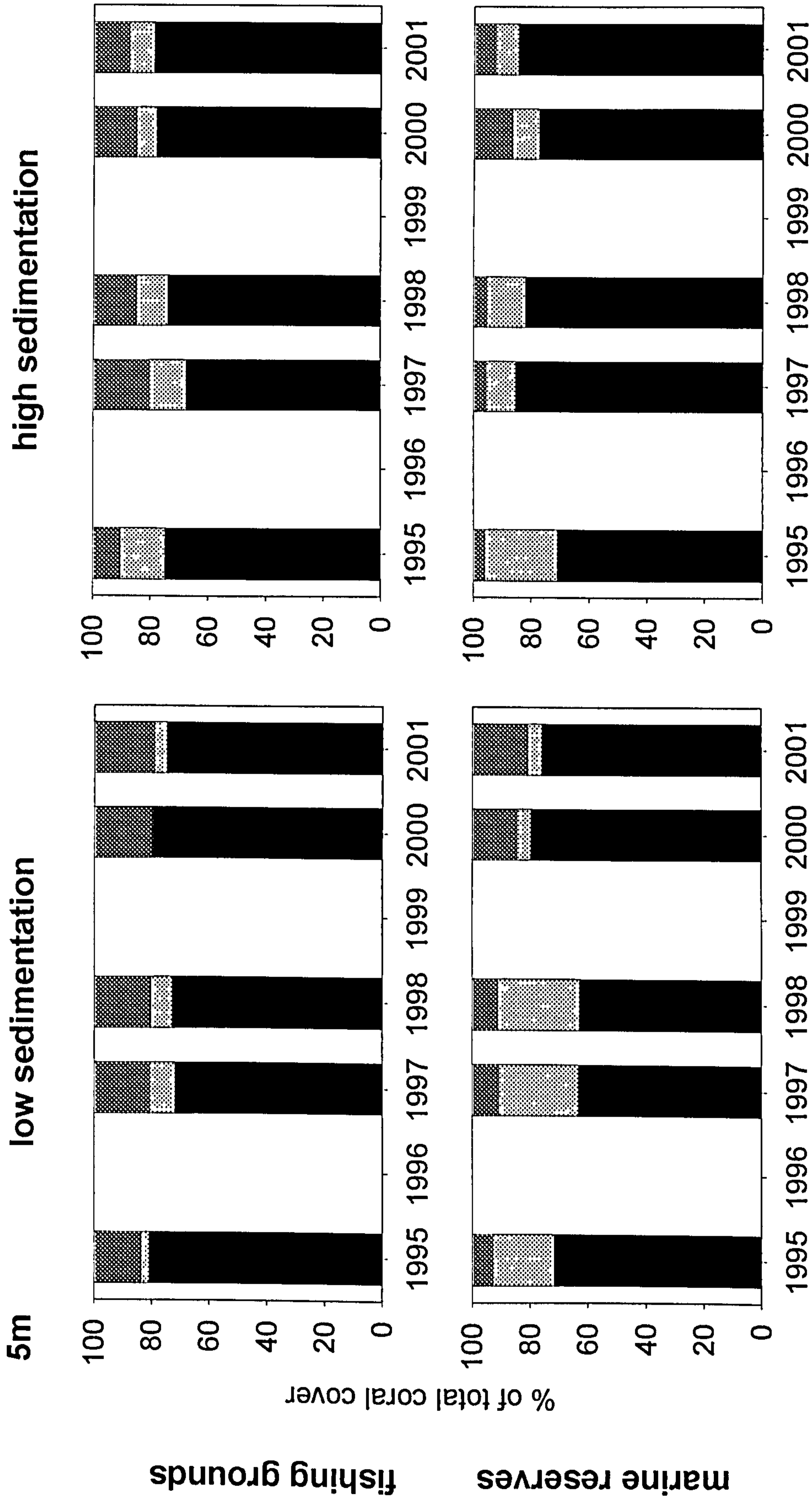
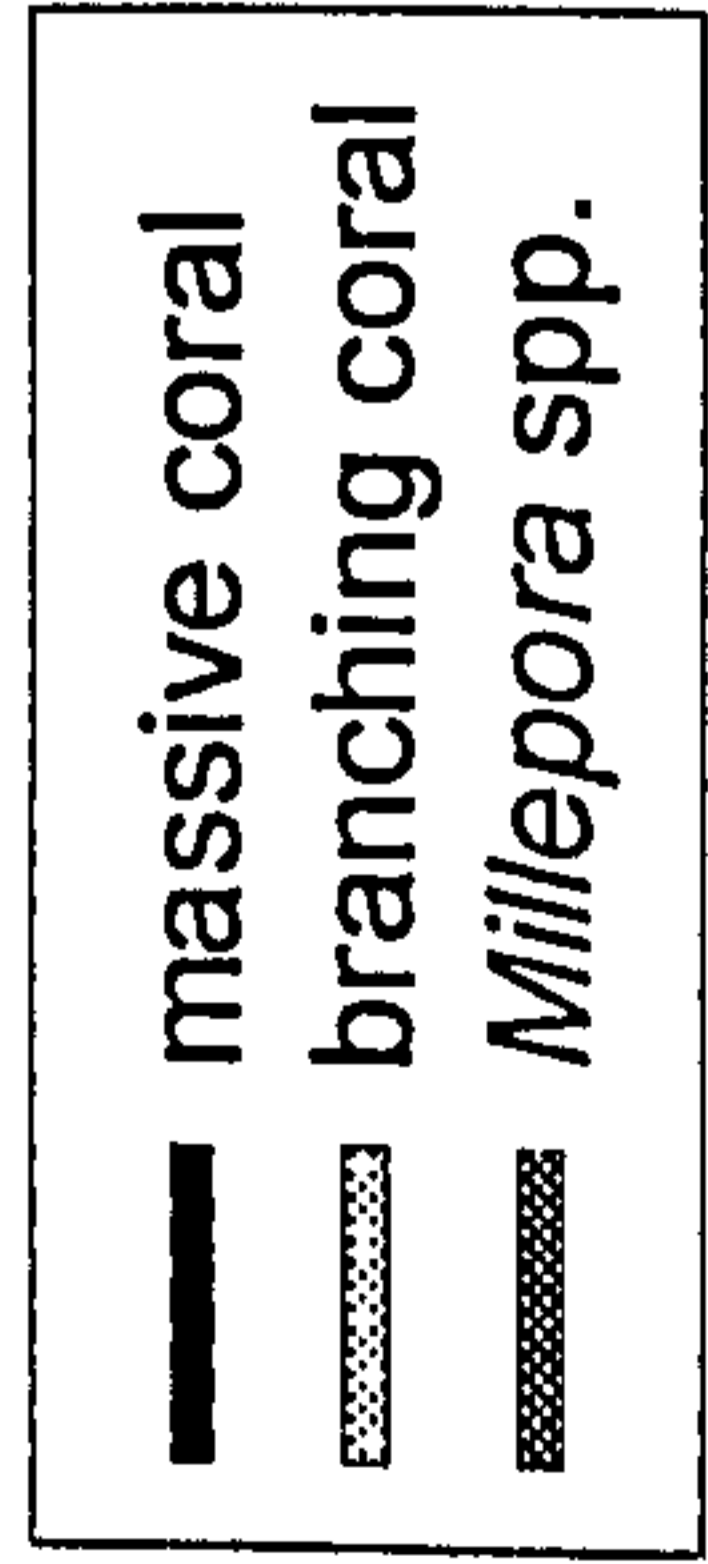


Fig. 8: Patterns of variation in percentage composition of coral assemblages including massive coral, branching coral and *Millepora* spp. from 1995 to 2001 at 5m depth for reefs in fishing grounds and marine reserves with low and high sedimentation conditions.



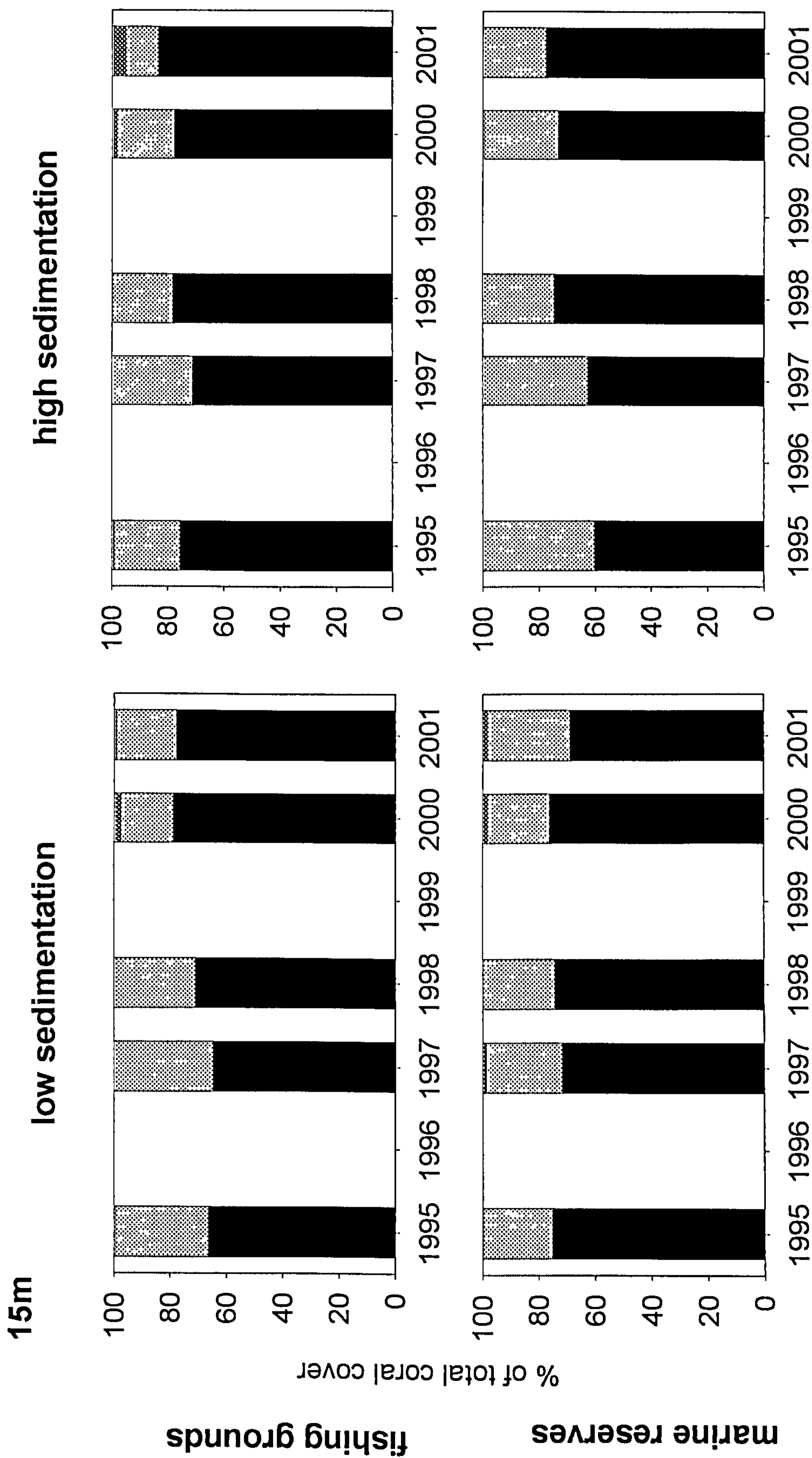


Fig. 9: Patterns of variation in percentage composition of coral assemblages including massive coral, branching coral and *Millepora* spp. from 1995 to 2001 at 15m depth for reefs in fishing grounds and marine reserves with low and high sedimentation conditions.

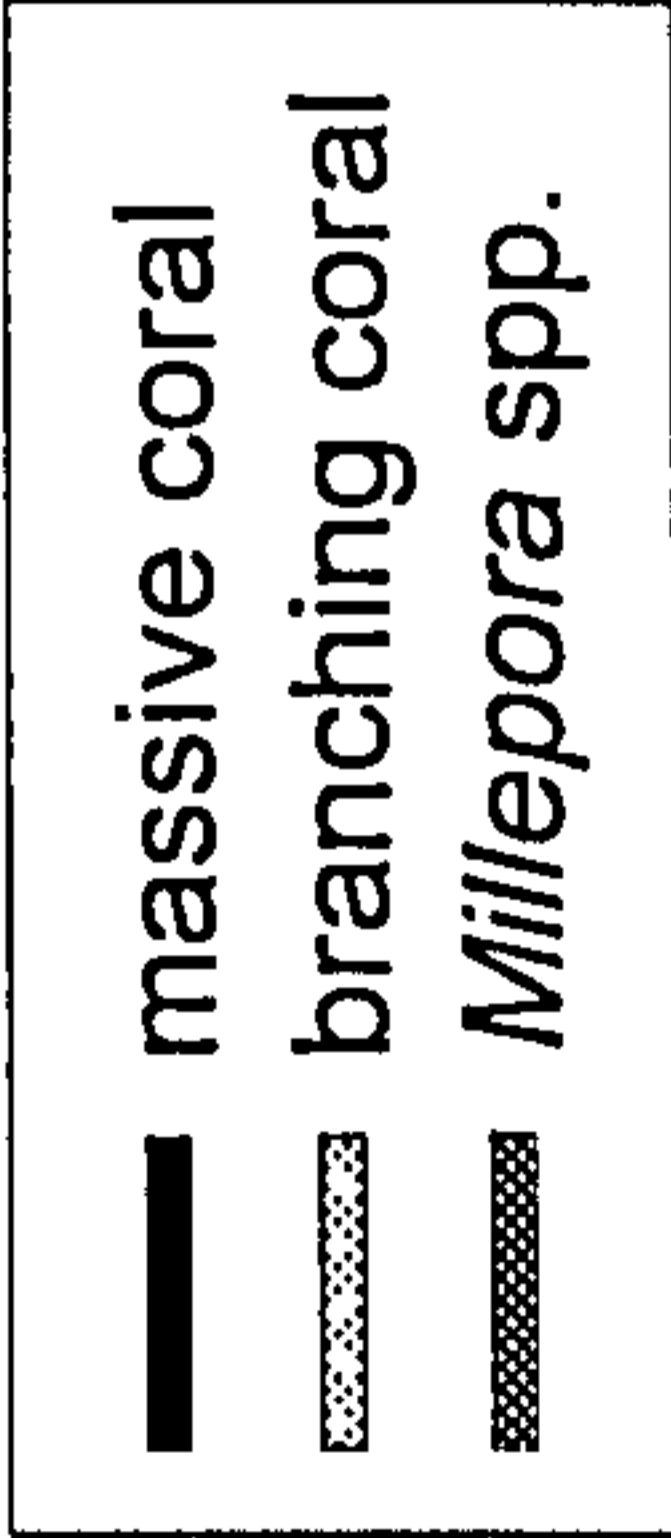


Table 7: Results of the four-way ANOVA analysis testing the effects of the factors ‘Depth’ (5m, 15m), ‘Sedimentation Level’ (low, high), ‘Protection Level’ (reserve, fishing ground), ‘Year’ (from 1994/5 or 1996 to 2001) and their 2-way interactions on several independent reef factors.

Reef factors	Depth	Sed	Prot	Year	SxP	DxS	DxP	DxY	SxY	PxY
% massive coral	5<15***	L<H***	FG<R***	95>00***	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001	ns
% branching coral	5<15***	L>H *	FG<R***	95>00***	p<0.001	p=0.01	p<0.01	p<0.001	p<0.01	p=0.001
% <i>Millepora</i> spp.	5>15***	L<H *	FG>R ns	95>00***	p<0.001	p=0.001	ns	p<0.001	p<0.05	ns
% gorgonian	5>15***	L<H **	FG>R *	95>00***	p<0.001	ns	ns	p=0.001	p<0.01	ns
% sponge	5<15***	L>H***	FG>R ns	95>00***	p<0.001	p<0.05	p<0.001	p<0.05	p<0.001	p<0.01
% others	5<15 *	L>H *	FG>R ns	95>96***	p<0.001	ns	ns	p=0.001	p<0.001	p<0.001

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. *p≤0.05, **p≤0.01, ***p≤0.001, ns=non-significant. For sample sizes see Appendix 1.

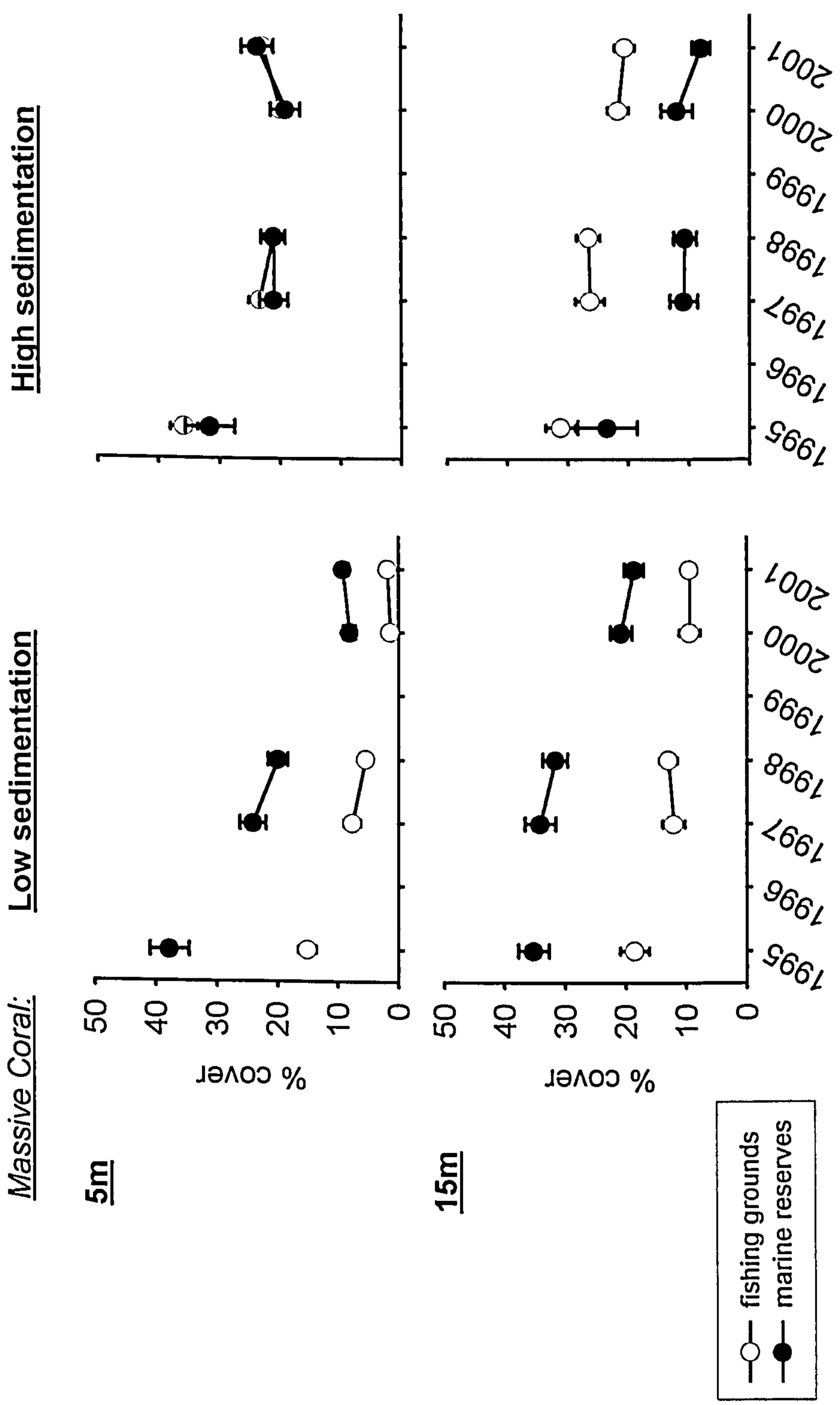


Fig. 10: Percentage massive coral cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

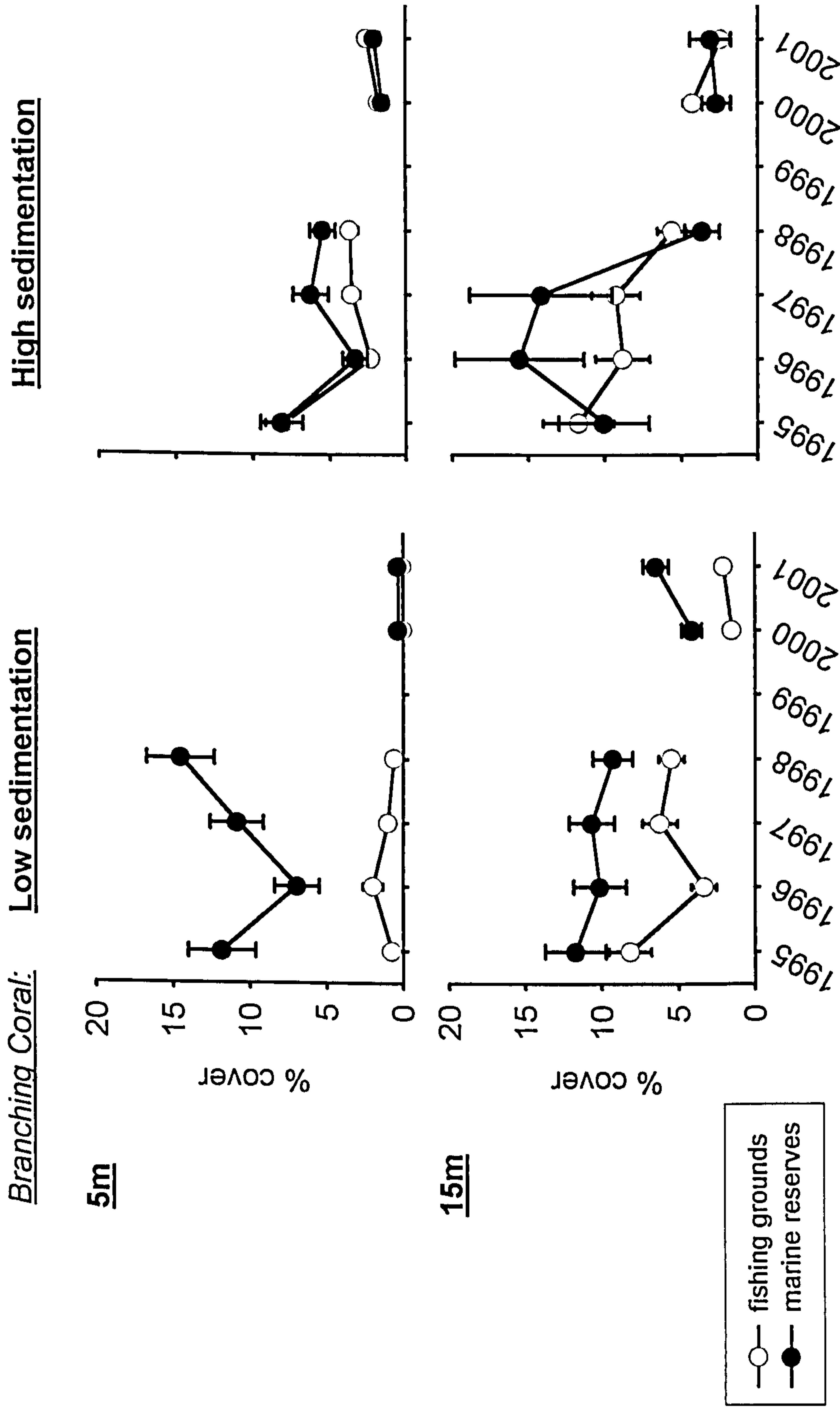


Fig. 11: Percentage branching coral cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

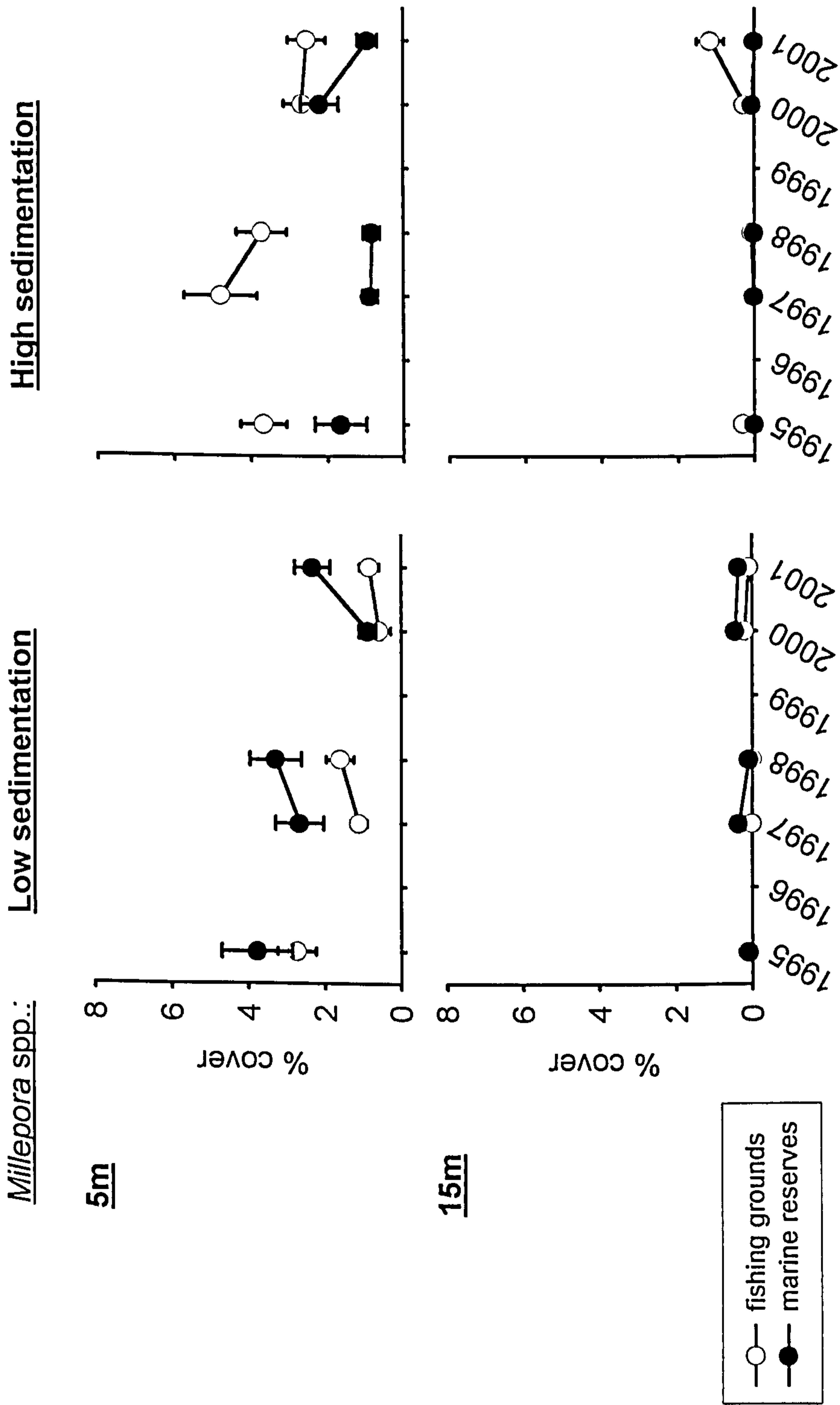


Fig. 12: Percentage *Millepora* spp. cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

grounds (Table 7, Figs. 10-11). Again, a difference in cover existed at the time reserves were implemented and, hence, cannot be identified as a positive marine reserve effect (Figs. 10-11). *Millepora* spp. appear to not be significantly affected by protection from fishing (Table 7, Fig. 12). Hurricane Lenny in 1999 caused substantial losses in branching corals and some loss of massive corals and *Millepora* spp. mainly in the reserves of the low sedimentation sites (Figs. 10-12). At 5m depth in the marine reserves branching coral cover increased steeply from 1996 to 1999, the period where physical destruction by storms and hurricanes was absent, even exceeding coverage before 1996. This shows that branching corals have the ability to recover fast under suitable conditions after physical damage. Generally, all three coral groups show slightly higher coverage in 2001 compared to 2000 (Figs. 10-12), possibly indicating a recovery process.

Looking at the interactions affecting massive, branching and *Millepora* spp., we find that many are significant (Table 7). The interaction 'Protection and Year' is not significantly affecting massive coral cover, since changes in coverage of massive coral over the years in the low and high sedimentation areas are very much the same (Table 7, Fig. 10). All other significant interactions describing massive and coral cover are the same as described for total coral cover since these two coral groups are most dominant (see above). *Millepora* spp. is more abundant in the marine reserves than in the fishing grounds in the low sedimentation areas, but less abundant in the marine reserves than in the fishing grounds in the high sedimentation areas which is reflected in the significant interaction between 'Sedimentation Level' and Protection Level' (Table 7, Fig. 12). Additionally, *Millepora* spp. coverage fluctuates in both depth and sedimentation areas over the years which leads to significant interactions of both factors with the factor 'Year' (Table 7, Fig. 12).

Functional algal groups

Figures 13 and 14 show that the low sedimentation areas at 5m and 15m depth are not as dominated by filamentous algae as the high sedimentation reefs. In general, filamentous algae is the main component of all algal communities at 5m depth, whereas at 15m depth they cover less substrate (Table 8, Figs. 13-14). It is notable that at 15m depth in the fishing grounds of the high sedimentation areas,

filamentous algal cover decreased steadily from 1996 to 2001 and that of other functional algal groups increased (Figs.14).

All algal functional groups show a significant increase over the years in coverage of the benthic substrate (Table 8, Figs. 15-19). In addition, all functional algal groups are found in higher abundance in shallow water except macroalgae that were more common at 15m depth (Table 8, Figs. 15-19). Filamentous algal cover is greater in high sedimentation than in low sedimentation sites, whereas macro- and blue-green algae are more abundant in low than in high sedimentation sites (Table 8, Figs. 15-18). Coralline and encrusting algae were not significantly affected by sedimentation (Table 8, Figs. 17 and 19). Macroalgae and encrusting algae groups are found in greater abundance in fishing grounds than in marine reserves (Table 8, Figs. 16-17), except blue-green algae that are more common in marine reserves (Table 8, Fig. 18). Filamentous and coralline algae were not clearly affected by protection from fishing (Table 8, Figs. 15 and 19). Specifically, it is notable that after the hurricane events in 1995/96 and 1999 blue-green algae increased significantly, more dramatically at 15m depth, especially in the low sedimentation areas, but then it dropped steeply in 2001 (Fig. 21).

The ANOVA results showed many significant interactions for all functional algal groups (Table 8). Interactions including the factor 'Year' were significant mainly due to changes between 1998 and 2000 that varied between both the depths, sedimentation levels and protection levels (Table 8, Figs. 15-19). This is mainly because waves produced by Hurricane Lenny hit the low sedimentation areas more severely than the high sedimentation areas, opening new space for fast algal colonisation. Filamentous algae show highest coverage after Hurricane Lenny in 1999, whereas all other functional algal groups were most abundant in 2001.

The interaction that is of greatest interest for this study is the one between the factors 'Sedimentation Level' and 'Protection Level'. Most functional groups show different patterns for the combination of these factors. Macroalgal cover is higher in the fishing grounds of the low sedimentation areas than of the high sedimentation areas, whereas in the marine reserves coverage stays the same (Fig. 16). Comparing all combinations, highest macroalgal cover occurs in the fishing grounds of the low sedimentation areas (Fig. 16).

Table 8: Results of the four-way ANOVA analysis testing the effects of the factors 'Depth' (5m, 15m), 'Sedimentation Level' (low, high), 'Protection Level' (reserve, fishing ground), 'Year' (from 1994/5 or 1996 to 2001) and their 2-way interactions on several independent reef factors.

Reef factors	Depth	Sed	Prot	Year	SxP	DxS	DxP	DxY	SxY	PxY
% filamentous algae	5>15***	L<H***	FG>R ns	96<00***	p<0.01	p<0.001	p<0.01	p<0.001	p<0.001	p<0.001
% macroalgae	5<15***	L>H***	FG>R***	96<01***	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001
% encrusting algae	5>15 *	L<H ns	FG>R***	96<01***	p<0.001	p<0.001	ns	p<0.001	p<0.05	ns
% blue-green algae	5>15***	L>H***	FG<R *	98<01***	p<0.05	p<0.001	p<0.001	p<0.001	p<0.001	p<0.05
% coralline algae	5>15***	L<H ns	FG<R ns	96<01***	p<0.001	p<0.01	ns	p<0.001	ns	p<0.05

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. *p≤0.05, **p≤0.01, ***p≤0.001, ns=non-significant. For sample sizes see Appendix 1.

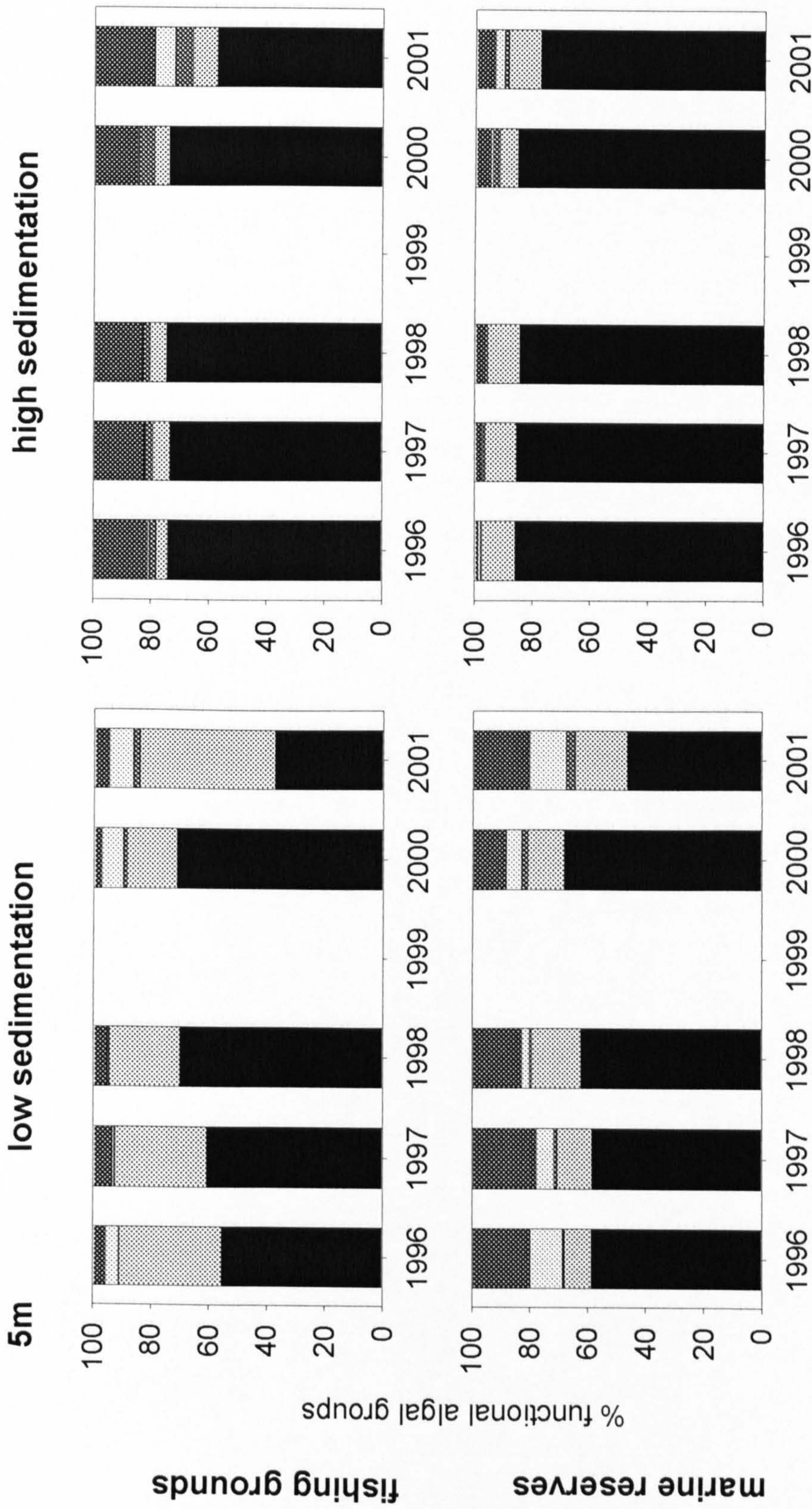


Fig. 13: Patterns of variation in percentage cover of the different functional algal groups from 1005 to 2001 at 5m depth for reefs in fishing grounds and marine reserves with low and high sedimentation conditions.

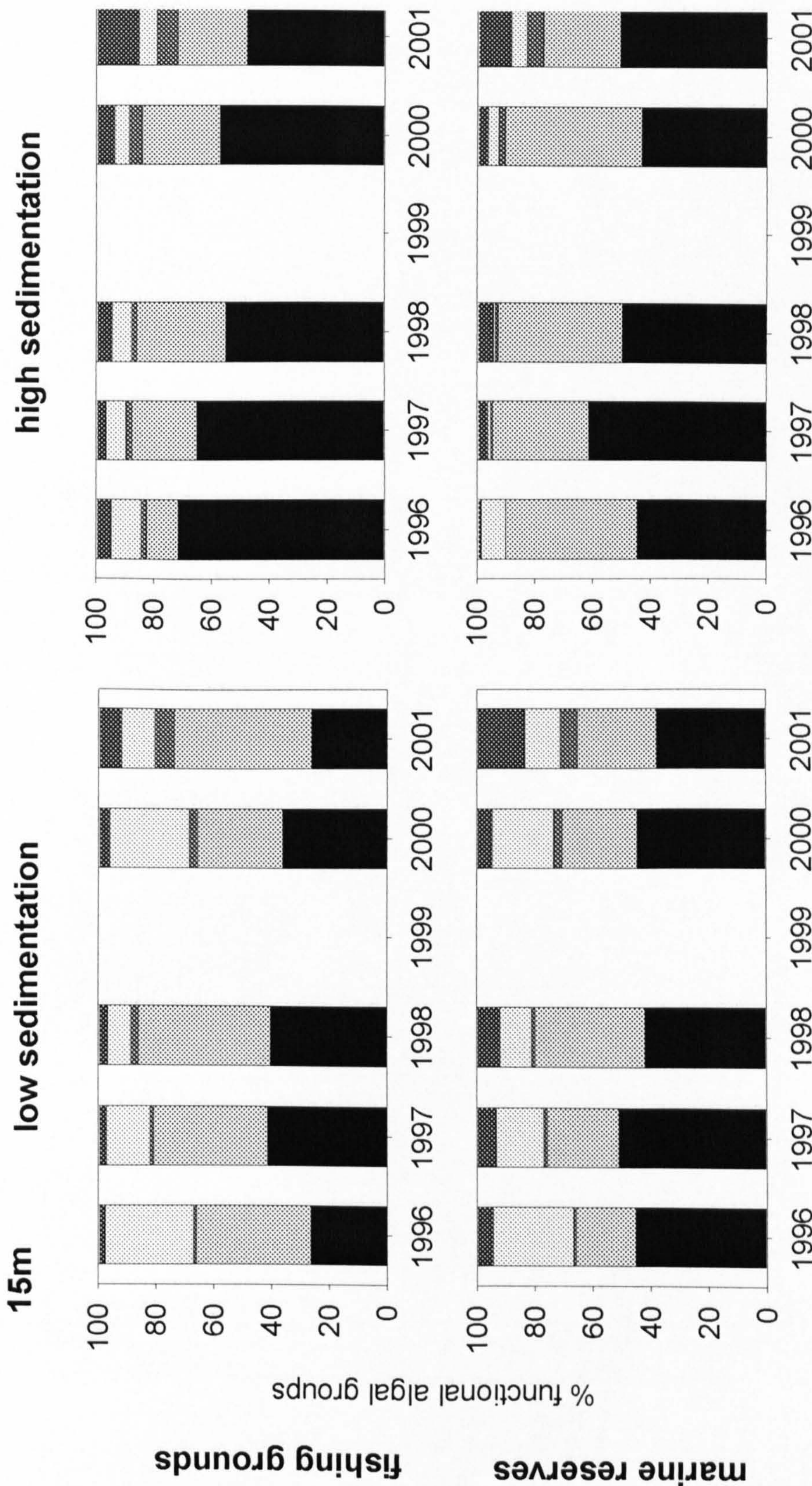
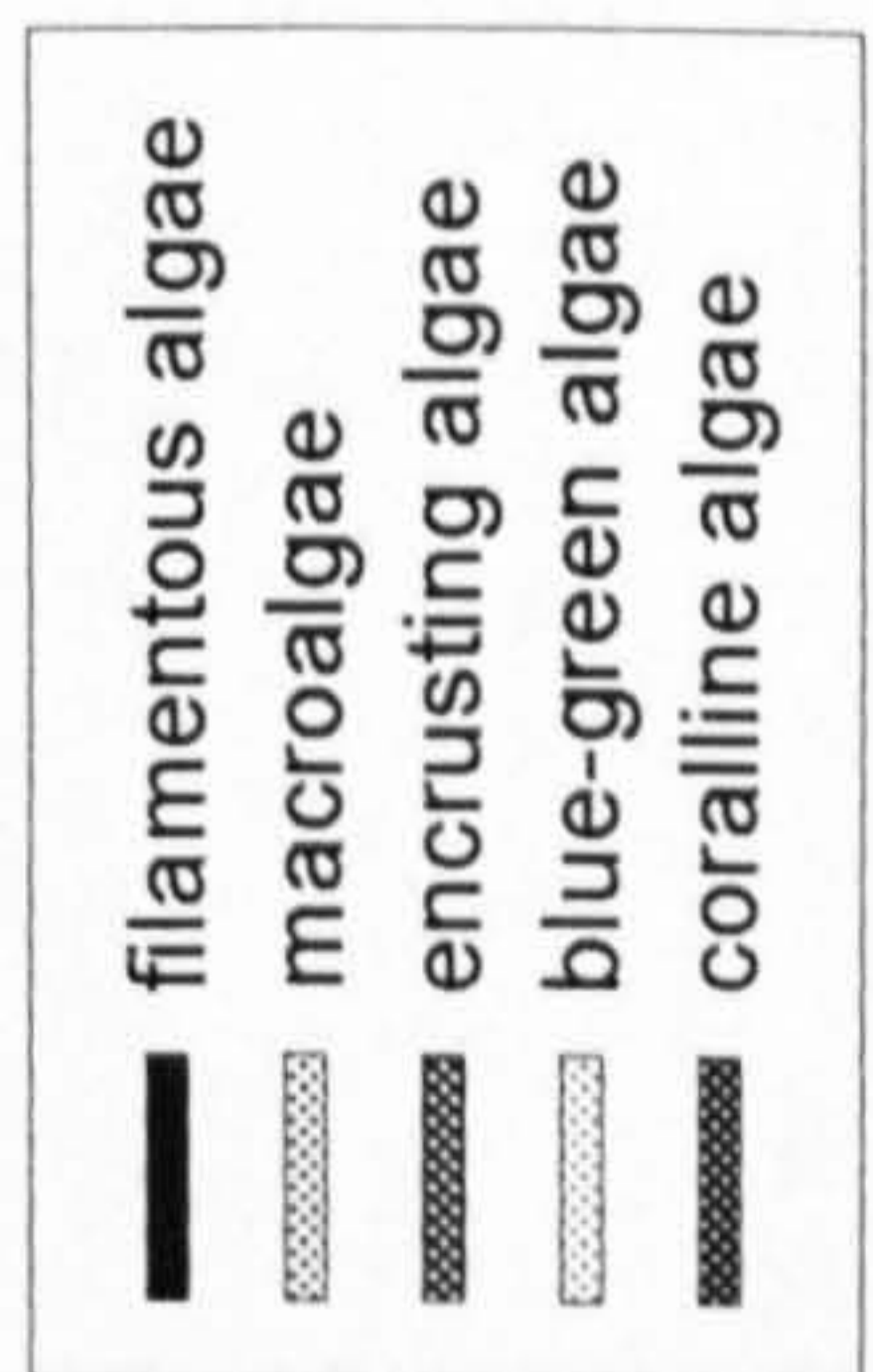


Fig. 14: Patterns of variation in percentage cover of the different functional algal groups from 1995 to 2001 at 15m depth for reefs in fishing grounds and marine reserves with low and high sedimentation conditions.



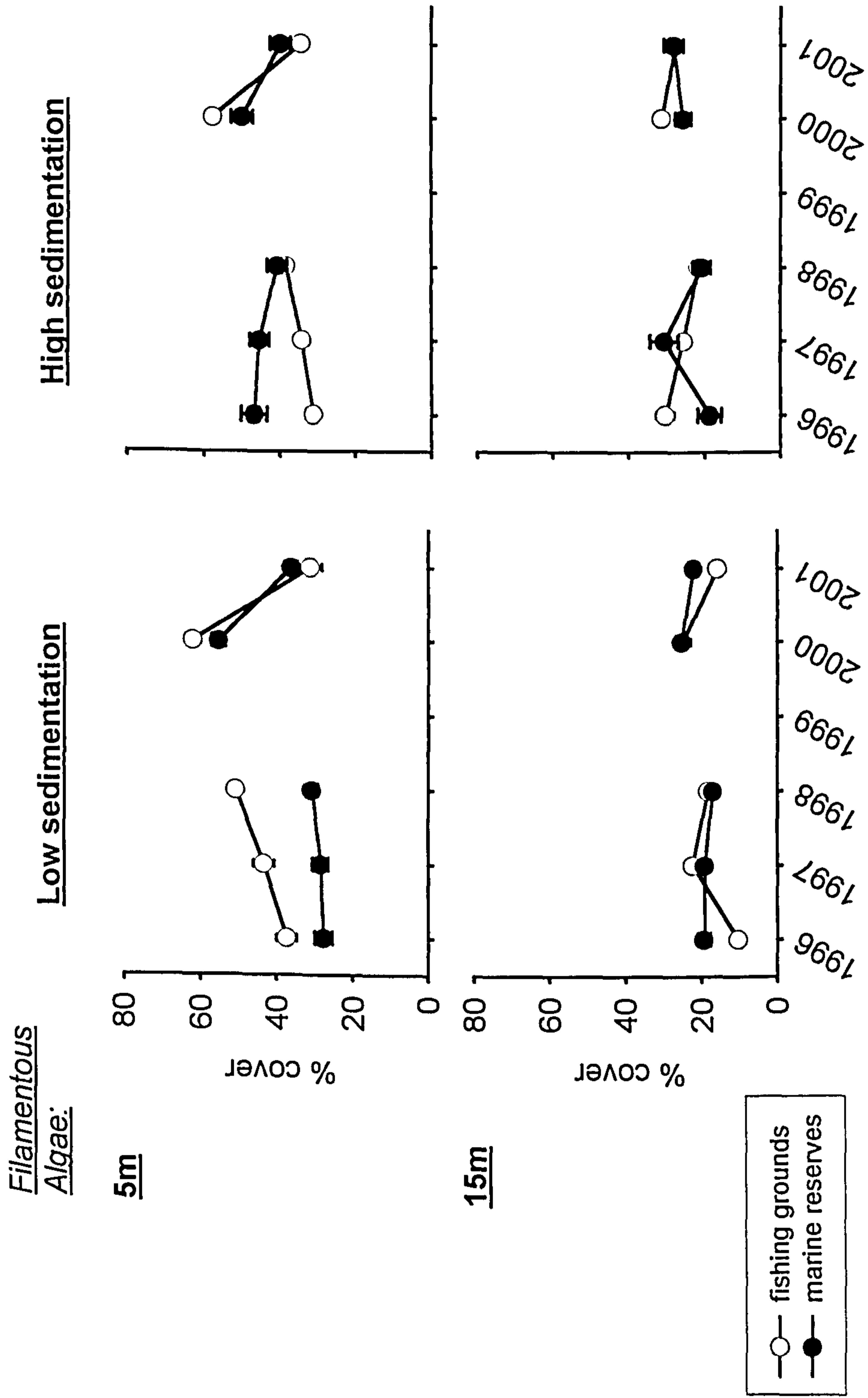


Fig. 15: Percentage filamentous algal cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

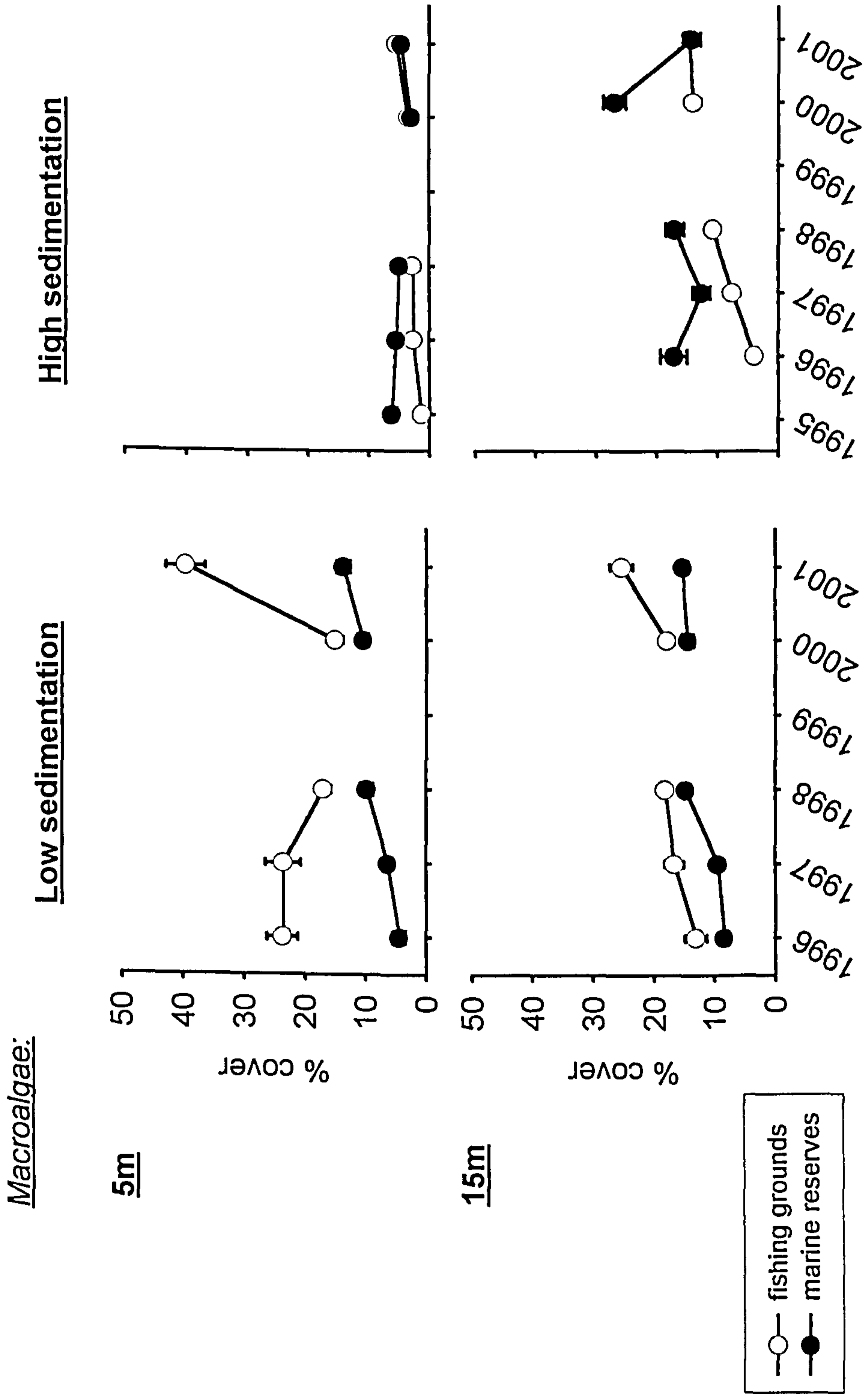


Fig. 16: Percentage macroalgal cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

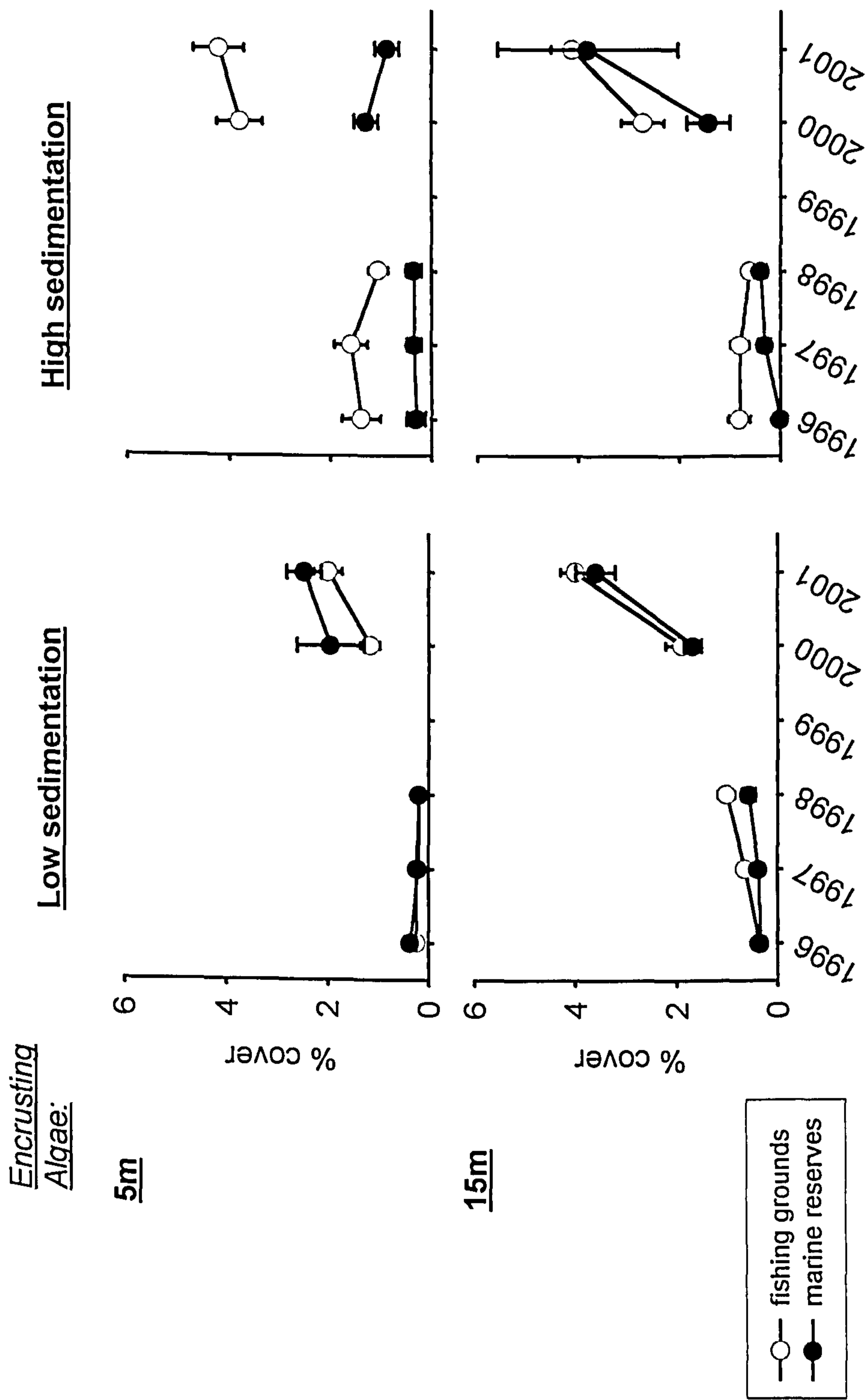


Fig. 17: Percentage encrusting algal cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

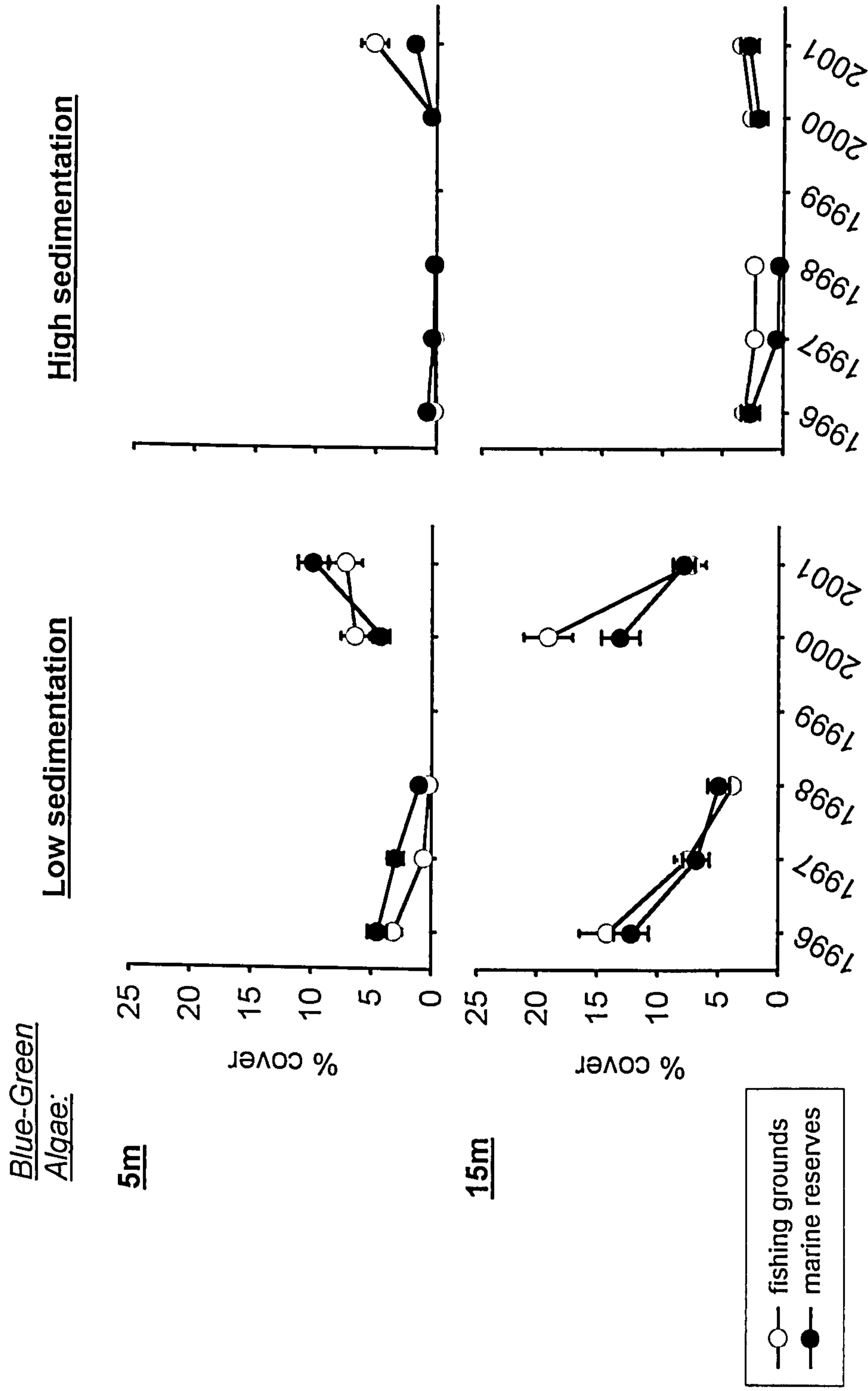


Fig. 18: Percentage blue-green algal cover in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

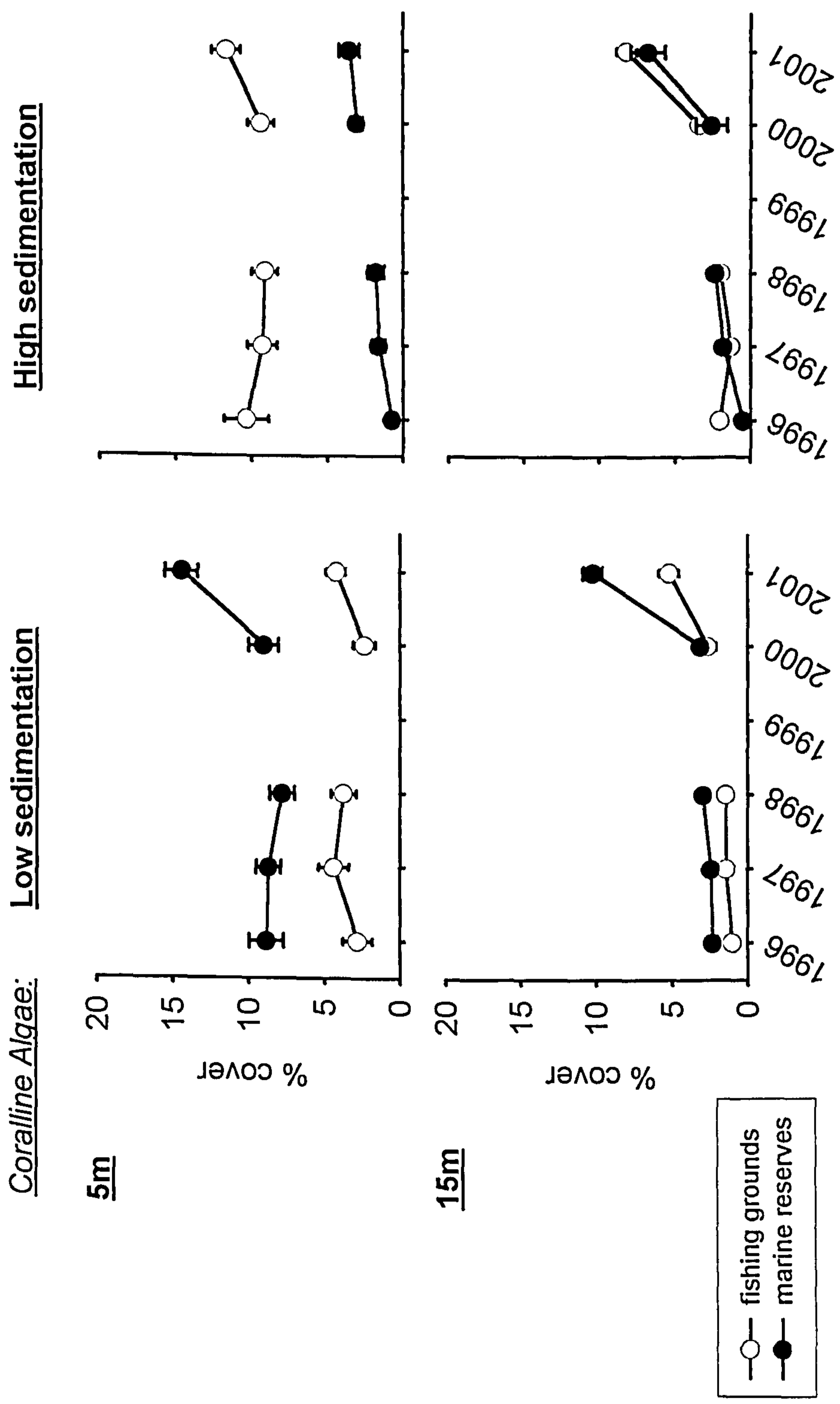


Fig. 19: Percentage coralline algal cover in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

Encrusting and blue-green algae show the same pattern for 'Sedimentation Level' and 'Protection Level', that is the opposite pattern of filamentous algae (Figs. 15, 17-18). There is no difference in filamentous algal cover between the fishing grounds and marine reserves in the low sedimentation areas, whereas in the high sedimentation areas, filamentous algae are more abundant in the fishing grounds (Fig. 15). Encrusting and blue-green algae are more abundant in the marine reserves than in the fishing grounds of the low sedimentation areas, whereas for encrusting and blue-green algae there is no difference (Figs. 17-18). Coralline algae are more common in the marine reserves than in the fishing grounds of the low sedimentation areas, but more common in the fishing grounds than in the marine reserves of the high sedimentation areas (Fig. 19). These results indicate that functional algal groups react differently to hurricane, sedimentation and fish grazing disturbances.

Herbivorous grazers (herbivorous fish and Diadema antillarum)

Generally, herbivorous fish biomass is greater at 5m than 15m depth (Table 9, Fig. 20). Marine reserves have helped to rebuild herbivorous fish stocks over the years (Table 9). In 2001 biomass of herbivorous fish was around 3 times greater than in 1995 (Table 9, Fig. 20). Sedimentation did not have any significant effect on herbivorous fish biomass (Table 9, Fig. 20). However, the interaction between 'Protection Level' and 'Sedimentation Level' was significant (Table 8). In the fishing grounds, herbivorous fish biomass is lower in the low sedimentation areas and higher in the high sedimentation areas, whereas in marine reserves, biomass is greater in the low sedimentation areas and lower in the high sedimentation areas (Fig. 20). Of all combinations, lowest herbivorous fish biomass is found in the fishing grounds of the low sedimentation sites (Fig. 20). In Figure 20 it is notable that Hurricane Lenny in 1999 had an impact on the biomass of herbivorous fish. In the low sedimentation areas that were hit by the Hurricane more severely than the high sedimentation areas, there is a stop in the steady increase of herbivorous fish biomass in the marine reserves between 1998 and 2000, and in the fishing grounds of the low sedimentation areas, there is even a drop in the biomass (Fig. 20).

Table 9: Results of the four-way ANOVA analysis testing the effects of the factors 'Depth' (5m, 15m), 'Sedimentation Level' (low, high), 'Protection Level' (reserve, fishing ground), 'Year' (from 1994/5 to 2001) and their 2-way interactions on two independent reef factors.

Reef factors	Depth	Sed	Prot	Year	DxS	DxP	DxY	SxP	SxY	PxY
Herbivorous fish biomass	5>15***	L>H ns	FG>R***	95>01 **	ns	ns	ns	p<0.001	ns	ns
# <i>Diadema antillarum</i> (sea urchin) / m ²	5>15***	L<H***	FG>R ns	95>01 *	p<0.001	ns	p=0.01	p<0.001	p<0.001	p<0.05

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. *p≤0.05, **p≤0.01, ***p≤0.001, ns=non-significant. For sample sizes see Appendix 1.

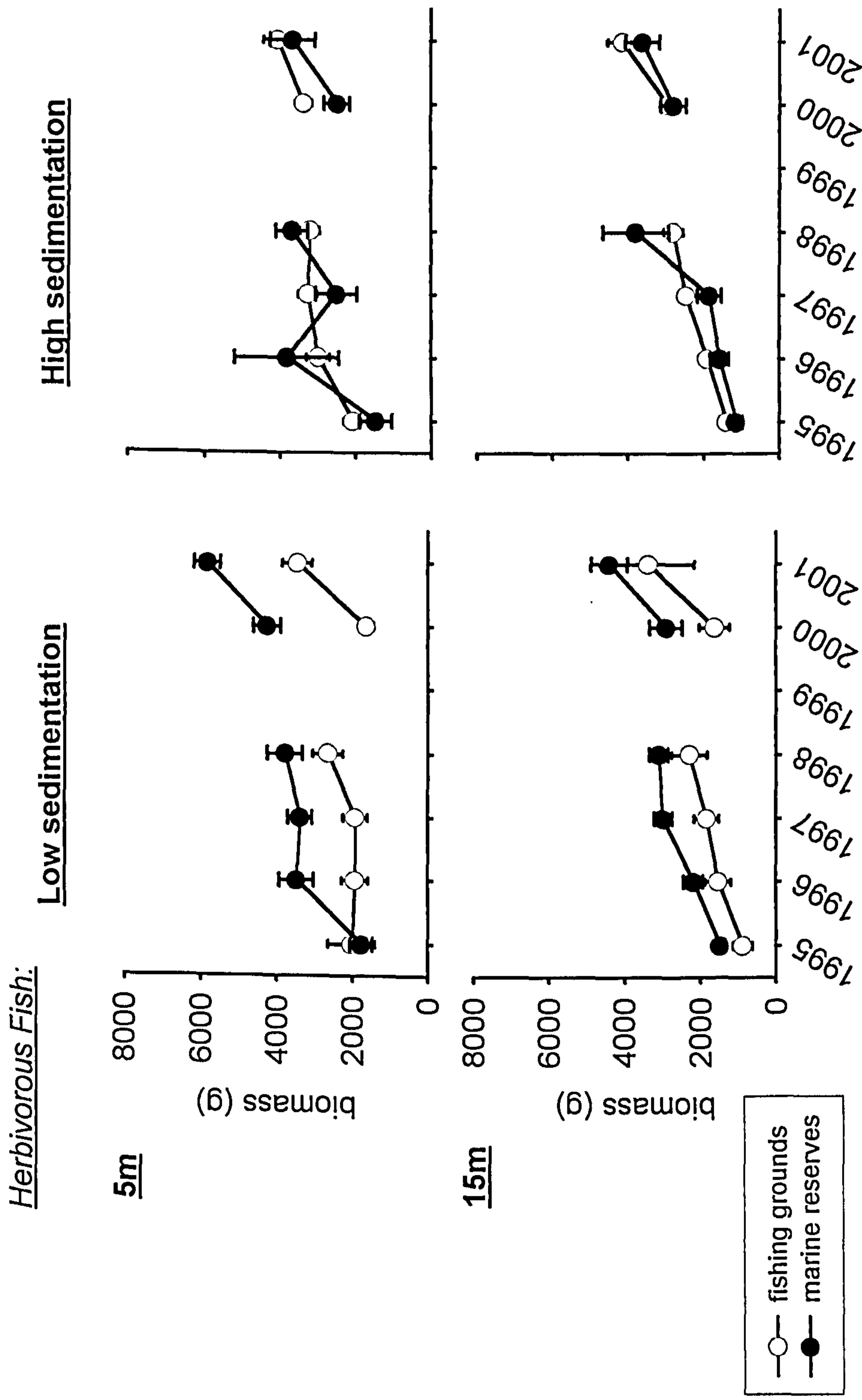


Fig. 20: Herbivorous fish biomass (g) in low and high sedimentation areas in fishing grounds and marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

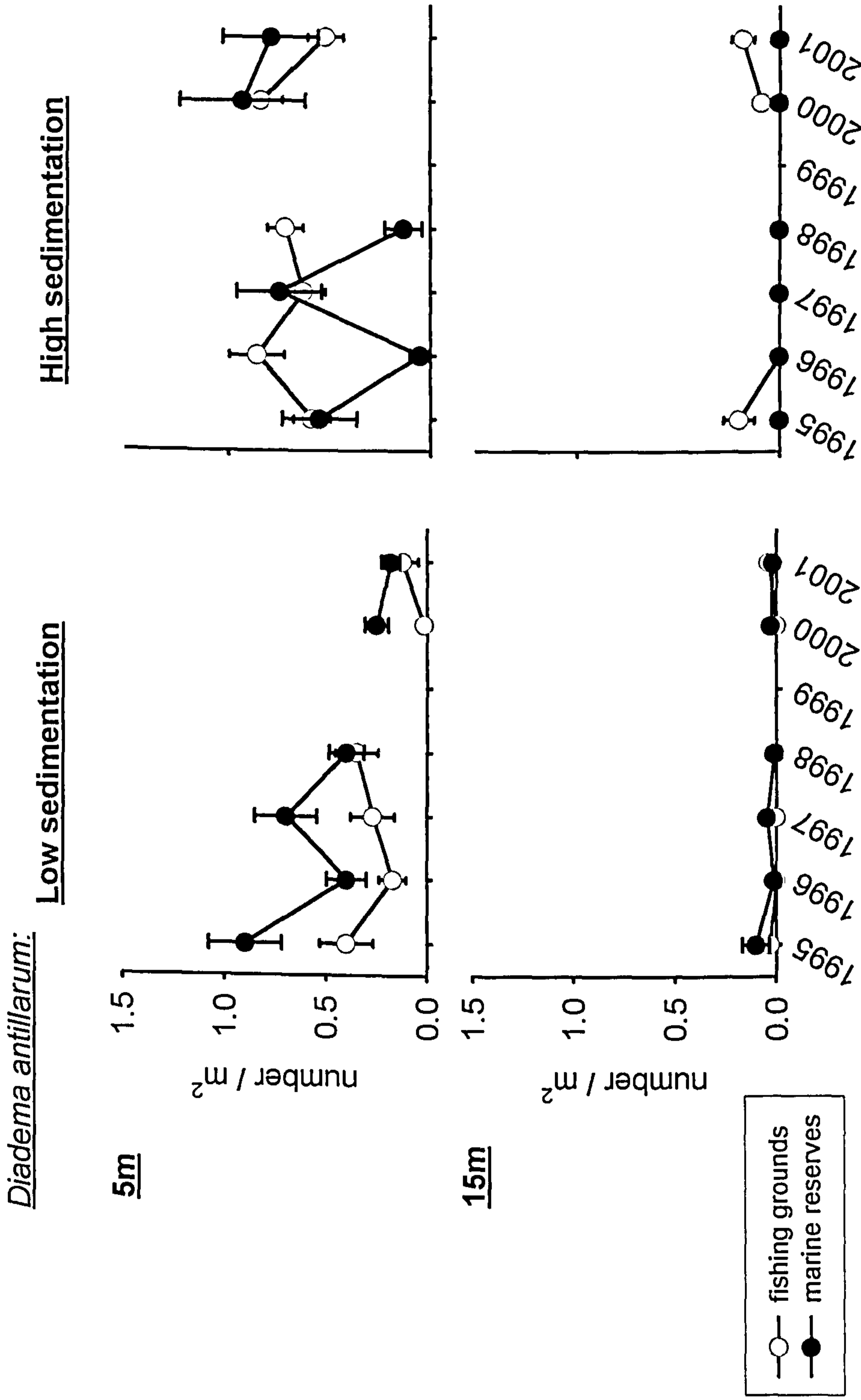


Fig. 21: Number of *Diadema antillarum* (no./m²) in low and high sedimentation areas in fishing grounds marine reserves and at 5m and 15m depth from 1995 to 2001. Error bars represent one standard error.

The abundance of the grazing sea urchin *D. antillarum* was much higher at 5m than at 15m depth (Table 9, Fig. 21). Sedimentation level had a significant effect (Table 9, Fig. 21). The number of *D. antillarum* was higher in the high sedimentation sites (Table 9, Fig. 21). All two-way interactions between 'Protection Level', 'Sedimentation Level' and 'Depth' showed significance in the ANOVA analysis (Table 9). At 15m depth in both sedimentation levels, there is not a lot of variation in the abundance of *D. antillarum* (Fig. 21). In the low sedimentation sites at 5m depth, *D. antillarum* abundance is higher in the marine reserves than in the fishing grounds, whereas at 5m depth in the high sedimentation sites, *D. antillarum* abundance varies a lot in the marine reserves and fishing grounds over the study period (Fig. 21). Overall, *D. antillarum* was more common in 1995 than in 2001, and since they were also more common in shallower water and low sedimentation areas, as described above, the interaction between 'Years' and these two factors respectively are significant (Table 9, Fig. 21).

Gorgonian cover, sponge cover and 'other' cover

The percentage substrate covered by gorgonians was measured using the base of an individual gorgonian fan. Gorgonians were more common at 5m compared to 15m depth (Table 10, Fig. 22). Sedimentation and protection from fishing both had a significant effect on gorgonian cover (Table 10, Fig. 22). Gorgonians are more common in high than in low sedimentation areas and in fishing grounds than marine reserves (Fig. 22).

Sponges were more prevalent in deeper water (Table 10, Fig. 23). They covered more substrate on low sedimentation reefs compared to high sedimentation reefs (Table 10, Fig. 23). However, there was no significant difference in coverage of sponges in fishing grounds and marine reserves (Table 10, Fig. 23). In the low sedimentation areas there is a decrease of sponge cover at 5m and 15m depth and in both marine reserves and fishing grounds due to Hurricane Lenny, that cause damage in these areas in 1999 (Fig. 23).

Table 10: Results of the four-way ANOVA analysis testing the effects of the factors 'Depth' (5m, 15m), 'Sedimentation Level' (low, high), 'Protection Level' (reserve, fishing ground), 'Year' (from 1994/5 to 2001) and their 2-way interactions on several independent reef factors.

Reef factors	Depth	Sed	Prot	Year	DxS	DxP	DxY	SxP	SxY	PxY
% gorgonian	5>15***	L<H **	FG>R *	95>00***	p<0.001	ns	ns	p=0.001	p<0.01	ns
% sponge	5<15***	L>H***	FG>R ns	95>00***	p<0.001	p<0.05	p<0.001	p<0.05	p<0.001	p<0.01
% others	5<15 *	L>H ns	FG>R *	95>96***	p<0.001	ns	ns	p=0.001	p<0.001	p<0.001

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns=non-significant. For sample sizes see Appendix 1.

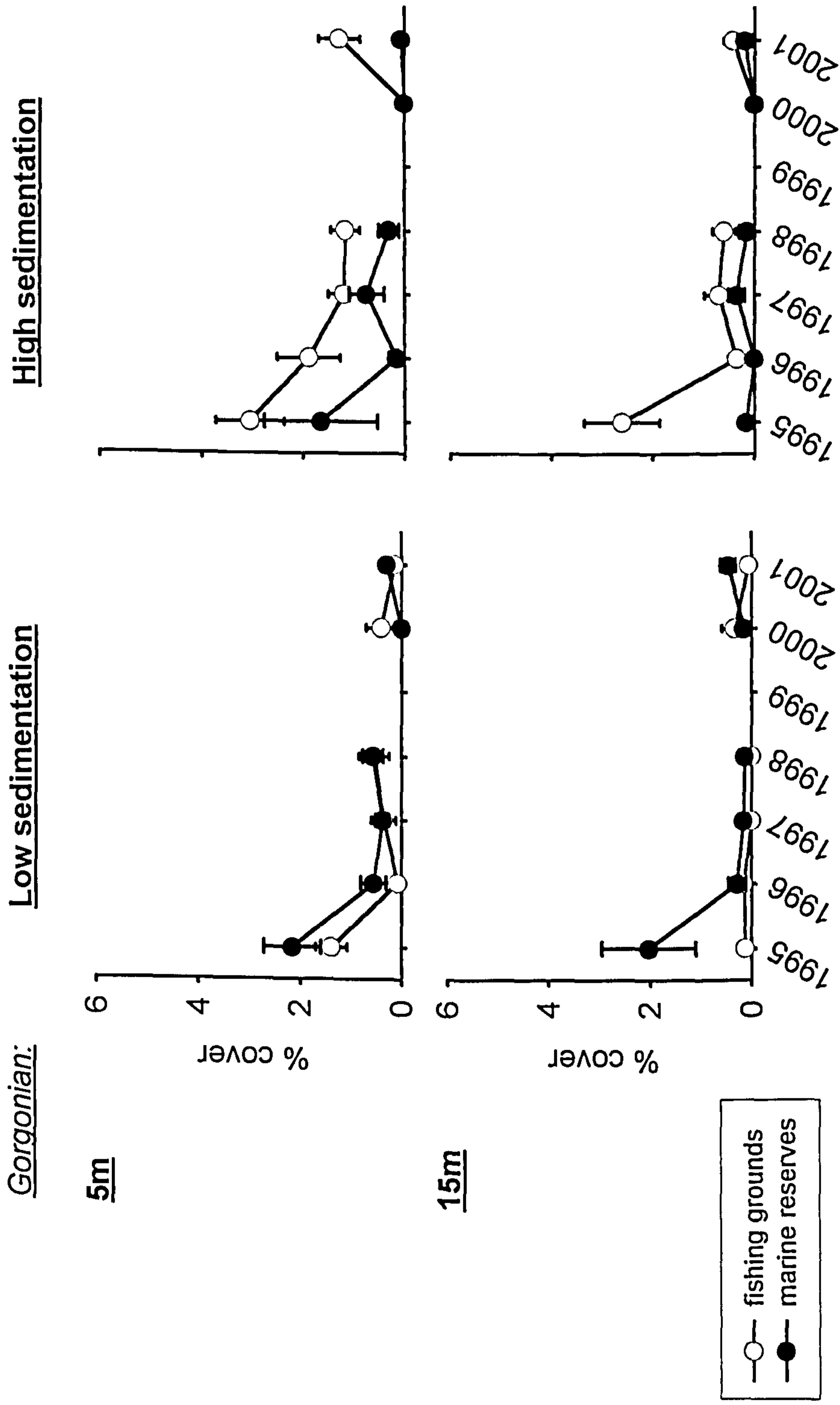


Fig. 22: Percentage gorgonian cover in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

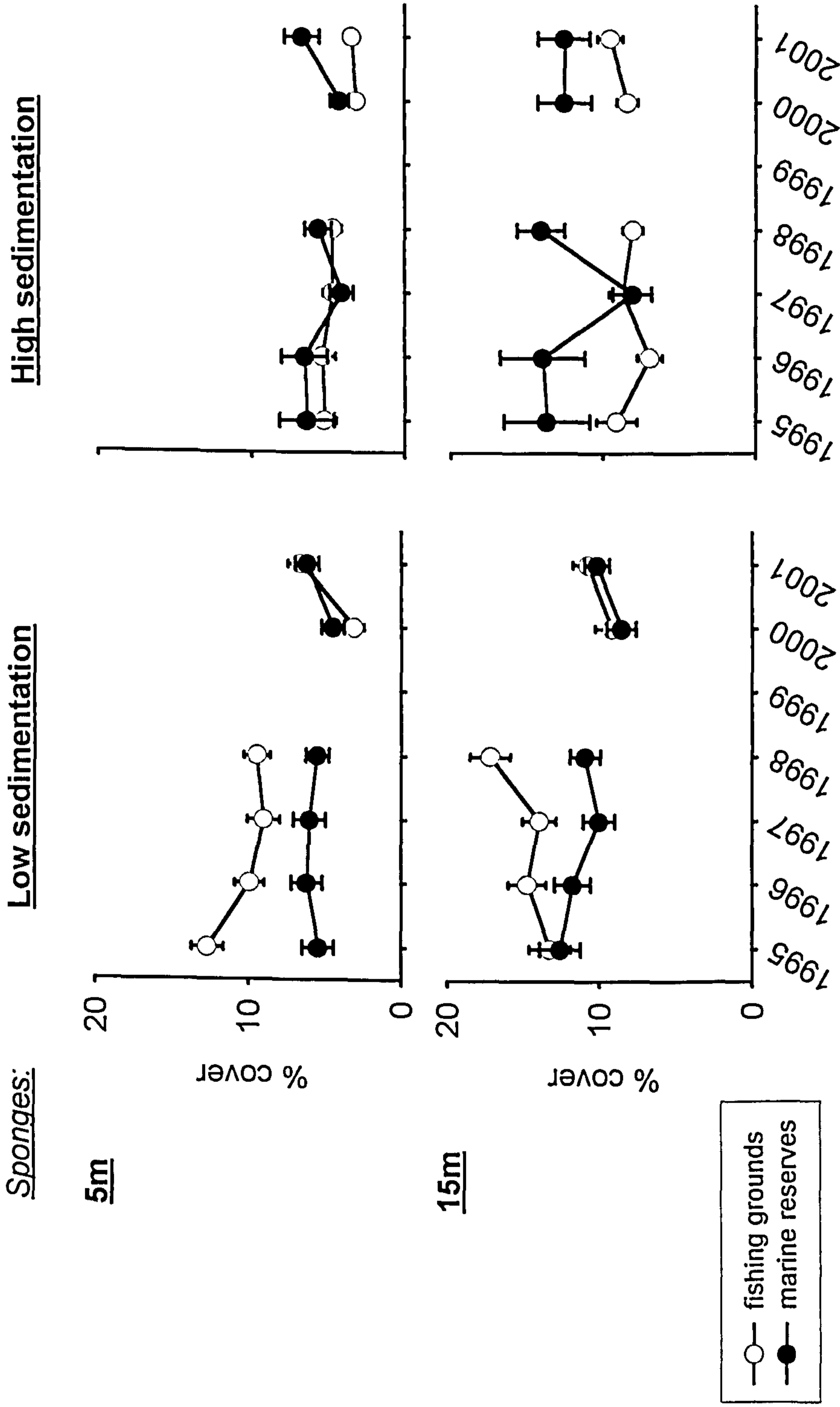


Fig. 23: Percentage sponge cover in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

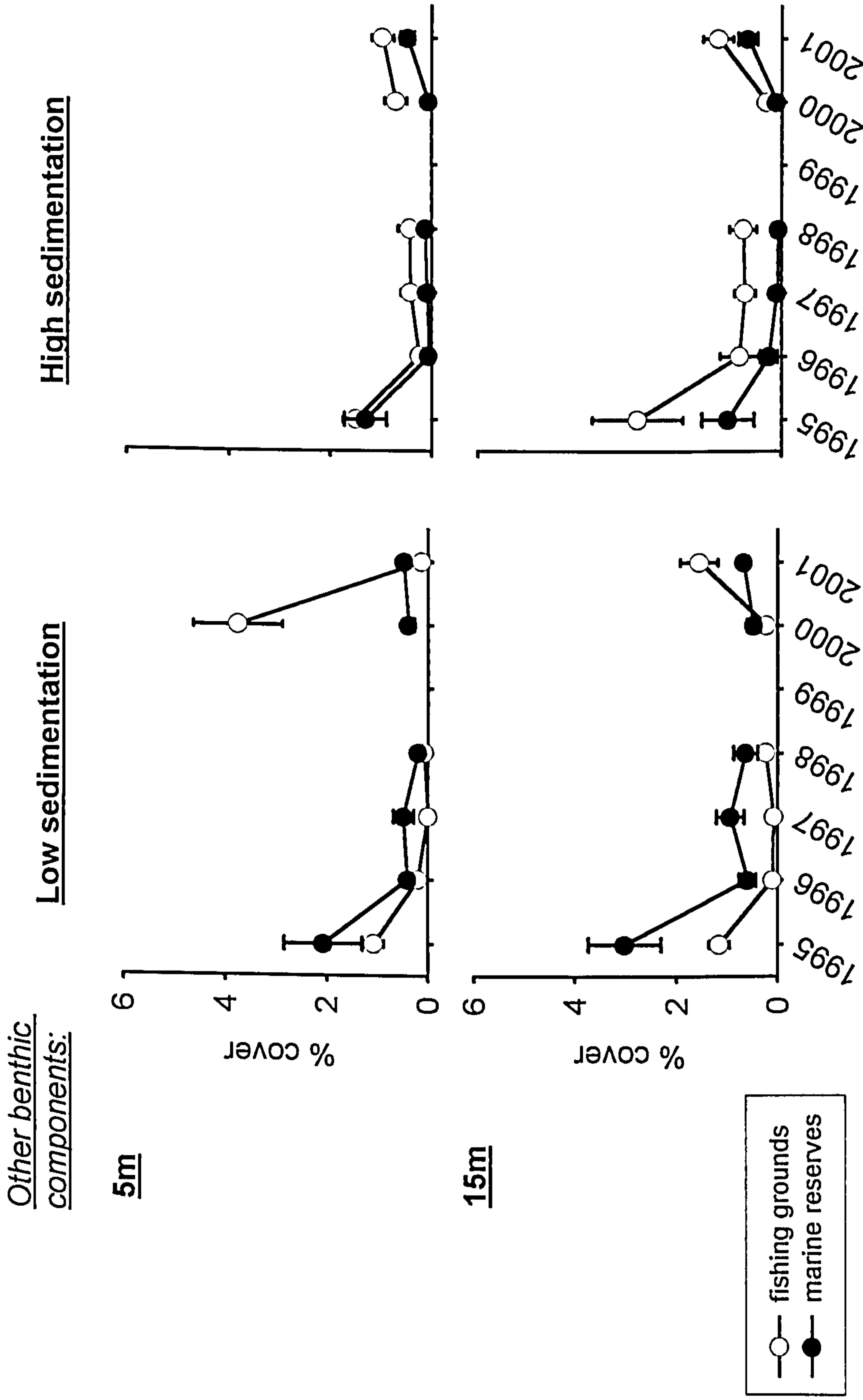


Fig. 24: Percentage cover of other benthic components in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

Cover of other benthic substrate components such as hydroids and ascidians was greater in deeper water and in the fishing grounds (Table 10, Fig. 24). Protection from fishing had no effect on the abundance of these 'other' benthic substrate components (Table 10, Fig. 24).

The interaction 'Protection Level' and 'Sedimentation Level' is significant for gorgonians, sponges and 'other' benthic components (Table 10). In the low sedimentation areas, gorgonian cover is higher and sponge cover is lower in the marine reserves than in the fishing grounds, whereas in the high sedimentation areas, gorgonians are more and sponges less common in fishing grounds than in the marine reserves (Figs. 22 and 23). Highest coverage of gorgonians occurs in the fishing grounds of the high sedimentation areas (Fig. 22). The difference between sponge cover is greater between the fishing grounds than between the marine reserves (Fig. 23). The abundance of 'other' benthic components is quite stable in all combinations, except in the marine reserves of the high sedimentation areas where it is much lower (Fig. 24). For gorgonians, sponges and 'other' benthic components, significant interactions between 'Depth' and 'Year' and 'Sedimentation Level' and 'Year' are due to different increases and decreases at 5m and 15m depth and between low and high sedimentation areas in the different years (Table 10, Fig. 22).

Bare substrate, rubble and sand

The non-living substrate component rubble showed higher coverage in fishing grounds compared to marine reserves (Table 11, Figs. 26). Bare substrate and sand is equally common in both fishing grounds and reserve sites (Table 11, Figs. 25 and 27). The interaction 'Sedimentation Level' and 'Protection Level' is significant for all three non-living substrate components (Table 11). In the marine reserves, bare substrate is equally common in the high and low sedimentation areas, but it is less common in the fishing grounds of the low sedimentation areas than in the fishing grounds of the high sedimentation areas (Fig. 25). Rubble covers more substrate in the marine reserves than in the fishing grounds in the high sedimentation areas, whereas in the low sedimentation areas more rubble

Table 11: Results of the four-way ANOVA analysis testing the effects of the factors depth (5m, 15m), sedimentation level (low, high), protection level (reserve, fishing ground), year (from 1994/5 to 2001) and their 2-way interactions on several independent reef factors.

Reef factors	Depth	Sed	Prot	Year	DxS	DxP	DxY	SxP	SxY	PxY
% bare substrate	5<15***	L<H***	FG>R ns	95<01***	ns	ns	p<0.001	p<0.001	p<0.001	ns
% rubble	5<15 ns	L<H***	FG>R***	95>01***	ns	p=0.001	p<0.001	p<0.001	p<0.001	ns
% sand	5>15***	L>H***	FG>R ns	95>01***	ns	p<0.001	p<0.001	p<0.001	p<0.01	p<0.001

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. *p≤0.05, **p≤0.01, ***p≤0.001, ns=non-significant. For sample sizes see Appendix 1.

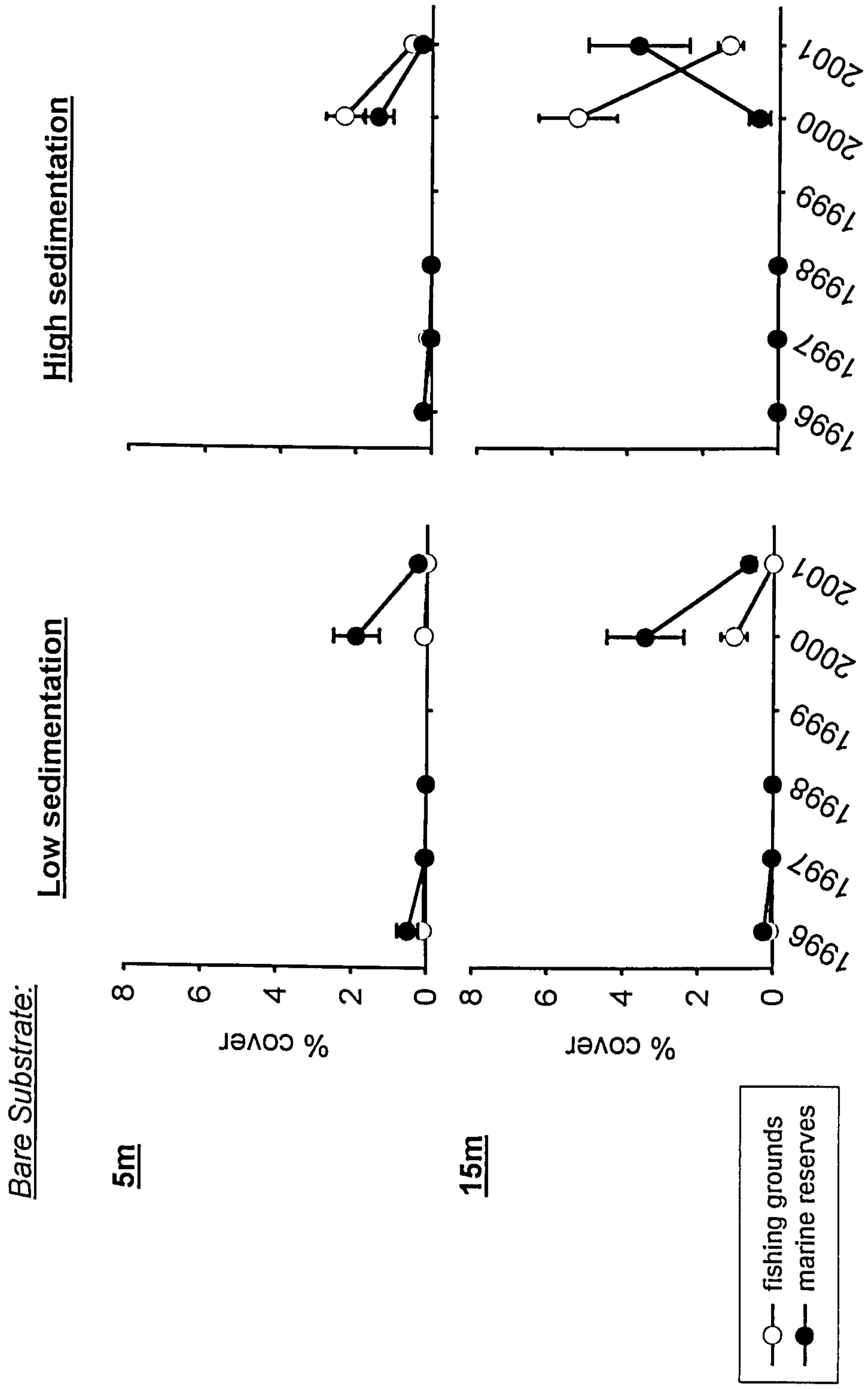


Fig. 25: Percentage bare substrate in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

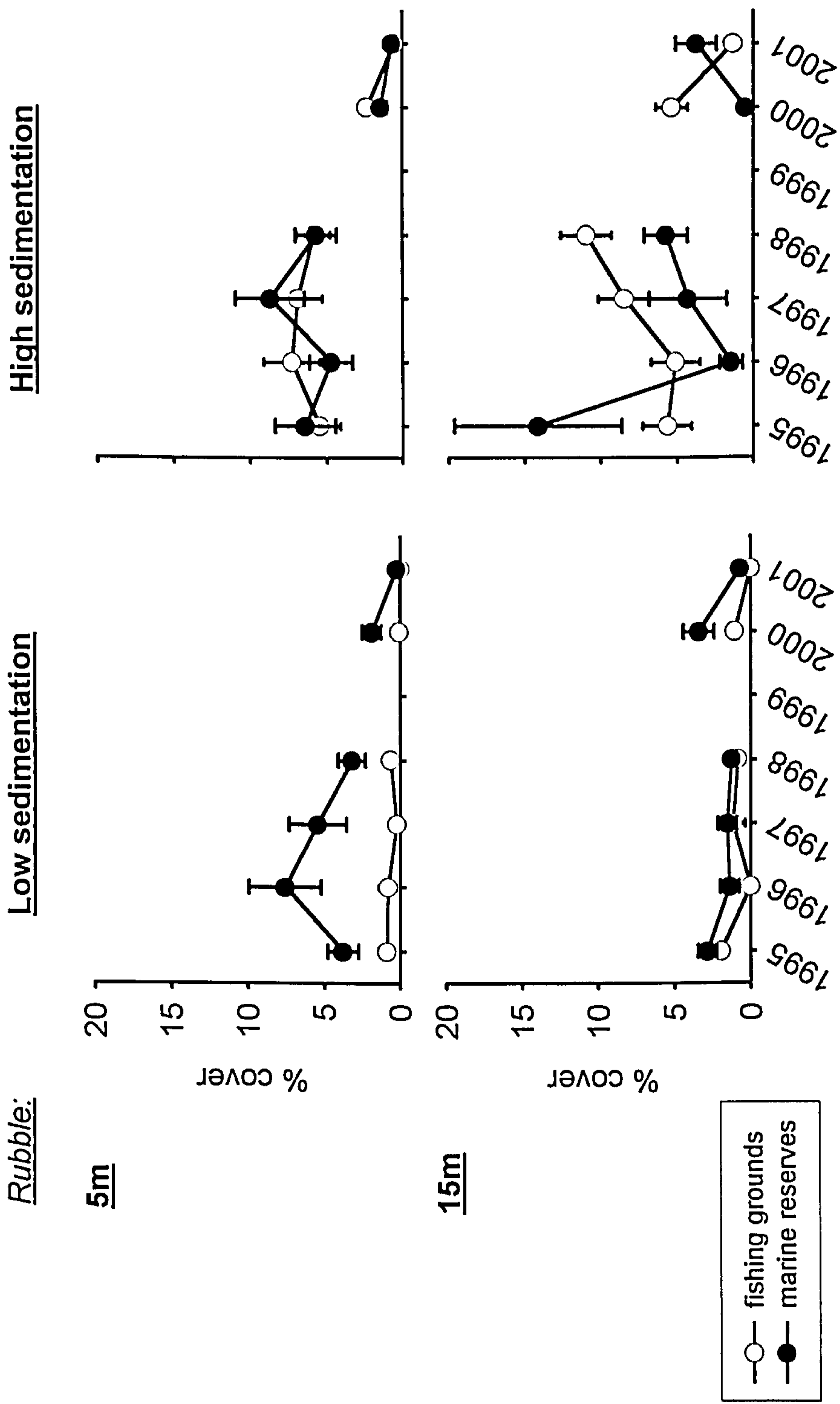


Fig. 26: Percentage rubble in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

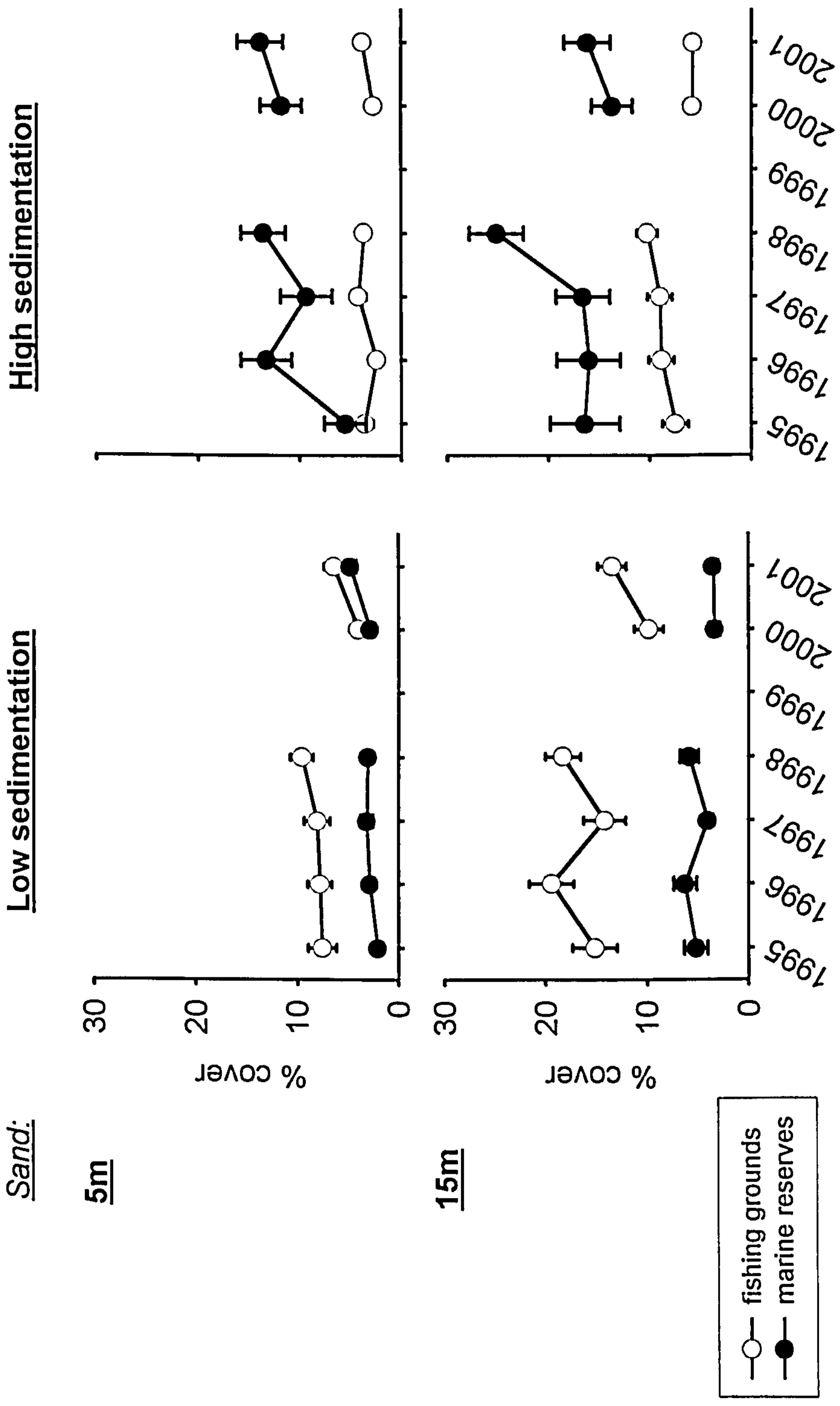


Fig. 27: Percentage sand in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

occurs in the fishing grounds than in the marine reserves (Fig. 26). Sand is more common in fishing grounds of the low sedimentation areas and in the reserves of the high sedimentation areas (Fig. 27). There was a lack of bare substrate up to 1998, but Hurricane Lenny in 1999 opened new space due to coral damage (Fig. 25). Sand and rubble decreased on some reefs after hurricane Lenny in 1999 (Figs. 26-27), probably because the sand and rubble pieces were transported into deeper water by strong wave activity. Both interactions 'Depth' and 'Year' and 'Sedimentation Level' and 'Year' were also significant for all three non-living substrate, which shows that from 1995 to 2001, abundance of non-living substrate differed between 5m and 15m depths and between the high and low sedimentation areas over the years (Table 11, Figs. 25-27).

Live loose coral fragments, branching coral breakages and health status of corals

Live loose coral fragments and the number of breakages did not differ between 5m and 15m depths and between fishing grounds and reserves (Table 12, Figs. 28-29). There was no significant difference in the number of breakages from 1995 to 2001 (Fig. 29). The lack of an increase in breakages after Hurricane Lenny in 1999 is probably because the branching coral populations decreased steeply in all sites from 1995 and, were at a level too low to show significant changes in breakage events (Table 12, Fig. 10). The number of live loose fragments differed significantly between years. Coral fragment numbers were stable in at both depths from 1995 to 1997. At 15m depth, the number of fragments decreased. At 5m depth, was highest in 1998 and then decreased again, shown by the significant interaction between 'Depth' and 'Year' (Table 12, Fig. 28).

Percentage cover of recently dead corals was generally very low during the study, apart from 1996 to 1997 at 15m in both low and high sedimentation areas when it increased steeply (Fig. 30). This was due to a disease outbreak (white plague type II and, to a lesser extent, black band disease) (Nugues 2002) and is evident in Figure 32, which shows the number of diseased corals. Additionally, the frequency of bleaching was highest in 1997 (Fig. 31). Sedimentation level had a significant effect on the percentage cover of recently dead corals, but not on coral bleaching and disease events (Table 12, Figs. 30-31).

Table 12: Results of the four-way ANOVA analysis testing the effects of the factors depth (5m, 15m), sedimentation level (low, high), protection level (reserve, fishing ground), year (from 1994/5 or 1996 to 2001) and their 2-way interactions on several independent reef factors.

Reef factors	Depth	Sed	Prot	Year	DxS	DxP	DxY	SxP	SxY	PxY
# broken corals / 1% branching coral cover	5<15 ns	L<H ns	FG<R ns	95>01 ns	ns	ns	ns	ns	ns	ns
# live loose coral frags / 1% bran. coral cover	5<15 ns	L<H *	FG<R***	95>01***	ns	ns	p<0.01	ns	ns	ns
% recently dead corals	5<15 ns	L<H***	FG<R***	95>01***	ns	ns	p<0.001	ns	p<0.001	p<0.01
% bleached corals	5>15 **	L<H ns	FG>R***	95>01***	ns	ns	p<0.001	p<0.001	p<0.01	p<0.01
# diseased corals / m ²	5<15 *	L<H ns	FG<R ns	95<01 ns	ns	ns	ns	p<0.05	ns	ns

D=depth, Sed/S=sedimentation, Prot/P=protection level, Y=year, R=reserves, FG=fishing grounds, L=low, H=high. *p≤0.05, **p≤0.01, ***p≤0.001, ns=non-significant. For sample sizes see Appendix 1.

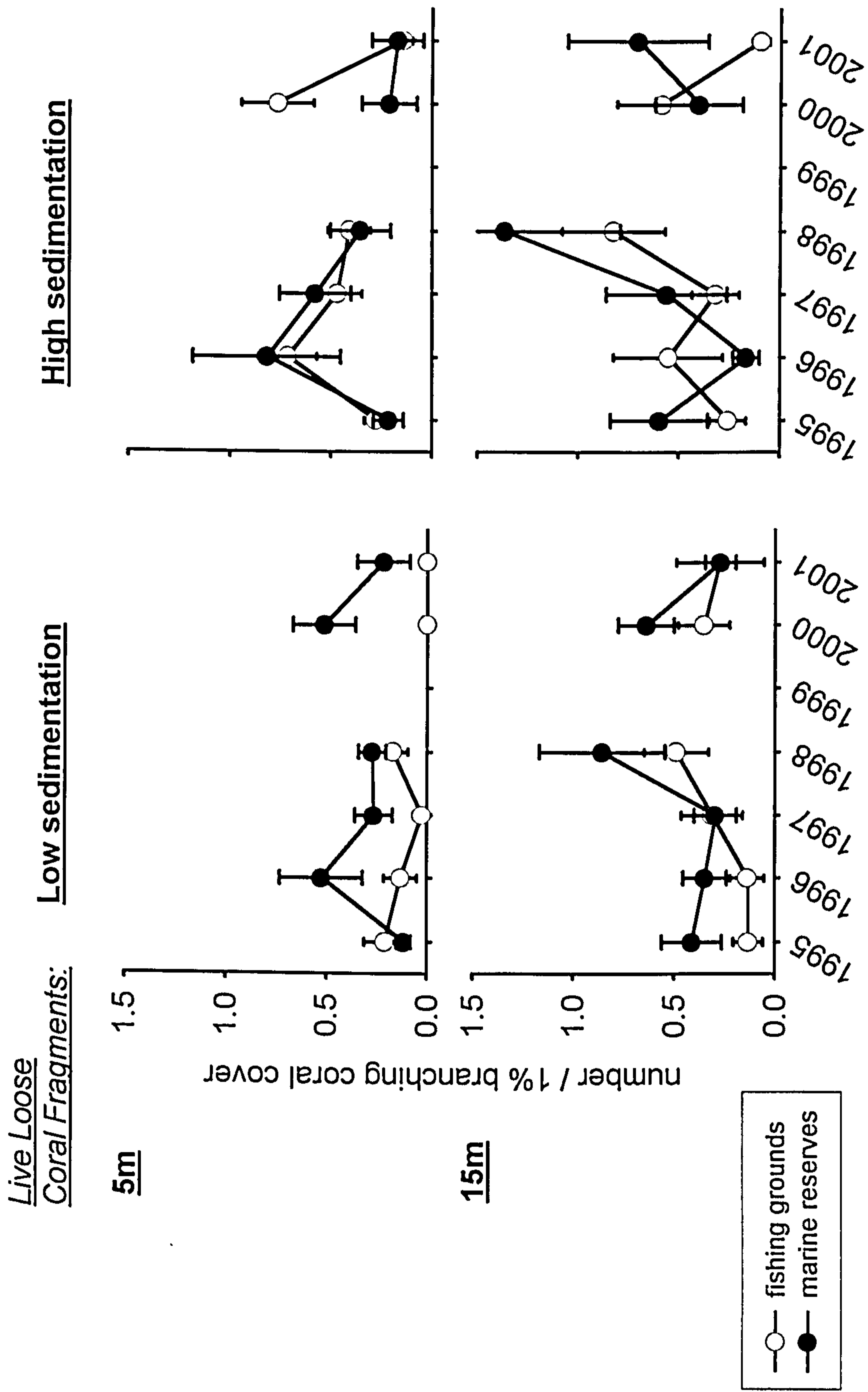


Fig. 28: Number of live loose coral fragments per 1% branching coral cover in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

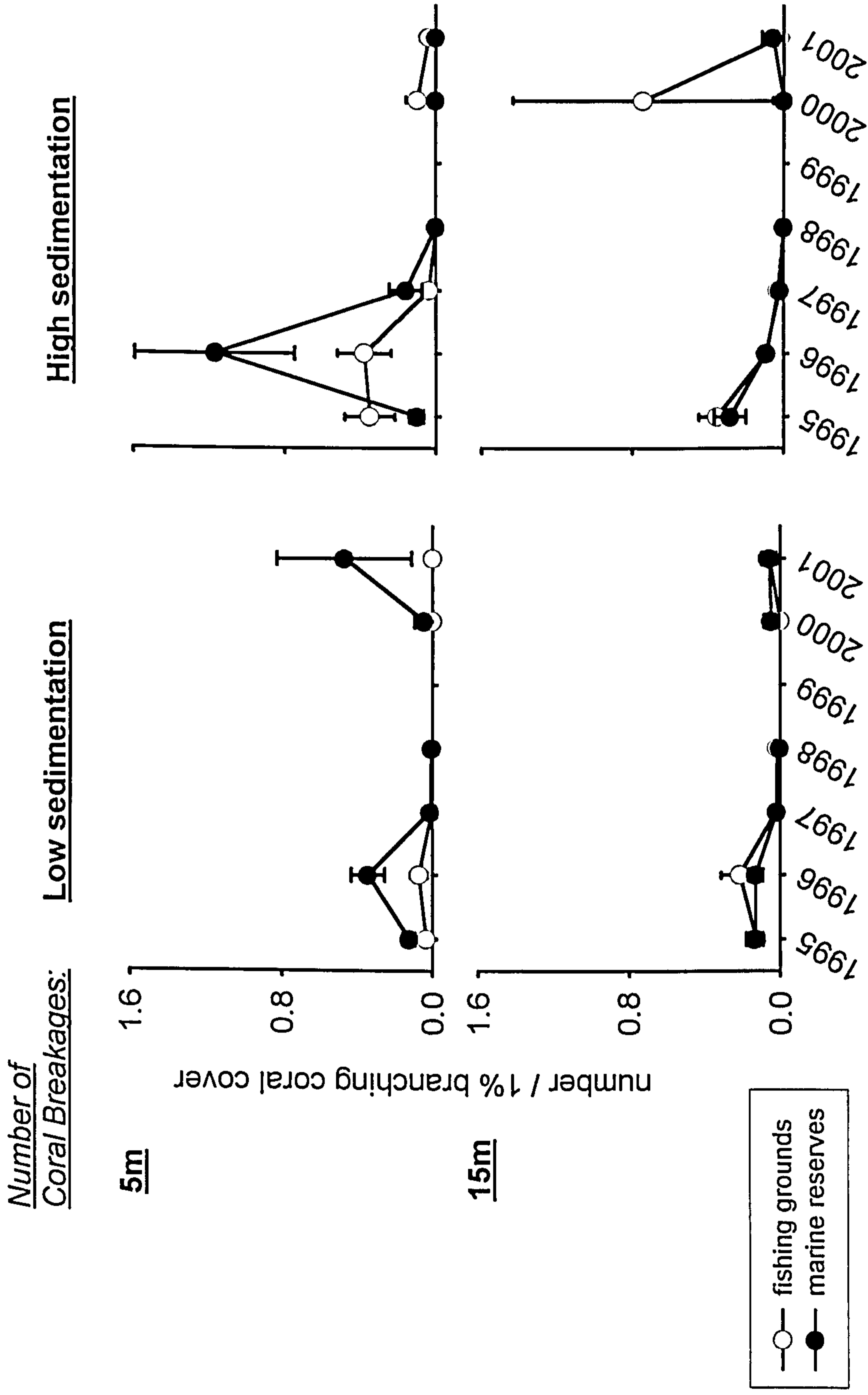


Fig. 29: Number of broken corals per 1% branching coral cover in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

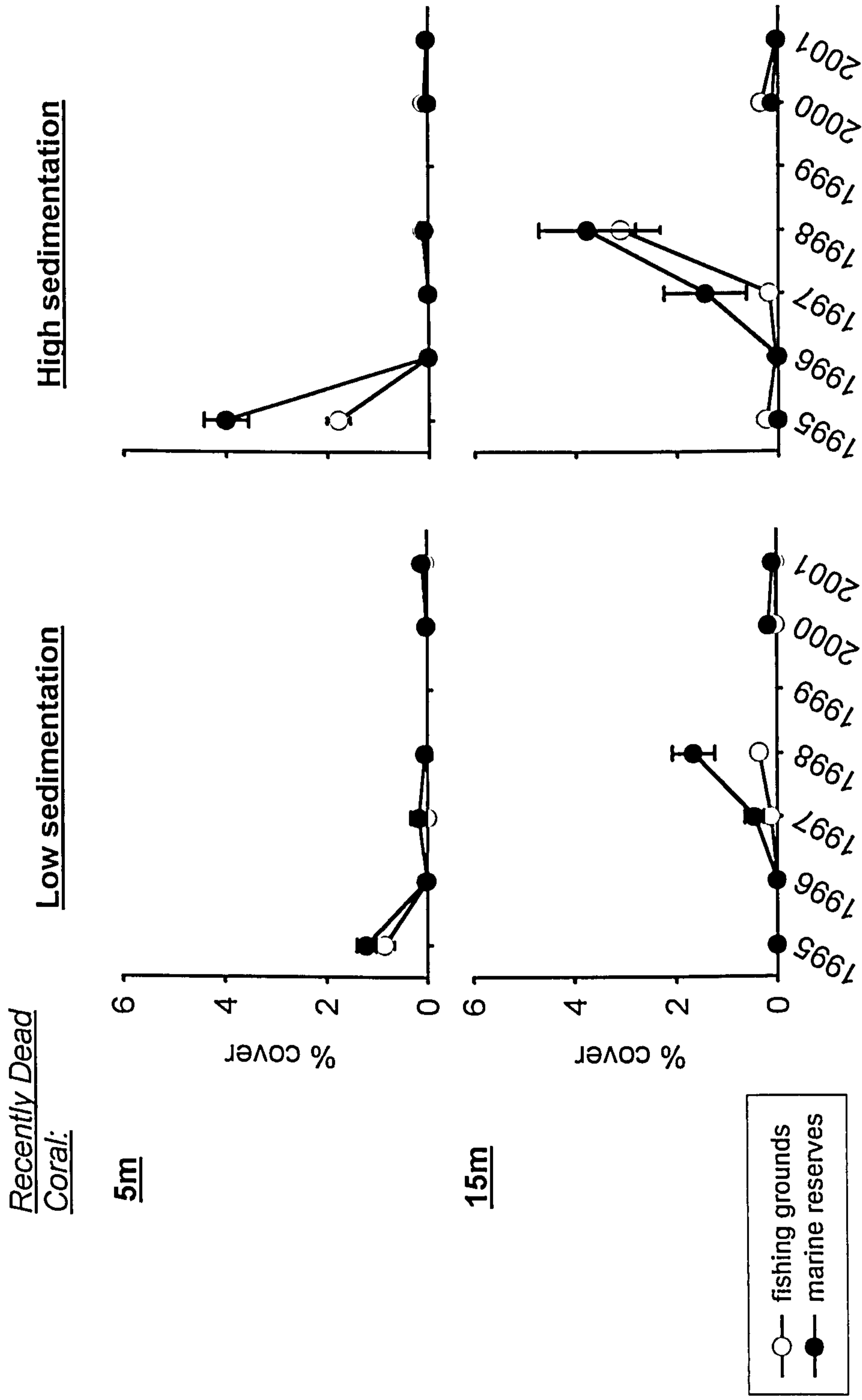


Fig. 30: Percentage cover of recently dead corals in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

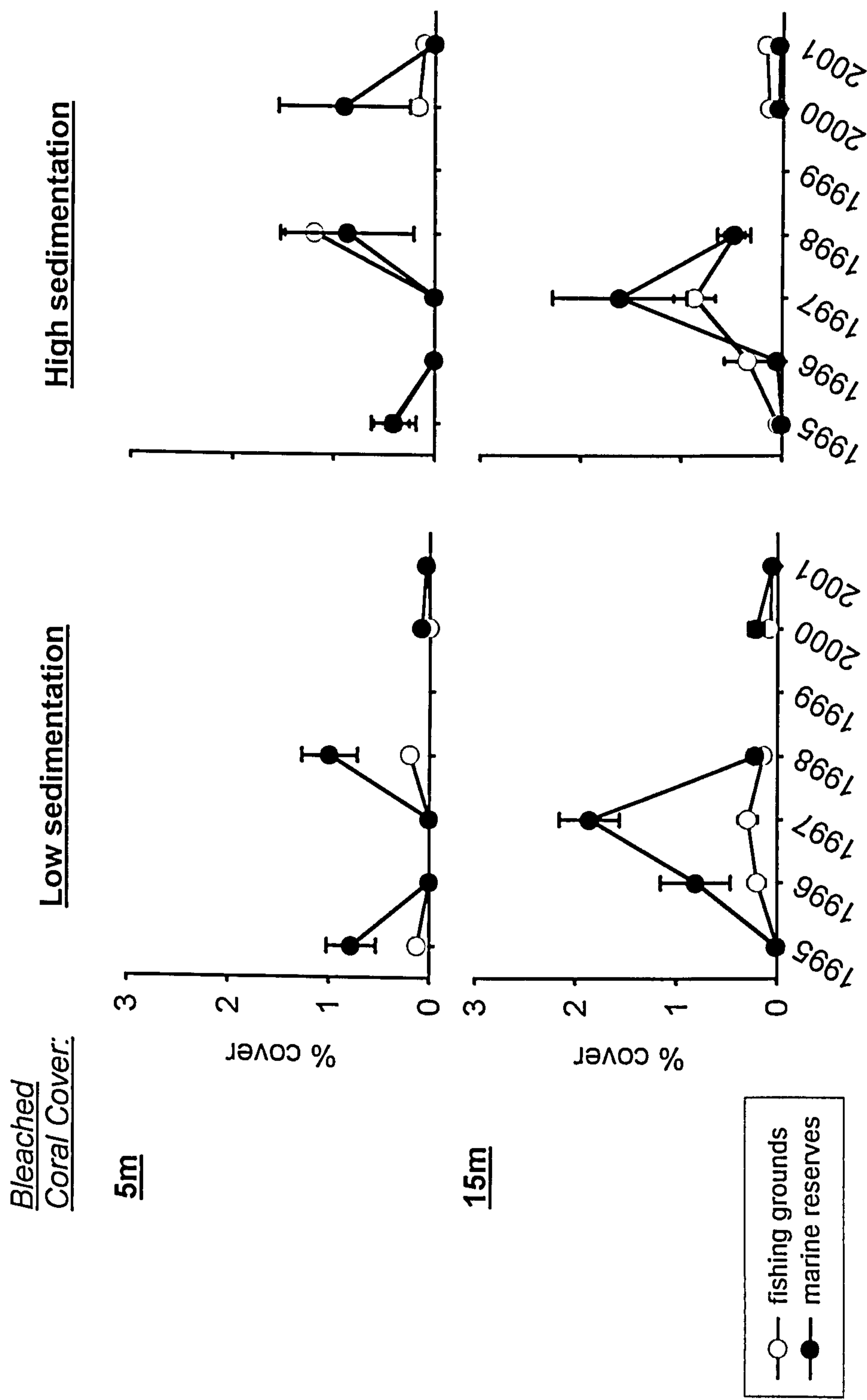


Fig. 31: Percentage bleached coral cover in low and high sedimentation areas in fishing grounds and marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

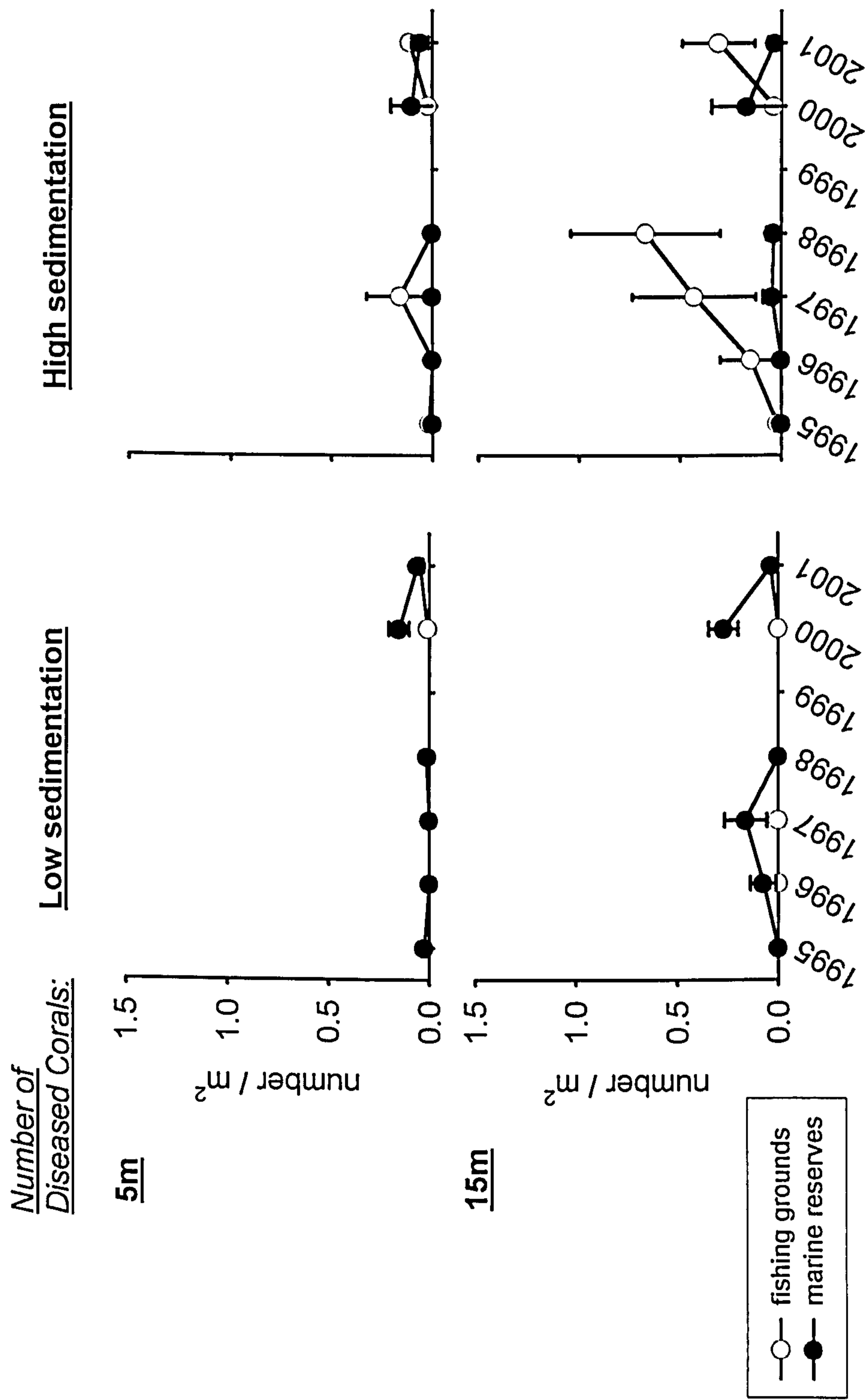


Fig. 32: Number of diseased corals in low and high sedimentation areas in fishing grounds marine reserves and in 5 and 15m depth from 1995 to 2001. Error bars represent one standard error.

Recently dead corals were found more often in high sedimentation areas (Table 12, Figs. 30-31). Less coral bleaching occurred in marine reserves, but there were more recently dead corals in marine reserves than in fishing grounds (Table 12, Figs. 30-31). The number of diseased corals did not differ between marine reserves and fishing grounds (Table 12, Fig. 32). The interaction 'Protection Level' and 'Sedimentation Level' was significant for percentage bleached and number of diseased corals (Table 12). Both bleaching and diseases occurred less in the fishing grounds of the low sedimentation areas than of the high sedimentation areas (Figs. 31-32). The percentage of bleached coral cover was quite similar in marine reserves of the low and high sedimentation areas, whereas the number of corals affected by a disease was slightly higher in the marine reserves of the low sedimentation areas than of the high sedimentation areas (Table 12, Figs. 31-32).

2.4.3 Coral cover changes and sedimentation rates

I calculated coral loss for 5m and 15m depth from 1995 to 1998 and from 1995 to 2001 by taking the difference in percentage total coral cover between 1995 and 1998 and between 1998 and 2001 (see Table 5). Coral loss is then expressed as absolute and relative loss (Figs. 33-36). The periods, 1995 to 1998 and 1995 to 2001, were examined separately to explore trends prior to and following the hurricane disturbance that occurred in 1999. Taking the full period from 1995 to 2001, there were no significant relationships between relative and absolute coral loss and sedimentation rates measured in sediment traps (Figs. 33-36). However, there were significant relationships between absolute and relative coral loss from 1995 to 1998 and sedimentation rate (25cm and 65cm traps). Coral loss decreased with decreasing sedimentation (Figs. 33-36). This shows that prior to Hurricane Lenny, there were clear damaging effects of sedimentation on coral cover. However, Hurricane Lenny in 1999 was responsible for a dramatic coral loss, which obscures these sedimentation effects when considering data from the full span of the study.

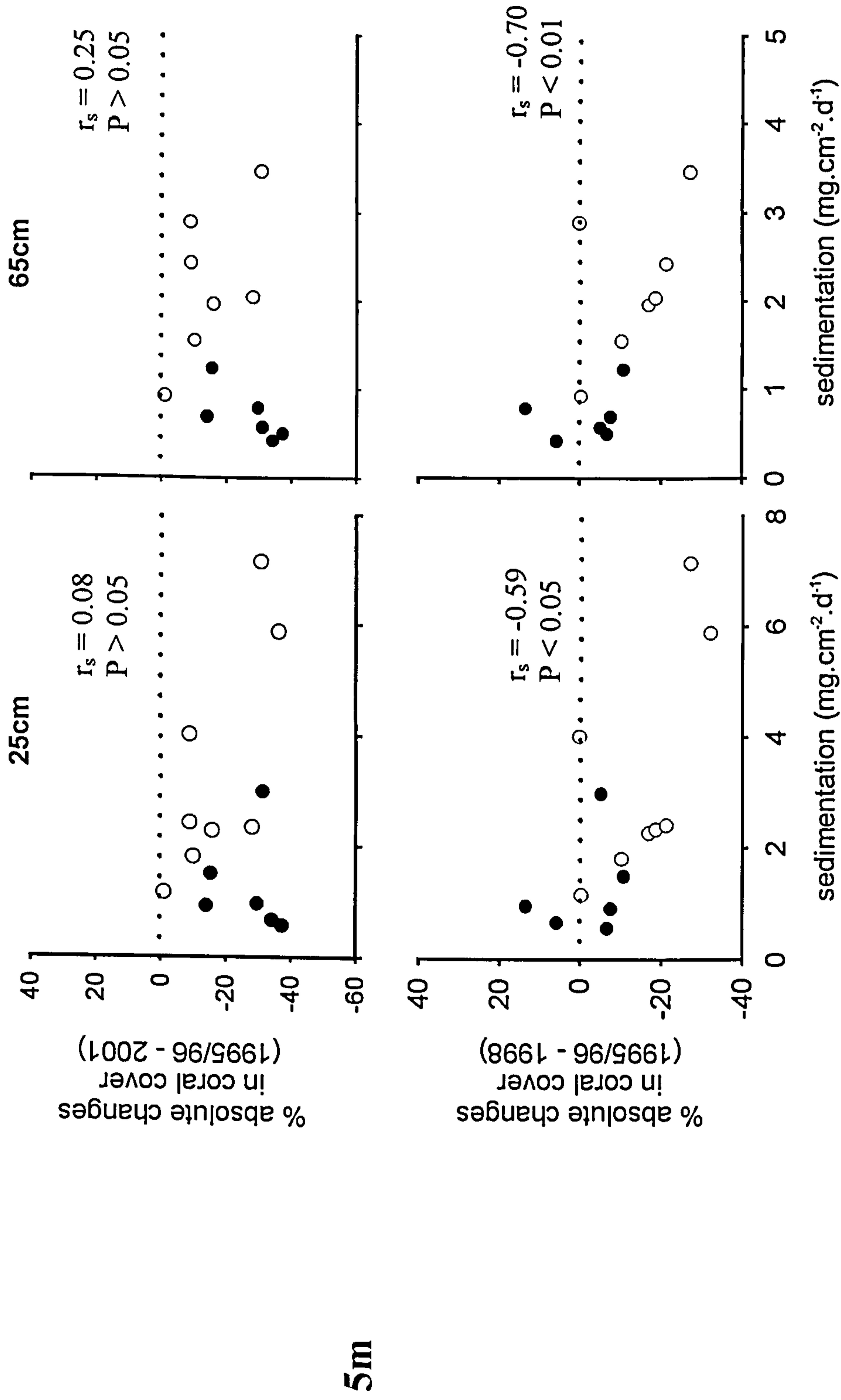


Fig. 33: Relationship between sedimentation rate (mg.cm².d⁻¹) of 25cm and 65cm traps and percentage absolute coral cover loss from 1995/96 to 2001 and from 1995/96 to 1998 in the sites with low and high sedimentation conditions at 5m depth. ● = low sedimentation, ○ = high sedimentation, r_s = Spearman correlation coefficient (n = 14).

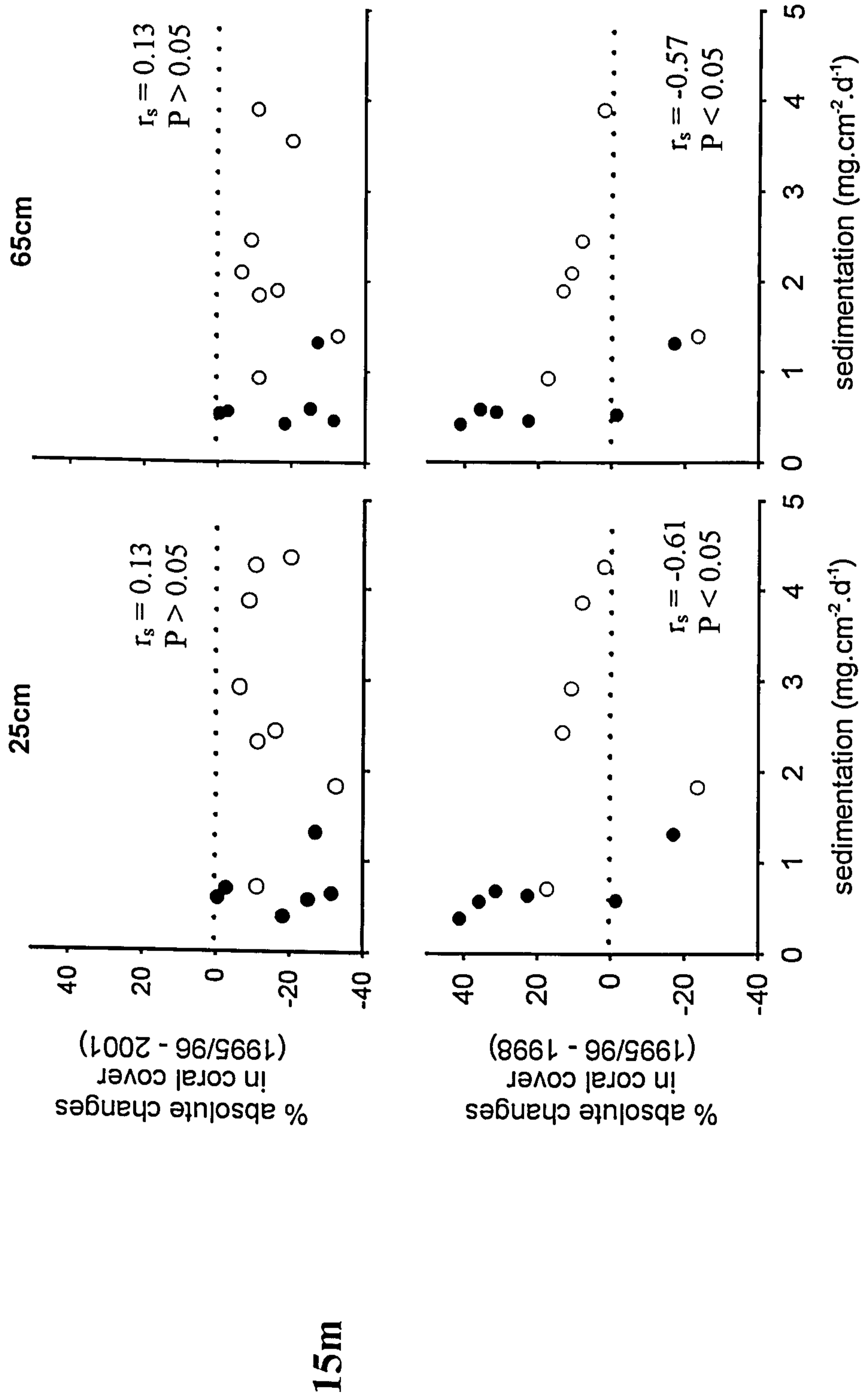


Fig. 34: Relationship between sedimentation rate (mg.cm⁻².d⁻¹) of 25cm and 65cm traps and percentage absolute coral cover loss from 1995/96 to 2001 and from 1995/96 to 1998 in the sites with low and high sedimentation conditions at 15m depth. ● = low sedimentation, ○ = high sedimentation, r_s = Spearman correlation coefficient (n = 14).

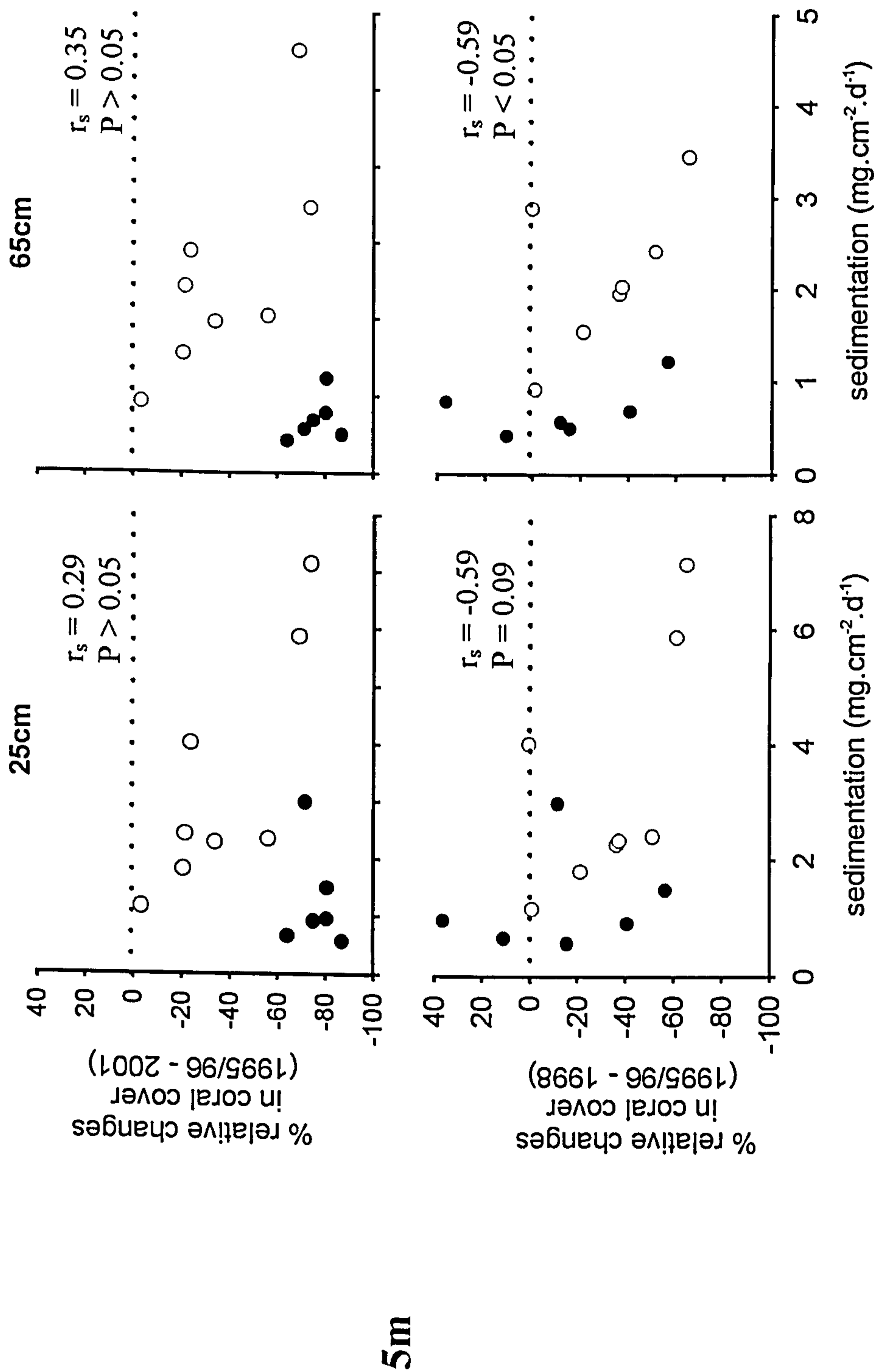


Fig. 35: Relationship between sedimentation rate (mg.cm⁻².d⁻¹) of 25cm and 65cm traps and percentage relative coral cover loss from 1995/96 to 2001 and from 1995/96 to 1998 in the sites with low and high sedimentation conditions at 5m depth. ● = low sedimentation, ○ = high sedimentation, r_s = Spearman correlation coefficient (n = 14).

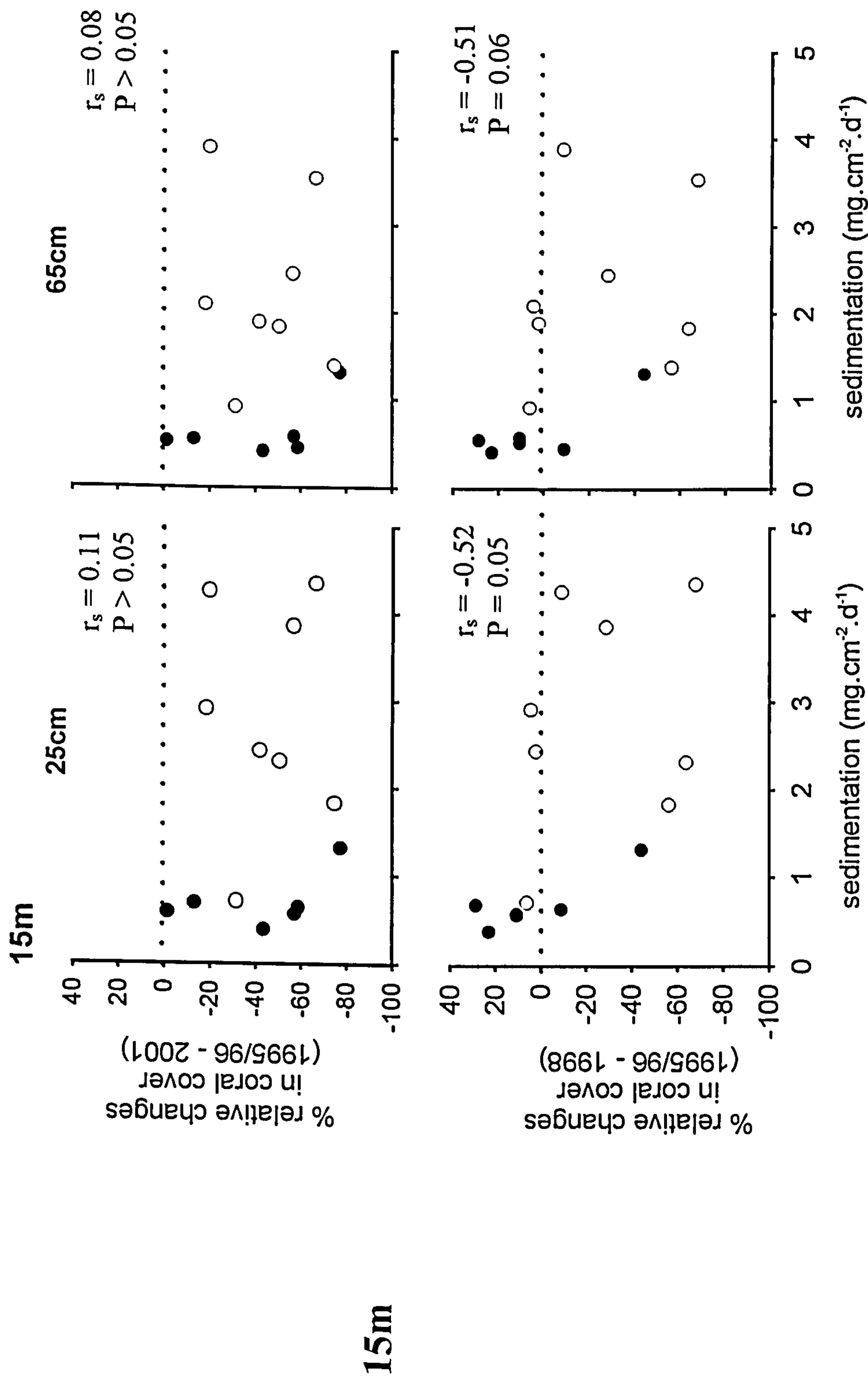


Fig. 36: Relationship between sedimentation rate ($\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) of 25cm and 65cm traps and percentage relative coral cover loss from 1995/96 to 2001 and from 1995/96 to 1998 in the sites with low and high sedimentation conditions at 15m depth. ● = low sedimentation, ○ = high sedimentation, r_s = Spearman correlation coefficient ($n = 14$).

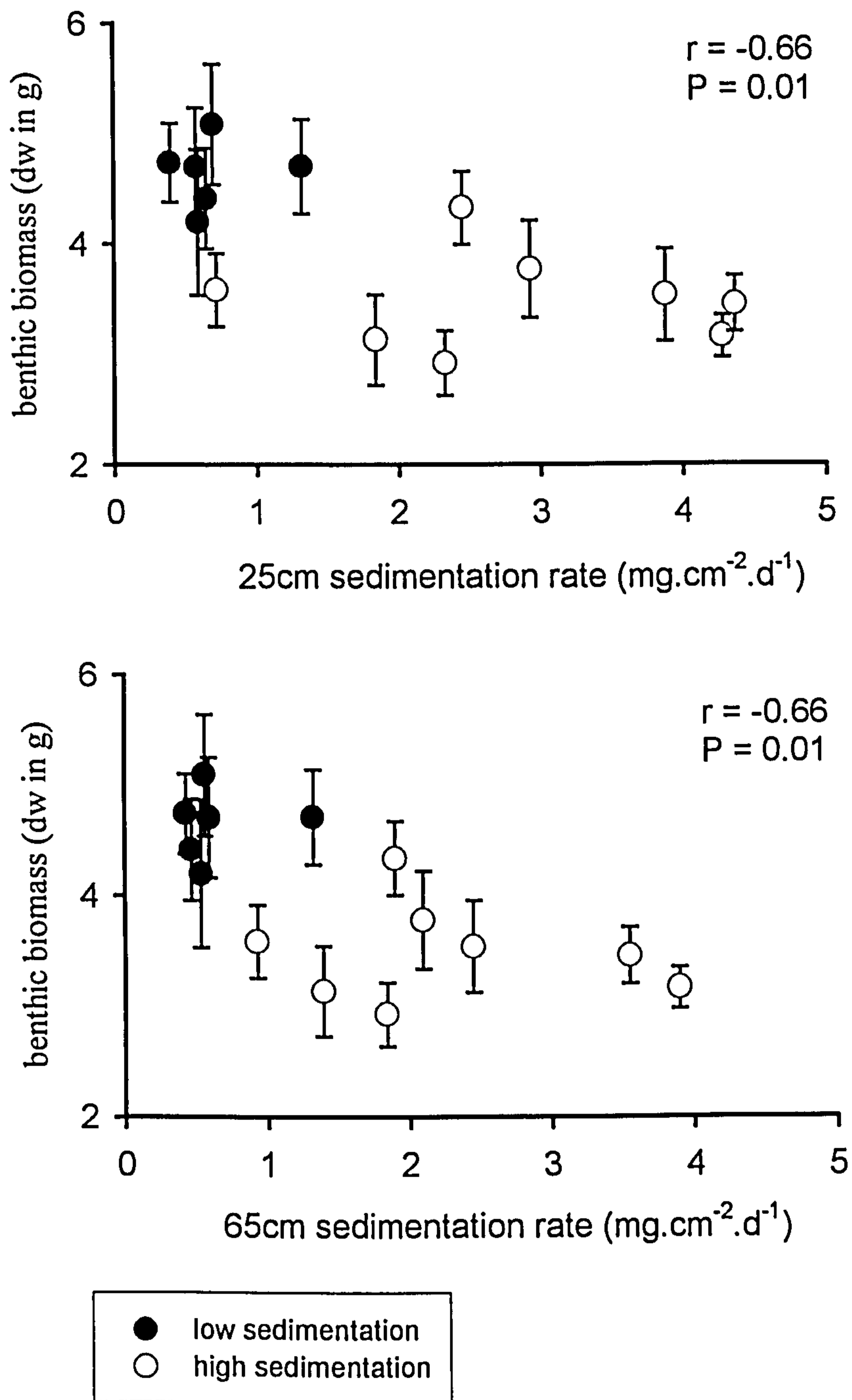


Fig. 37: Relationship between benthic biomass (dry weight (dw) in g) on high and low sedimentation reefs and sedimentation rate of 25cm and 65cm trap at 15m depth in low and high sedimentation reefs. Error bars represent one standard error. Pearson correlation coefficient is based on mean values per site ($n = 14$).

2.4.4 Biomass of benthic overgrowth

Benthic overgrowth of high and low sedimentation areas was measured at 15m depth only and included overgrowth by ascidians, hydroids but also, to a lesser extent macroalgae. Figure 37 shows that sedimentation had a strong negative effect on the biomass of benthic overgrowth. With increasing sedimentation the dry weight of benthic overgrowth decreased. The highest biomass of the different benthic substrate components occurred in the sites with low sediment input (Fig. 37).

2.5 Discussion

Like many other studies, my results show that storms and hurricanes have detrimental effects on coral cover (e.g. Woodley et al. 1981, Rogers et al. 1991, Bythell et al. 1993). Tropical storm Debbie in 1994 brought a lot of sediment that was washed off the land onto reefs on the west coast of St. Lucia causing immediate mortality of corals exceeding 50% at some sites (Sladek Nowlis et al. 1997). Sediment deposited onto reefs by Tropical Storm Debbie, continued to affect corals negatively due to resuspension effects and, hence, coral loss was higher in the high than in the low sedimentation sites (this Chapter, Nugues 2000). Hurricane Lenny in 1999 physically devastated many coral reefs in the study area and total coral cover declined steeply. Coral cover at 5m depth suffered in total a relative loss of 44%, and in deeper water a total relative loss of for 29%. Overall, the low sedimentation sites suffered far more damage by Hurricane Lenny than high sedimentation sites. In some shallow areas branching corals disappeared totally due to strong waves that also turned over large coral boulders. This opened up space for fast colonisation by algae. After Hurricane Lenny, algal cover increased by 48% at 5m and by 29% at 15m depth. This supports prior research documenting dramatic changes in benthic substrate composition favouring algal recolonisation after hurricane events (Woodley 1989, Rogers et al. 1991).

My results show that sedimentation in St. Lucia is a chronic pollution problem that has contributed to serious impacts on coral reefs over the study

period. Coral reefs closest to river mouths have been most affected, but also corals further along the coast line have suffered from sedimentation input from the rivers. In the high sedimentation areas, relative coral loss from 1996 to 1998, a period when natural disturbances were only moderate, was 3% at 5m depth and 19% at 15m depth. Coral loss at the low sedimentation sites in this period occurred only in shallow water (7%), whereas in deeper water I observed an increase in coral cover of 3%. In the study area, none of high sedimentation sites at 5m depth showed coral cover increases (Figs. 33 and 35). After Tropical Storm Debbie in 1994, three out of eight high sedimentation sites showed positive coral cover growth at 15m depth (Fig. 36). However, compared to increases of coral cover in the low sedimentation sites at the same time, the coral cover increases in the high sedimentation sites were much lower. Hence, even if sedimentation does not decrease the amount of coral coverage, it slows down reef growth. This is an especially detrimental effect since after uncontrollable destruction of reefs caused by, hurricanes for example, recovery of corals is essential to sustain the reef framework and processes. Hunter and Evans (1995) reported that recovery of coral reefs in Kaneohe Bay, Hawaii, occurred only after the chronic sewage discharge was diverted. This re-iterates that chronic pollution can prevent replenishment of coral reefs.

In St. Lucia, the establishment of marine reserves in 1995 are responsible for the rapid build up of fish stocks (Roberts et al. 2001). In six years herbivorous fish biomass tripled at 5m and 15m depths in the areas closed to fishing and in the adjacent areas fish biomass doubled at both depths (see also Hawkins in prep.). The SMMA is an important example showing that marine reserves are an effective management tool to rebuild exploited fish stocks and support the reef fishery (Roberts et al. 2001). However, do marine reserves also help in preventing or reversing phase-shifts?

In this study, greatest herbivorous fish biomass occurred in the marine reserves where blue-green and macroalgal cover was highest. Macroalgae may affect corals more severely compared to other functional algal groups by shading corals, preventing post-settlement survival and physically harming coral tissue when they are swept around with water movement (De Ruyter van Steveninck et

al. 1988, Barnes and Chalker 1990, Coyer et al. 1993, Miller and Hay 1996). Observations exist of herbivorous fish feeding on macroalgal as well as avoiding them (e.g. Randall 1967, Carpenter 1986, Lewis 1986, Morrison 1988, Choat 1991, McClanahan et al. 2001). However, species such as *Caulerpa* spp., *Laurencia* spp., *Dictyota* spp. and *Lobophora* spp. are reported to be moderately to highly herbivore resistant (Littler et al. 1983, Hay 1984b, Lewis 1986, Hay et al. 1987). All these species also occurred mainly on the low sedimentation reefs in St. Lucia (pers.obs., Nugues 2000), and previous research on my study reefs reported that grazing fish mainly avoid feeding on macroalgae in this area (Low 2000). This is further supported by the results of this study that show that macroalgal cover increased steadily over the years, even as the biomass of herbivorous fish did so too.

One further explanation for increased macroalgal cover despite increases in fish stocks might be that the storm and hurricane events in St. Lucia opened up areas for fast algal colonisation leading to the grazing capacity of herbivorous fish stocks being exceeded. Increased macroalgal cover after Hurricane Hugo hit coral reefs of St. John, British Virgin Island, was similarly reported by Rogers et al. (1991). This situation may have been further exacerbated by a levelling off or even decrease in herbivorous fish biomass after Hurricane Lenny (Fig. 23) as reported after other hurricanes in the Caribbean (e.g. Fenner 1991). However, in St. Lucia after Hurricane Lenny, there was only a delayed increase in macroalgal cover on low sedimentation reefs in fishing grounds at 5m depth. It seems more likely that macroalgal growth increased steadily over time, then exponentially due to rapid colonisation of free space opened by Hurricane Lenny.

Macroalgal cover was lower on reefs with high sedimentation disturbance. Therefore, it seems more likely that on the high sedimentation reefs sedimentation is a controlling factor preventing macroalgal growth confirming previous research by Nugues (2000). Generally, it may be possible that on reefs with extensive grazing fish stocks probably combined with high sea urchin abundance and low macroalgal cover, herbivores may inhibit the growth of macroalgae through unselective grazing, scraping off newly colonising macroalgae that are still small in size (Lewis 1986). Once macroalgae reach a particular size and develop

defence mechanisms, herbivores avoid them (Hay 1984a). This is also reflected in the significant interaction between protection from fishing and sedimentation level for macroalgae, that showed highest macroalgal cover in the fishing grounds of the low sedimentation areas. These are also the reefs where herbivorous fish biomass is lowest and, hence, macroalgae are able to flourish. From these results I can conclude that algae cannot be controlled by herbivorous fish grazing and we should consider a potential active and controlled removal of macroalgae as a management tool.

On several Caribbean reefs, a return of the grazing sea urchin *Diadema antillarum* has been reported (Hunte and Younglao 1988, Knowlton 2001). It seems that *D. antillarum* grazes on macroalgae avoided by herbivorous fish (Szmant 2001). This observation is supported by Edmunds and Carpenter (2001) who reported increased *D. antillarum* populations from Jamaican reefs leading to decreased macroalgal cover and increased abundance of juvenile corals. Williams and Polunin (2001) who surveyed macroalgal cover and grazer biomass at several locations in the Caribbean suggest that the herbivorous fish populations cannot control algal growth and argue that a reduction of macroalgal cover is only possible with *D. antillarum* population recovery. However, *Diadema* abundance was still very low on the reefs that I studied with highest numbers found at 5m and virtually non at 15m depth. After Hurricane Lenny, there was also a reduction in *Diadema* abundance in the 5m low sedimentation areas. This also corresponds with observations on Jamaican coral reefs where densities of *D. antillarum* fell in shallow areas after Hurricane Allen in 1980 and in areas of severe hurricane impact, urchins were almost eliminated (Woodley et al. 1981). Generally, I observed that *D. antillarum* occurred only in some sites where it was distributed in patches. Hence, it may be that the random quadrat sampling was not the best way to estimate the abundance or effects of *D. antillarum*.

Blue-green algae was the only functional algal group that was found in significantly greater abundance in the marine reserves compared to the fishing grounds. Blue-green algae is reported not to be common diet of herbivorous fish (Littler and Littler 1999, Low 2000). Furthermore, its cover was greater on reefs with low sedimentation levels. However, there might also be other factors than

sedimentation operating since I observed rapid colonisation of blue-green algae forming large mats after Hurricane Lenny in 1999, mainly in the low sedimentation sites where hurricane damage was concentrated. Increases in blue-green algae after hurricanes may be due to nutrients that are released from resuspended sediments (Rogers et al. 1997, Stimson and Larned 2000). Alternatively, blue-green algae may be an opportunistic algal group, which covers the bare space created by the wave activity of hurricanes faster than other algae (Woodley 1989). Similar observations have been made on the Great Astrolabe Reef in Fiji, where the green algae *Trichosolen* sp., colonised carbonate substrate newly exposed by Cyclone Gavin within two to three days (Littler and Littler 1999) and following the grounding of the freighter *Wellwood* on Molasses Reef in Key Largo National Marine Sanctuary, Florida, when there was a rapid recolonisation by *Trichosolen molassensis* (Littler et al. 1987). However, there is a lack of knowledge on the persistence of *Trichosolen* sp. since it remained beyond the several week observation periods in these studies.

The reason why massive and branching coral cover was lower in low sedimentation sites and fishing grounds, was that they suffered more severe damage by waves caused by hurricanes in 1995/1996 and 1999. Much of the decline occurred in shallow water, where waves inflicted high mortality on branching corals. One would expect to have seen an increase in coral rubble, especially after the destructive Hurricane Lenny in 1999. However, this was not the case, probably because the broken coral pieces were dumped on beaches or moved into deeper water by waves. This shows that strong waves, even if destructive, might be helpful in removing deposited sediment, sand and rubble from the reefs into deeper water.

Coralline algae are important for coral larval settlement (Morse and Morse 1984, see also Chapter 5) and may contribute to coral recovery through recruitment. Hunte and Wittenberg (1992) found lower coralline algae on artificial settlement plates installed on eutrophic reefs in Barbados, where coral larval settlement rates were also lower. Fabricius and De'ath (2001) showed that on reefs of the Great Barrier Reef crustose coralline algal cover was relatively higher on reefs with low sediment deposits. This inverse relationship between the

abundance of coralline algae and sedimentation has implications for organisms depending on coralline algae for settlement such as corals and for rates of reef calcification (Fabricius and De'ath 2001). However, on reefs in St. Lucia, coralline algae appeared unaffected by sedimentation. On the other hand, sediment particles may cover coralline algal substrate and could impact on settlement processes (Richmond 1997).

In Chapters 4 and 5, I investigate the effects of sedimentation on coral larval settlement on artificial and natural substrata in the same study area. My results indicate that the location in the bay is more important than sedimentation level. Lowest settlement rates were found in the inner regimes of bays (the closest locations to a potential source of sedimentation). However, since the location in the bay is linked to different sediment input, sedimentation might negatively affect the settlement process. This can have detrimental effects for reefs and may prevent reef recovery through new coral settlement after reefs fall victim to destructive storms and hurricanes. Porter et al. (2001) who studied loss and changes in Floridian reef coral communities observed relative losses of coral cover ranging between 7.2% and 43.9% over a period of seven years (1984 and 1991) without severe hurricanes. Sources of coral mortality that could be identified were black band disease and bleaching. Throughout their study they did not observe a single sexual settlement event in any of their permanent photoquadrats. Hence, they concluded that coral losses of this magnitude could not be sustained. Settlement rates on natural substrata in my study area averaged 21 settlers.m⁻².yr⁻¹ (see Chapter 5). This is higher than reported from other studies in the Caribbean. Hence, it remains open if St. Lucia's coral reefs may be on a trajectory towards algal domination (see also Chapter 5).

Gorgonians, sponges and other benthic reef organisms also occupy hard reef substrate, as corals do, and, hence, contribute to spatial competition (e.g. Aerts 1997, Fairfull and Harriott 1999). Protection from fishing had no apparent effect on sponges, gorgonians and other benthic reef organisms. Gorgonians have been reported to be little affected by sedimentation stress (see Rogers 1990). Reefs with greater swells and surf (as found in shallower water) were found to be more suitable habitat than lagoonal calmer areas (Sanchez et al. 1997) and even

increasing densities with increasing turbidity have been reported for gorgonians (Schroeter et al. 1993). I also found greater density of gorgonians in shallower water and on high sedimentation reefs supporting these observations.

In St. Lucia, sponges and other benthic components such as bryozoans, ascidians and anemones, are more common in deeper water and low sedimentation reefs. A contrary observation was made by Hunte and Wittenberg (1992) who used artificial settlement plates that were installed on reefs in Barbados along a eutrophication/sedimentation gradient to look at coral larval settlement. They found greater biomass of non-coralline organisms on high eutrophic/sedimentation reefs. The reason for the different results is not clear but may be because Hunte and Wittenberg estimated cover of non-coralline organisms on concrete block that had been exposed for three weeks, whereas I estimated coverage on natural reef substrata. Since I found higher coverage on low sedimentation reefs in St. Lucia, spatial competition pressure may be greater on these reefs and combined with a greater macroalgal abundance, survival and recovery of corals of the low sedimentation reefs may be limited.

After Hurricane Lenny in 1999, coverage of sponges was decreased at 5m and 15m depth. However, there is a slight trend in 2001 that sponge cover increased again. Fast recovery of sponges after physical destruction by Hurricane Gilbert in 1988 was also reported on reefs in Cozumel, Mexico (Fenner 1991).

A disease outbreak in 1997 on reefs in the study area killed 6.6% of total coral cover in eight months (Nugues 2002). This is also reflected in this study where data in 1998 showed highest number of recently killed coral colonies and number of diseased corals. Bleaching was also highest during that period. Nemeth and Sladek Nowlis (2001) found a positive relationship between sedimentation and bleaching events. They monitored reefs from 1997 to 1999 of St. Thomas, U.S. Virgin Islands, during coastal land development constructions that caused sedimentation rates up to $14\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ (Nemeth and Nowlis 2001). Average sedimentation rates in St. Lucia were much lower, even in the high sedimentation areas. Hence, sedimentation might have not been high enough to induce coral bleaching. Overall, more recently killed corals were found in high sedimentation areas, whereas percentage of bleached and number of diseased corals was

generally not affected by sedimentation. Consequently, cause of death of the recently killed corals is not known.

2.6 Conclusions

This study shows that St. Lucia's coral reefs suffer from chronic sediment pollution but also that hurricanes and storms have severe impacts on the survivorship of corals. Coral loss caused by sedimentation impact and storms is directly replaced by an increase in algal cover. Algae immediately take over new space opened by storm damage. While functional algal groups react differently to hurricane impacts, sedimentation stress and herbivorous fish grazing pressure, St. Lucia's coral reefs are turning into algal-dominated reefs linked to human-induced stress and natural catastrophes. Marine reserves are important management tools to increase overexploited fish stocks and could have a positive effect on total coral cover by helping control algal abundance and growth. However, it seems that the herbivorous fish populations in St. Lucia have not yet been able to control algal growth (see also Williams and Polunin (2001) for other Caribbean reefs). It may also be speculated whether six years are not long enough to increase fish stocks to a high enough level to have a significant impact in reducing algal cover.

One important observation of this study is that marine reserves do not protect from natural impacts such as heavy rain and hurricanes. Neither can marine reserves save coral reefs from chronic sedimentation. While increased herbivorous grazing may open new substrate for settlement, sediment particles depositing on the substrate could prevent this process. Hence, natural disturbances such as hurricanes can have a greater impact on stressed coral reefs than on reefs that are in an environment free of human influences.

2.7 References

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Chapter 3

The effects of human-induced sedimentation on juvenile coral assemblages

3.1 Abstract

The persistence of coral reefs depends on the balance between coral mortality and new coral growth and recruitment. Reef framework degradation arises when carbonate erosion exceeds carbonate deposition by framework building corals and coralline algae. Degradation may be a consequence of sedimentation, mainly caused from river run off. Several studies show that sedimentation inhibits settlement of coral larvae. In contrast, little is known about its impacts on juvenile coral assemblages. In this chapter I describe the density and diversity of juvenile corals at three locations (inbay, midbay, offbay) along four bays on the west coast of St. Lucia, West Indies, two exposed to river discharge (high sedimentation bays) and two not exposed (low sedimentation bays). The density of juvenile corals was significantly lower inbay, but did not differ between high and low sedimentation bays. However, there was a significant negative relationship between actual sedimentation rate and numbers of juvenile corals per location. The number of juvenile coral species was significantly lower in the high sedimentation bays compared to low sedimentation bays. I also found increasing densities of juvenile corals with decreasing sedimentation rates. This was linked

to an altered juvenile coral composition, probably towards more sediment tolerant species in areas of high sedimentation. *Agaricia agaricites* and *Porites astreoides* were the most abundant juvenile coral species in all four bays. In general, densities of juveniles of massive coral species (e.g. *Colpophylia natans*, *Meandrina meandrites* and *Diploria spp.*) were very low in all areas. With increasing adult coral cover I observed increasing numbers of juvenile corals, but there was a near significant opposite effect of algal cover. The impact of herbivorous fish on juvenile corals is not clear. The percentage of totally healthy juvenile corals (i.e. no signs of overgrowth by other organisms or disease) decreased significantly with increasing sedimentation. Also average size of the juveniles decreased with increasing sediment input. Thus sedimentation detrimentally affects coral recruitment, intensifying reef degradation.

3.2 Introduction

Coral reefs represent one of the most diverse ecosystems on earth (Williams 1983, Reaka-Kudla 1995) and are among the most threatened (Birkeland 1997, Wilkinson 2000, Spalding et al. 2001). They are becoming degraded world-wide through excessive human use and the consequences of land use conversion. The major human-induced threats to coral reefs in recent times are over-fishing, sedimentation as a result of terrestrial erosion, coastal development and dredging, and nutrient pollution from sewage and agricultural run-off (Roberts 1993, Ginsburg 1994). Global climate change causing rising sea temperatures is a further severe stress to reefs leading to coral decline world-wide (Podesta and Glynn 1997, Sheppard 1999, Souter et al. 2000, Wilkinson 2000).

In many parts of the Caribbean, over-exploitation of herbivorous fish, combined with the mass mortality of the herbivorous echinoid *Diadema antillarum* due to a disease epidemic in 1983/84 (Lessios et al. 1984, Lessios 1988), has decreased grazing pressure on reefs. These events led to release of algae from grazing pressure resulting in phase shifts from coral to algal dominance on many reefs in the Caribbean (Done 1992, Hughes 1994). In addition, increasing levels of nutrients in coastal waters encourage algal rather

than coral growth (Lapointe 1997) and most corals thrive best in low-nutrient tropical water due to their symbiosis with zooxanthellae (dinoflagellate symbiotic algae that live in the coral tissue) (Muller-Parker and D'Elia 1997). The consequences are loss of biodiversity and reduced secondary production (Done 1992). Phase shifts may be compounded by the effects of sedimentation (Johannes 1975, Rogers 1990, Richmond 1993).

Many studies have reported a decline in the number of species and coral diversity with increasing sedimentation as well as a decrease in coral abundance (Van Moorsel 1985, Tomascik and Sander 1987a, Hunte and Wittenberg 1992). Reef degradation due to excessive sedimentation occurs in different ways: (a) corals are smothered by sediment leading to partial or whole mortality of the coral colony (see Rogers 1990), (b) inhibited reproduction (Kojis and Quinn 1984, Tomascik and Sander 1987b), (c) corals are weakened and become more susceptible to disease or other environmental changes due to tissue damages by abrasion of sediment particles and reduced photosynthesis from falling light levels (Rogers 1983), (d) reduced growth rate (Cortès and Risk 1985, Tomascik and Sander 1985), and (e) coral larval settlement is unsuccessful due to the sediment layer that covers the benthic substrate (Tomascik and Sander 1987b, Babcock 1991, Tomascik 1991, Te 1992, Wittenberg and Hunte 1992).

Most hermatypic corals have some form of sediment rejection ability (Bak 1978). To expel sediment particles, they have developed different mechanisms such as tissue expansion by uptake of water through the stomodeum, tentacular movements, ciliary action, and mucus production (Stafford-Smith and Ormond 1992). This constant energy expenditure by corals to remove sediment particles, combined with the reduction in light caused by suspended particles might be the main reasons for decreased growth rate and reproduction in sites with high sedimentation rates (Tomascik and Sander 1985, Edmunds and Davies 1989).

Even at low levels, sub-lethal to adult coral colonies, sedimentation may be detrimental to juvenile corals (Hodgson 1990a, Wittenberg and Hunte 1992, Richmond 1997), while algae are still thriving (Sammarco 1980, Van Moorsel 1985). Some studies have shown that small rather than large colonies are more susceptible to sediment (Hughes and Jackson 1985, Van Moorsel 1985,

Wittenberg and Hunte 1992, Connell et al. 1997), while others argue that smaller colonies can rid themselves more efficiently of sediment particles (Dodge and J.R. 1977).

Filamentous algae play an important part in sediment-affected areas by trapping sediment particles among their fronds, making the substrate less suitable for successful coral larval settlement (Walker and Ormond 1982, Birkeland 1988, Stafford-Smith and Ormond 1992). Herbivore grazing might enhance the survival of juvenile corals by removing algae (Harriott 1983, Rogers et al. 1984, Done 1992, Wittenberg and Hunte 1992).

The long-term vitality of coral reefs is dependent on new coral settlers and their survival. Just as forests will senesce if there is no regeneration from seeds, so also will coral reefs decline if recruitment ceases or falls below replacement rates. The sensitivity of the early life history process of corals to agents of reef decline, such as sedimentation and algae, are crucial to the resilience of reefs. The process of reef degradation is perhaps most likely to be seen first at the coral recruitment stage. In the longer term phase shifts may move the balance from calcium carbonate deposition (coral growth) to erosion, threatening the entire reef system (Done 1992, Sheppard et al. 2002).

In this study I investigate patterns of juvenile coral abundance, composition, average size and health status along reefs of two bays with high sedimentation and two with low sedimentation in St. Lucia, Eastern Caribbean. Furthermore, I analyse the effects of the abundance of herbivorous fish and urchins, living coral cover and algal cover on the juvenile coral assemblages.

3.3 Material and methods

3.3.1 Study sites

The study was conducted on fringing reefs and reef patches along the west coast of St. Lucia, West Indies. Study sites were selected on three nearshore to offshore stretches of an 11km long coastline within the Soufrière Management Area (SMMA) and on one nearshore to offshore stretch within the Anse La Raye area

7km to the north (Fig. 1). These four stretches are referred to as bays. The Soufrière and Anse La Raye/Anse Galet rivers provide two bays with high sedimentation inputs (H1 and H2), and two bays do not have any significant direct sediment input by rivers (L1 and L2). In each bay, I selected three locations, one closest to the head of the bay (inbay), one at the mouth of the bay (offbay) and one location between the inbay and offbay locations (midbay) (Fig. 1). Along the Soufrière high sedimentation bay five study locations (inbay, in-mid, midbay, mid-off, offbay) were established (Fig. 1). The inbay locations are characterised by calmer water whereas at the offbay locations wave exposure and currents can be strong. For the high sediment bays, the inbay locations were closest to the river mouth and the offbay locations furthest from it.

3.3.2 Sediment traps

In August 1997 sediment traps were set up at all of the above sampling locations (Fig. 1). At each location, two sets of sediment traps were established at 15m depth, consisting of 4cm diameter PVC plastic tubes with a height to width ratio of 4, as recommended for cylindrical traps with an internal diameter of 21-57mm by Blomkvist and Kofoed (1981) and Gardner (1980). The two sediment traps per set were fixed at 25cm and 65cm above the substrate. The differing heights of the traps allow the effects of sediment resuspension to be separated from new inputs. For this study the data from the lower trap were used since coral communities are affected by both new sediment input and sediment resuspension and the lower trap integrates these effects. The sedimentation rate measured from 1997 to 1999 was analysed by suction filtration of deposits through weighed filter papers (55 μ m, Whatman No. 1 papers), air dried for at least 24 hours and then weighed. Eleven sediment samples were collected from each set of traps at two week intervals during four trips spread over a period of 18 months. The mean deposition rate for each site is used in analyses in this study.

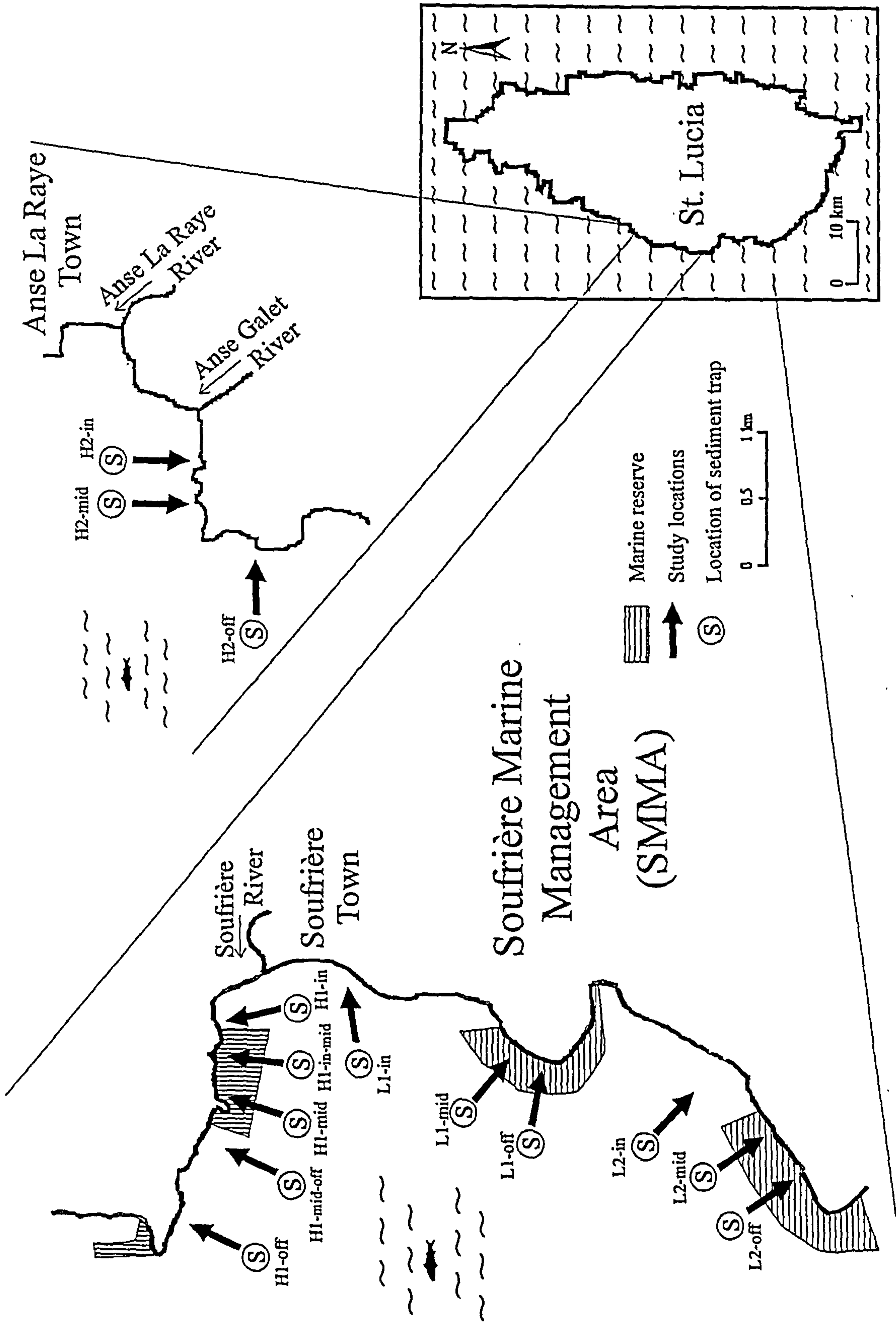


Fig. 1: Map of St. Lucia showing the study areas with the four bays (L1, L2, H1 and H2), sedimentation trap locations (S), study locations (black arrows: in-bay, in-mid, midbay, mid-off, offbay), marine reserves and the river systems.

3.3.3 Sampling of juvenile corals

Data on juvenile corals were collected between November and December 1998 by sampling with randomly placed 60 x 80cm quadrats on the reef at 15m depth using SCUBA. At each site a minimum of 12 quadrats were sampled. Quadrats having over 50% coral cover of one species, sand or rubble were not sampled because coral larvae require non-living hard bottom to settle. In each quadrat the number of juvenile corals was recorded and each individual identified, where possible, to species level. A juvenile coral was defined as primary polyps and intact coral colonies with a diameter of 40mm or less (Bak and Engel 1979). Juveniles of *Agaricia spp.* and *Scolymia spp.* could only be identified to the generic level. Solitary polyps of the genera *Scolymia* and *Mussa* are very much alike, as are those of *Manicina* and *Colpophyllia* (Bak and Engel 1979). These genera were, respectively, grouped (referred to as *Scolymia* and *Colpophyllia*). Also *Montrastrea annularis*, *M. faveolata* and *M. franksi* could not be identified separately and are grouped as *M. annularis*.

Only the greatest diameter of every recruit was measured, to the nearest millimetre, since most juveniles were approximately circular in outline (Wallace 1983). Additionally, I noted whether the juvenile coral was totally healthy, or if it had signs of overgrowth by other organisms or algae, disease infection, bleaching or physical damage.

3.3.4 Benthic substrate composition (coral and algal cover)

Surveys of the benthic substrate composition were undertaken at the same time and at the same locations as the survey of the assemblages of juvenile corals. Coral and algal cover were estimated visually using randomly placed 1m²-quadrats at 15m depth. The distances between quadrats (1-5m) were determined using computer-generated random numbers. The minimum sample size per location was 12 quadrats. Sand bottoms and dense monospecific *Madracis*

mirabilis and *Porites porites* coral beds were not included because these substrata were unavailable for coral larval settlement. In addition, I noted the number of sea urchins (*Diadema antillarum*) found in each quadrat.

3.3.5 Abundance of herbivorous fish

Data on abundance of herbivorous fish were collected in July 1998 at the same study sites. Using a modification of the stationary point count method developed by Bohnsack and Bannerot (1986), demersal fish were counted using SCUBA at 15m deep. A tape measure 10m long was placed across the reef at the point to be counted and all fishes observed within or passing through a 5m radius of the centre of the tape, extending upwards for 5m in a cylinder above the reef, were counted during a 15 minute period. The lengths of individuals present (parrotfish, Scaridae, and surgeonfish, Acanthuridae) were estimated visually to the nearest centimetre. For the data analysis, combined biomass of the herbivores present was calculated from length-weight equations in Bohnsack and Harper (1988).

3.3.6 Statistical analysis

3.3.6.1 Sedimentation

Differences in sedimentation rate were tested using a nested three-way analyses of variance (ANOVA). The factors analysed were the 'Sedimentation level' (high and low), 'Location' (inbay, midbay, offbay) and 'Bay' (L1, L2 and H1 and H2) which was nested in 'Sedimentation level'. Data were ln-transformed to fulfil the assumptions of normality and homoscedasticity. Significant differences between more than two groups were tested with Tukey's *post hoc* test (Zar 1996).

3.3.6.2 Juvenile density and species' abundance

After testing the data for homogeneity of variances (Levene's test, $P > 0.05$) and normality (Kolmogorov-Smirnov test, $P > 0.05$), data for the number of juvenile corals were $\sqrt{(x+0.5)}$ transformed. Nested two-way ANOVA were carried out using the general linear model (GLM) for unbalanced data to test the null hypothesis of no differences in mean juvenile coral density or species richness (number of species) between the high and low sedimentation bays and between the locations (inbay, midbay, offbay) of the bays. Two locations of the Soufrière bay (H1 in-mid, H1 mid-off) were excluded from this analysis in order to equalise the sample sizes for all locations. Tukey's post-hoc test was performed to distinguish significant levels of the factors (Zar 1996). In addition, Spearman rank-order correlation tests were carried out between sedimentation rate and the mean numbers of juvenile corals and juvenile coral species.

3.3.6.3 Juvenile coral species composition

Data were ordinated using a principal co-ordinate analysis (= classical scaling) available in the R-package computer program which has both similarity and distance measures (Legendre and Legendre 1983, Legendre and Vaudor 1991). For this study, similarity between the plots was calculated for species presence/absence per site using Jaccard's coefficient (Digby and Kempton 1987). Species diversity was calculated using the number of species and Shannon's Diversity Index H' . Spearman rank order correlation analysis was used to examine the relationships between sedimentation and juvenile coral community composition, Diversity H' , and the abundance of different juvenile coral species (data for species that showed a normal distribution were tested with Pearson's correlation).

3.3.6.4 *Benthic substrate, herbivorous fish, juvenile coral size and health status*

Spearman rank-order correlation analyses were used to examine the relation between the mean number of juvenile corals and species per site and coral/algal cover and herbivorous fish biomass. Spearman rank-order correlation was also used to test the relationship between sedimentation and percentage of totally healthy juvenile corals. Additionally, Pearson's correlation analysis was used to look at the influence of sedimentation on mean size of juveniles.

3.4 Results

During the study 1,003 juvenile corals were counted in 206 quadrats taken (mean of 4.9 juvenile corals per 0.48m²) over the whole study area. Together they represented 19 species belonging to 9 families. *Agaricia* spp. was the most common genus in the study area, contributing from 17% to 59% of the total recruit density per location, followed by *Porites astreoides* which accounted for up to 38% of the recruit density per location (see also Table 1). Correlation analyses of the abundance of different coral species against sediment input show that some coral species (5 out of 18 species) respond to an increase in sediment with a decrease in abundance (see Table 1). However, several species (3 out of 18 species) like *Meandrina meandrites* and *Siderastrea siderea*, become more common as sedimentation increases. The species *Diploria strigosa* and *D. labyrinthus* were only found in the mid bay location of the high sedimentation bay H2. The remaining 10 species did not react to different levels sediment input. This may be also because they were rare in the study area and, hence, not enough data were available.

Table 1: Species composition of juvenile corals shown as percentage of total juvenile coral abundance for the high sedimentation bays (% high), low sedimentation bays (% low), and for the whole study area. The results of the correlation tests between sedimentation rate and the number of juvenile coral colonies of the species for each location of each bay are also shown (n = 14). Pearson correlation test (r) are used for all data sets of species that had a normal distribution and non-normal data sets were analysed with a Spearman rank-order correlation test (marked with r_s). * = $P < 0.01$, ** = $P < 0.05$.

Species	% low	% high	% total	Correlation coefficient
<i>Agaricia</i> spp.	41.0	33.5	36.5	-0.49*
<i>Porites astreoides</i>	14.6	18.7	16.7	-0.46*
<i>Siderastrea siderea</i>	6.6	4.6	5.9	0.49*
<i>Meandrina meandrites</i>	8.3	2.2	6.0	0.61**
<i>Eusmielia fastigiata</i>	5.7	9.3	7.3	-0.49*
<i>Montastrea decactus</i>	5.7	7.0	6.4	0.06
<i>Scolymia</i> spp.	3.3	2.4	3.0	0.06
<i>Leptoseris cucullatus</i>	2.4.	8.4	5.0	-0.62**
<i>Montastrea annularis</i>	2.3	3.1	2.8	-0.28
<i>Favia fragum</i>	2.0	3.1	2.4	-0.42
<i>Madracis mirabilis</i>	1.7	2.4	2.0	0.56*
<i>Stephanocoenia michelinii</i>	1.6	0.2	0.9	0.43 (r_s)
<i>Porites porites</i>	1.5	4.0	2.6	-0.49*
<i>Montastrea cavernosa</i>	1.0	0.2	0.6	0.40 (r_s)
<i>Colpophyllia natans</i>	1.0	0.2	0.7	0.26
<i>Siderastrea radians</i>	0.8	0.8	0.9	0.34 (r_s)
<i>Diploria strigosa</i>	0.4	0	0.2	0.38 (r_s)
<i>Diploria labyrinthus</i>	0.2	0	0.1	-0.11 (r_s)

3.3.1 Sedimentation

The results of the sediment trap data confirm that the high sedimentation bays received significantly more sediment than the low sedimentation bays (Table 2). The factor 'Location' of the traps was also significant with more sediment input at the inbay than the mid- and offbay location ($P < 0.001$). In addition, there was a significant interaction ($P < 0.05$) between the factors 'Sediment' and 'Location' showing that sediment declines moving inbay to offbay in high sedimentation bays but not in the low sedimentation bays (Fig. 2). The high sedimentation bays form a sediment gradient, sedimentation decreases with increasing distance from head of the bay. There was no such sediment gradient found in the low sedimentation bays.

3.3.2 Juvenile coral density and species abundance

The ANOVA result shows that juvenile coral density did not differ significantly between high and low sedimentation bays (Table 3, Fig. 3). However, the factor 'Location' did affect density of juvenile corals with significantly more juvenile corals in mid- and offbay locations than in the inbay location. The interaction 'Bay' nested within 'Sedimentation level' and Location was significant, because the two high sedimentation bays show increasing number of juvenile corals from the inbay to the offbay location, whereas the pattern of the low sedimentation bays is not clear (Table 3, Fig. 3).

Sedimentation did affect species richness of juvenile corals (Fig. 4, Table 3). There were significantly more species in the low sedimentation compared to the high sedimentation bays ($P < 0.01$). A significant difference was also found in species richness between the in-, mid- and offbay locations. Number of species was significantly higher in the offbay than in the inbay location. The low sedimentation bay showed opposite patterns in the number of species in the three different locations. In the low sedimentation bay L1 species richness decreases with increasing distance from the head of bay to headland, whereas in the low

Table 2: Results of the nested three-way ANOVA used to test differences in sedimentation rates between ‘Sedimentation level / Sed’ (low, high), ‘Location / Loc’ (inbay, midbay, offbay), and ‘Bay’ (L1, L2 and H1, H2) nested within ‘Sedimentation level’. Sample sizes: $n(H1) = 110$, $n(H2, H3, H4) = 66$.

Factors	df	F	P
Sedimentation level	1	90.752	< 0.001
Location	2	18.071	< 0.001
Bay(Sedimentation)	2	2.619	= 0.051
Bay(Sed)*Loc	2	2.899	< 0.05
Sed*Loc	4	4.236	< 0.05
Error	296		
total	308		

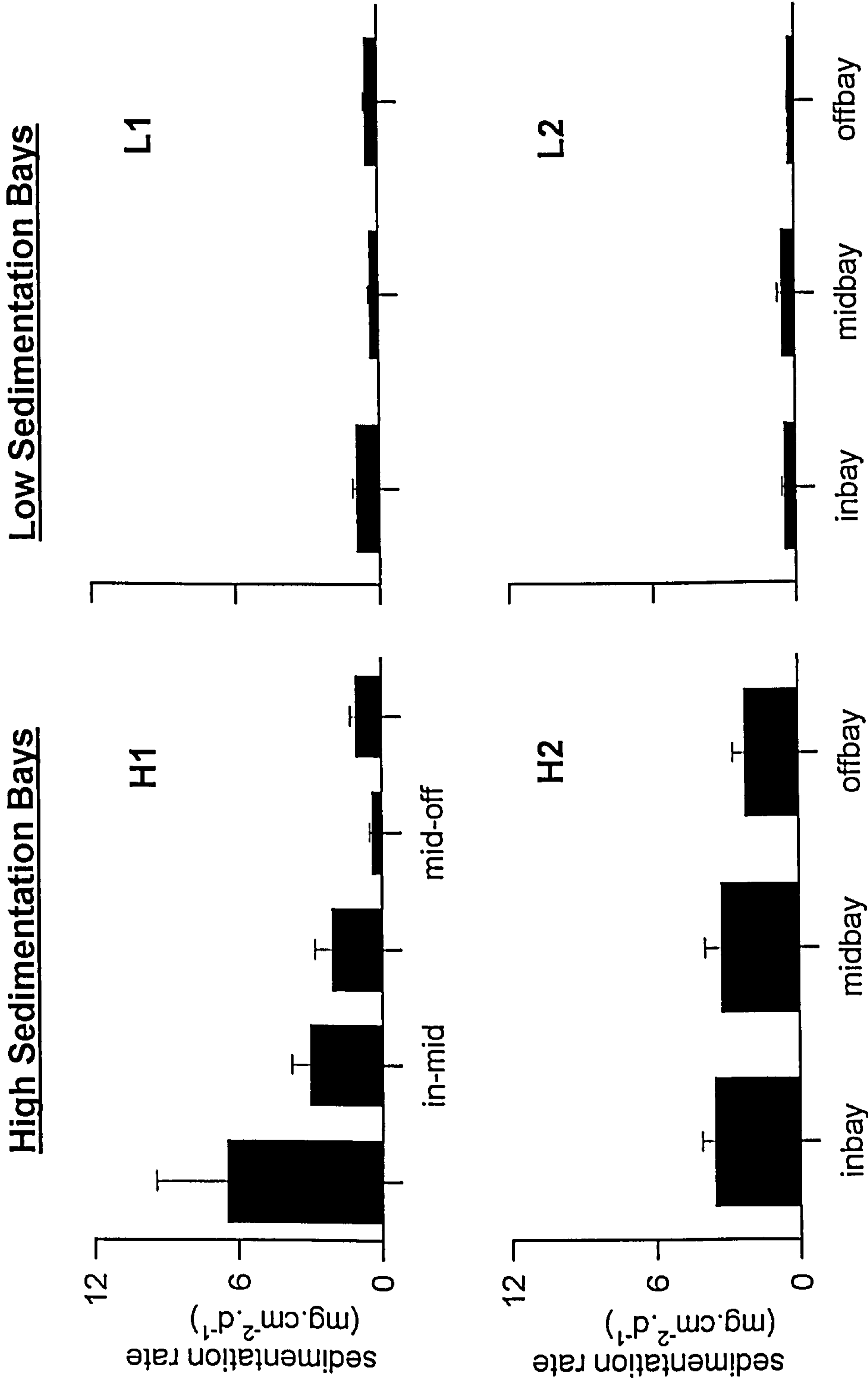


Fig. 2: Sedimentation rates ($\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) of the 25cm sediment traps measured under different periods from 1997 to 2001 at 15m depth at each location of each bay ($n = 22$). Error bars represent one standard error.

Table 3: Juvenile coral density and species richness were tested with a nested three-way ANOVA. The factors ‘Sedimentation level / Sed’ and ‘Location / Loc’ are fixed factors. The level of significance was $P = 0.05$. ns = non-significant.

Factors	juvenile coral density			juvenile species richness		
	df	F	P	df	F	P
Sedimentation level	1	2.394	ns	1	6.066	$P < 0.05$
Location	2	6.101	$P < 0.01$	2	3.136	$P < 0.05$
Bay(Sedimentation)	2	1.381	ns	2	1.792	ns
Bay(Sed)*Loc	4	5.215	$P = 0.001$	4	3.451	$P = 0.01$
Sed*Loc	2	0.561	ns	2	0.872	ns
error	166			166		
total	178			178		

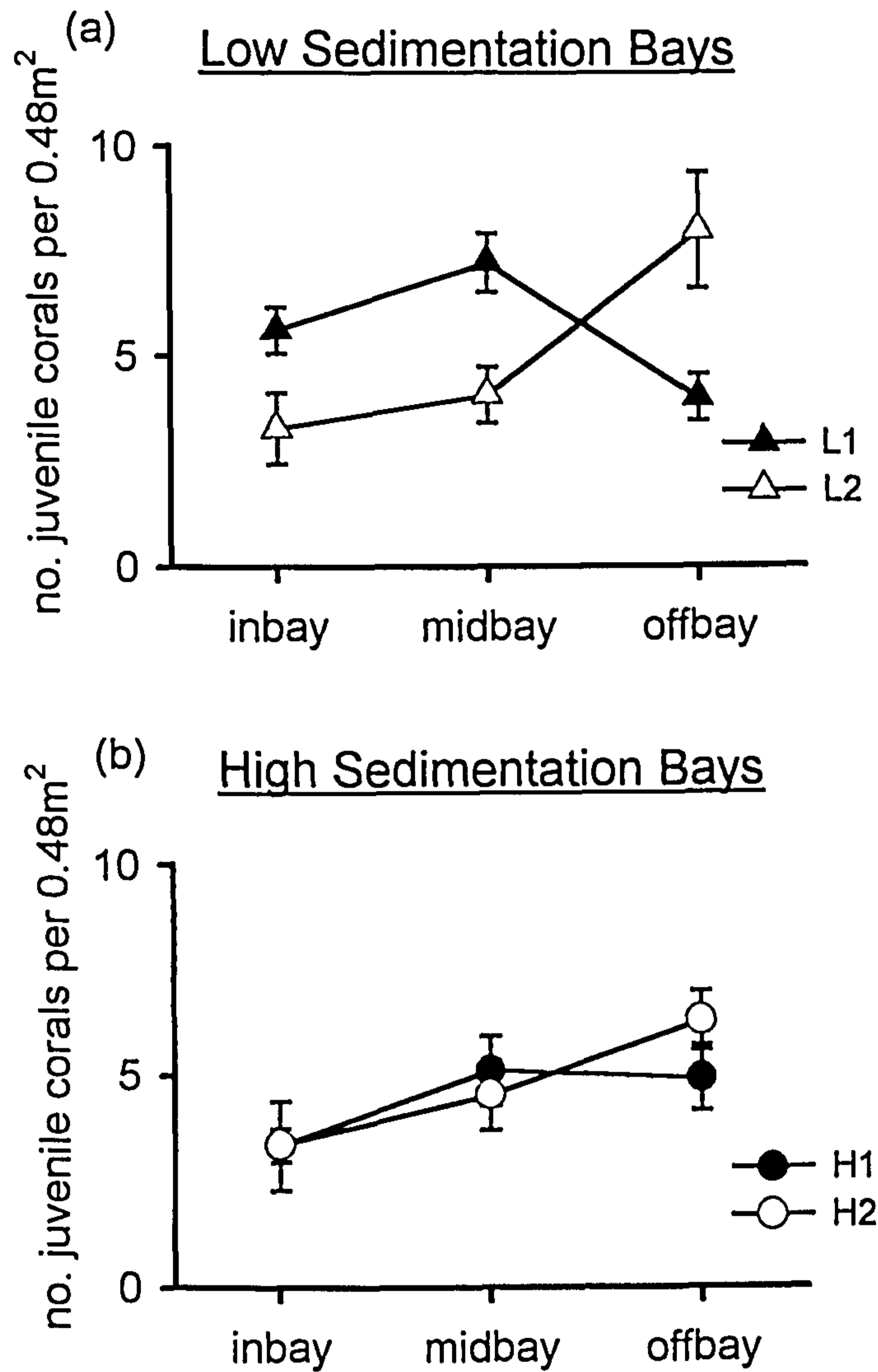


Fig. 3: Mean densities of juvenile corals (no. per 0.48m²) in the inbay, midbay and offbay location of the (a) low (L1, L2) and (b) high (H1, H2) sedimentation bays. Sample sizes were $12 < n < 19$ quadrats for each location of each bay. Error bars represent one standard error.

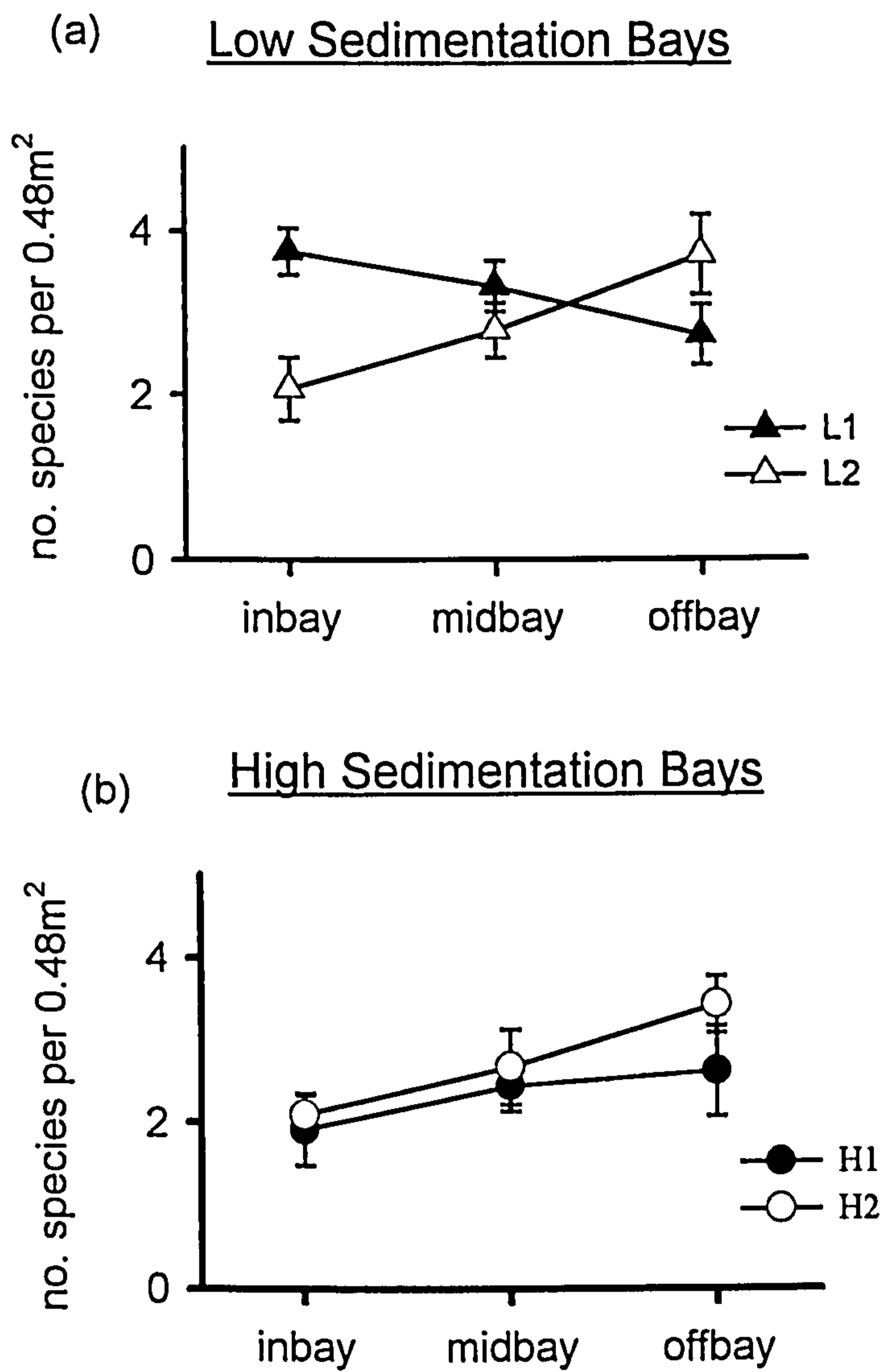


Fig. 4: Mean species richness of juvenile corals (no. per 0.48m^2) in the inbay, midbay and offbay location of the (a) low (L1, L2) and (b) high sedimentation bays (H1, H2) (\pm SE, $12 < n < 19$ quadrats for each location of each bay).

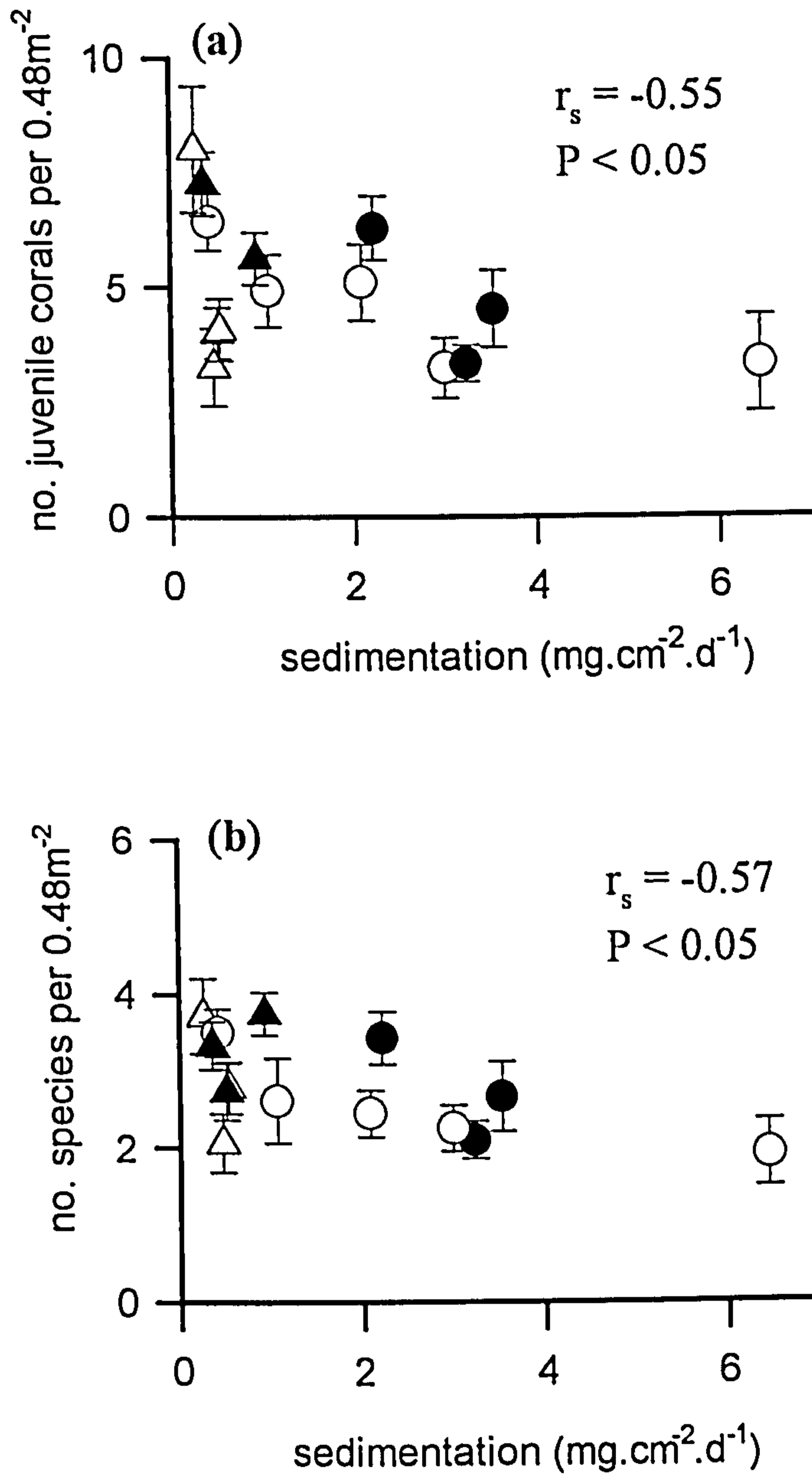


Fig. 5: Relationship between sedimentation rate ($\text{mg}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) and (a) mean number of juvenile coral colonies per 0.48m^2 and (b) mean number of juvenile coral species for a 0.48m^2 -area (\pm SE, $12 < n < 19$). Spearman correlation coefficient (r_s) is based on mean values per location of each bay ($n = 14$). \blacktriangle = low sedimentation bay L1, \triangle = low sedimentation bay L2, \circ = high sedimentation bay H1, \bullet = high sedimentation bay H2.

sedimentation bay L2 species richness decreases as it does in both high sedimentation bays H1 and H2 (Fig. 4a and b). This is reflected in the significant interaction between 'Bay' nested within 'Sedimentation level' and Location (Table 3).

'Location' is confounded with sediment input on high sediment gradients since rivers empty into the heads of bays. When the data were examined using Spearman's correlation test, the effect of sedimentation became clearer. There were significant negative relationships between sedimentation rate and juvenile coral density and species richness (Fig. 5a and b).

3.3.3 Juvenile coral species composition

The results of the principal co-ordinates analysis (PCO) are shown in Figure 6, where the first three dimensions are plotted against each other. Axis 1 and axis 2 (Fig. 6a) explain 42% of the total variation (see Table 4). This is not very high, so it does not give a very satisfactory picture. Nonetheless, one main feature is clear: the two axes show a good separation between the highest sedimentation locations (inbay and midbay of the high sedimentation bays) and other locations. This suggests that juvenile coral community structure is affected by high inputs of sediment. The inbay location of the low sedimentation bay L2 is also situated far from the main cluster of medium to low sediment sites. The third axis supports the view that sedimentation input affects structure of juvenile coral assemblages, although the total percentage of variance only rises to 56%. There is a strong relationship between the values of sites on axis 1 and sedimentation rate (Fig. 7) indicating that sediment is a key factor affecting juvenile coral assemblages.

Figure 8 shows that diversity (H') of juvenile coral assemblages decreases with rising sediment input. In areas where sedimentation is low, diversity H' can be either high or low, whereas it is consistently low in sites with high sedimentation stress.

Table 4: The results of the Principal Co-ordinates Analysis (PCO) showing the Eigenvalues and percentage of variance of the principal co-ordinate axis.

Principal Co-ordinate Axis	Eigenvalues	% of variances
PC1	0.365	22.70
PC2	0.289	18.50
PC3	0.210	14.10
PC4	0.171	11.95
PC5	0.127	9.50
PC6	0.041	4.67
PC7	0.039	4.56
PC8	0.032	4.20
PC9	0.012	3.10
PC10	0.002	2.53
PC11	0	2.42
PC12	-0.020	1.33
PC13	-0.035	0.45
PC14	-0.043	0

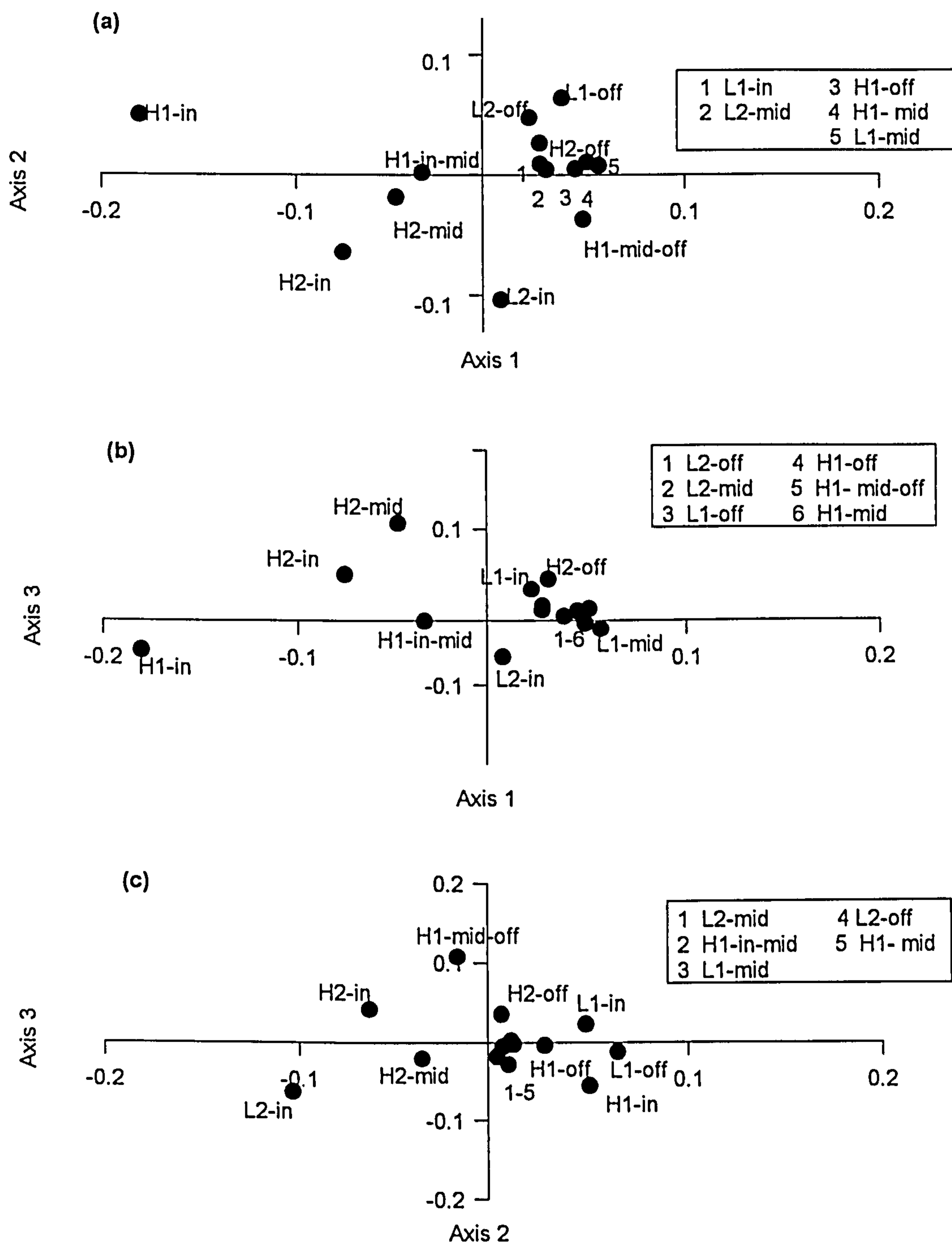


Fig. 6: The three first axes of the PCO analysis plotted against each other: (a) axis1 vs. axis2, (b) axis1 vs. axis3, (c) axis2 vs. Axis3. The distance between the points describes the similarity of the species composition between the sites. For abbreviations: L1 and L2 = low sedimentation bays, H1 and H2 = high sedimentation bays, in = inbay, mid = midbay, off = offbay. The locations in-mid and off-mid exist only for the high sedimentation bay H2.

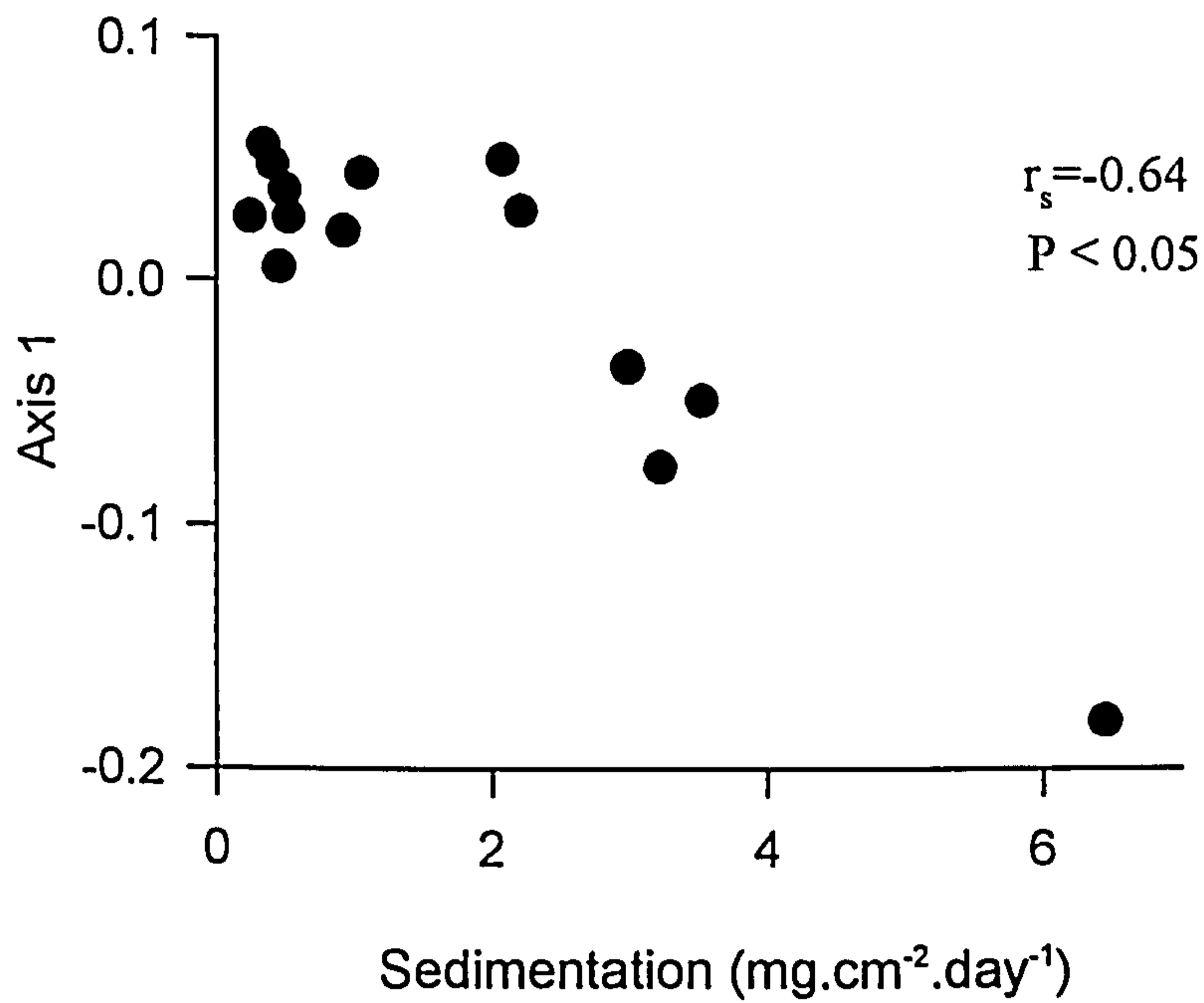


Fig. 7: Results of Spearman rank correlation analysis testing the relationship between score on axis 1 of the PCO and sedimentation rate (mg.cm⁻².d⁻¹) of each location. Spearman correlation coefficient (r_s) is based on mean values per location of each bay ($n = 14$).

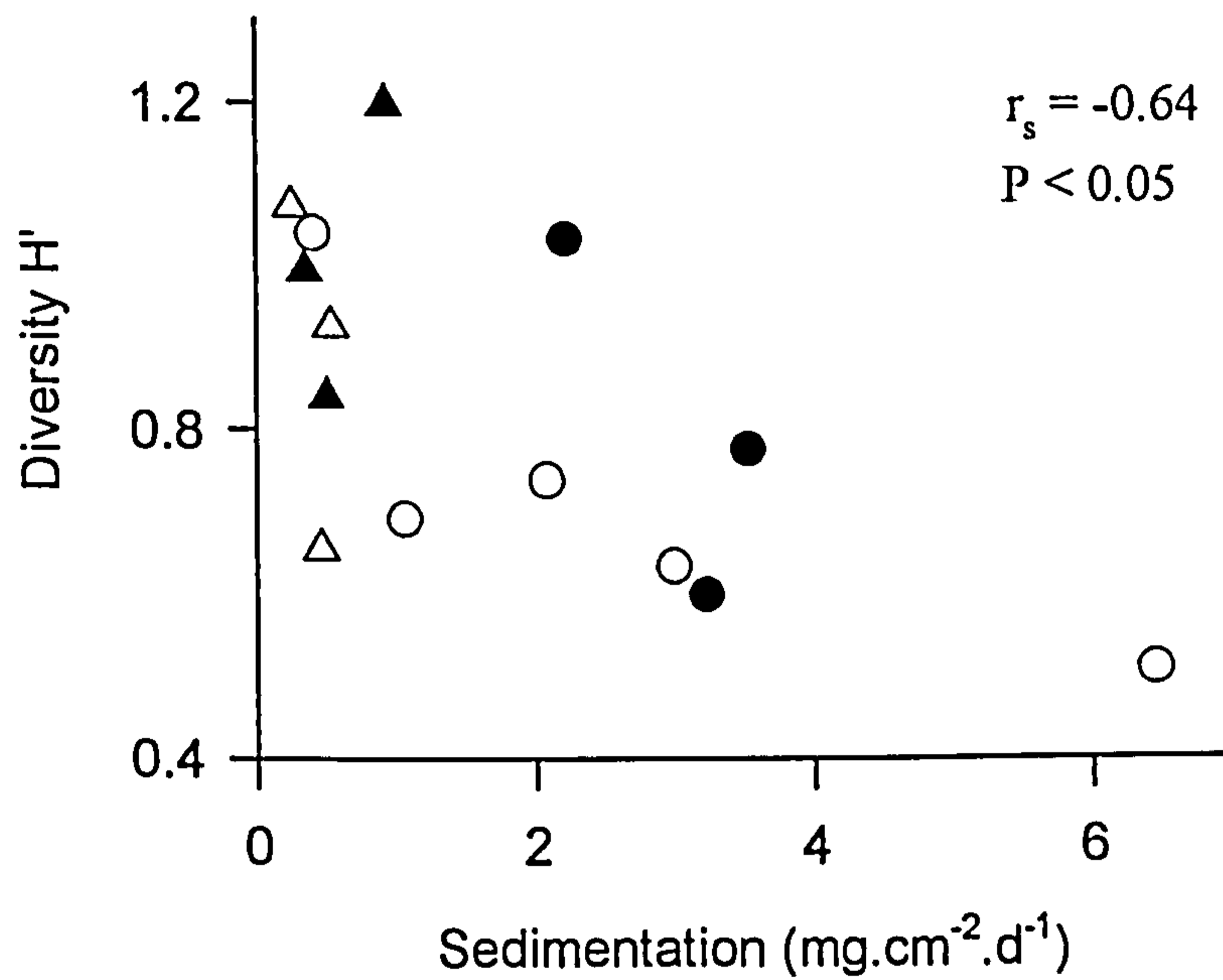


Fig. 8: Relationship between Shannon H' diversity index of each location of the low and high sedimentation bays and sedimentation rate (mg.cm⁻².d⁻¹) in each location measured between 1997 and 2001. Spearman correlation coefficient (r_s) is based on mean values per location of each bay ($n = 14$). ▲ = low sedimentation bay L1, △ = low sedimentation bay L2, ○ = high sedimentation bay H1, ● = high sedimentation bay H2.

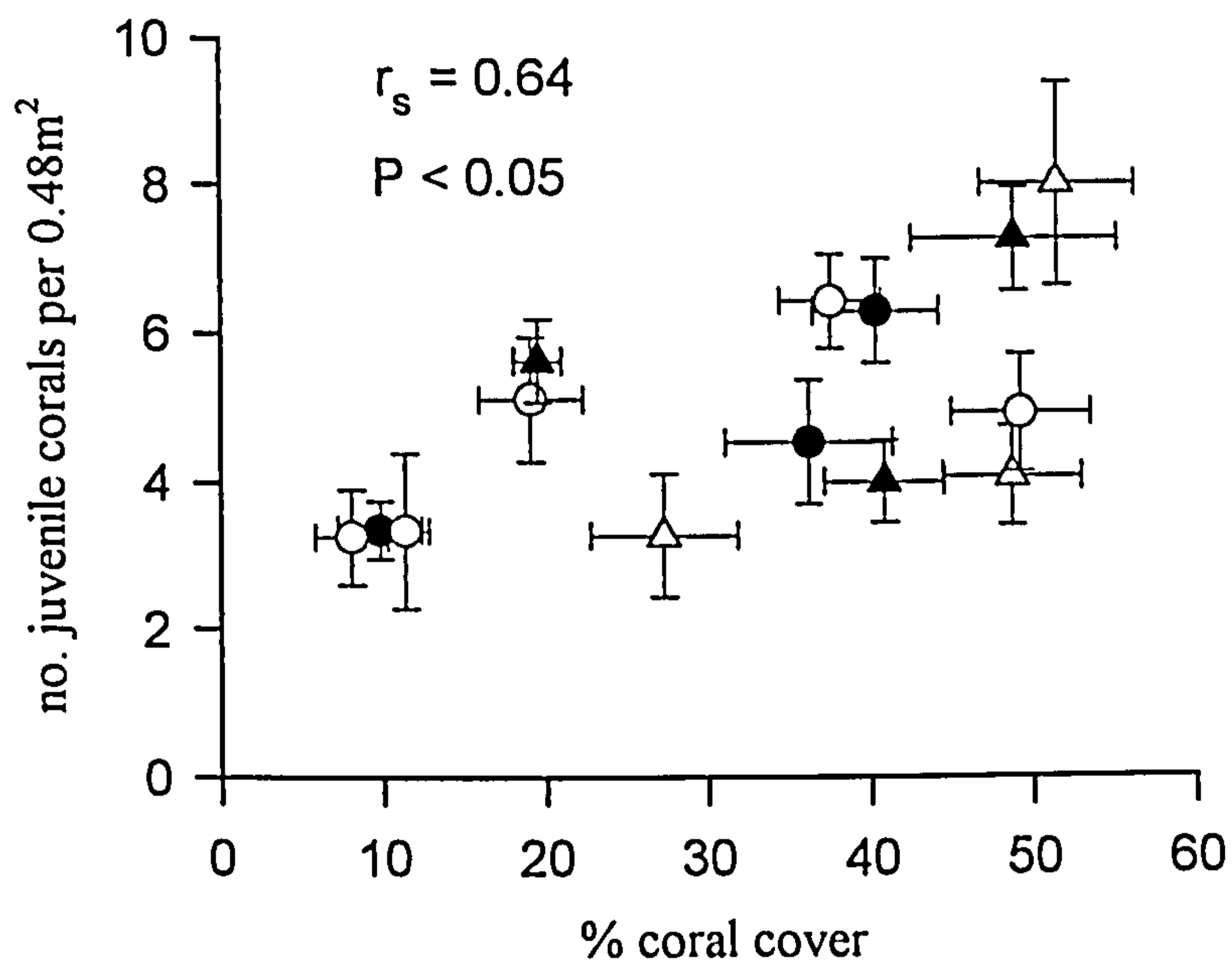


Fig. 9: Relationship between percentage adult coral cover and number of juvenile corals (no. per 0.48m²) per site (n = 14). Error bars represent one standard error. Spearman correlation coefficient (r_s) is based on mean values per location of each bay (n = 14). ▲ = low sedimentation bay L1, △ = low sedimentation bay L2, ○ = high sedimentation bay H1, ● = high sedimentation bay H2.

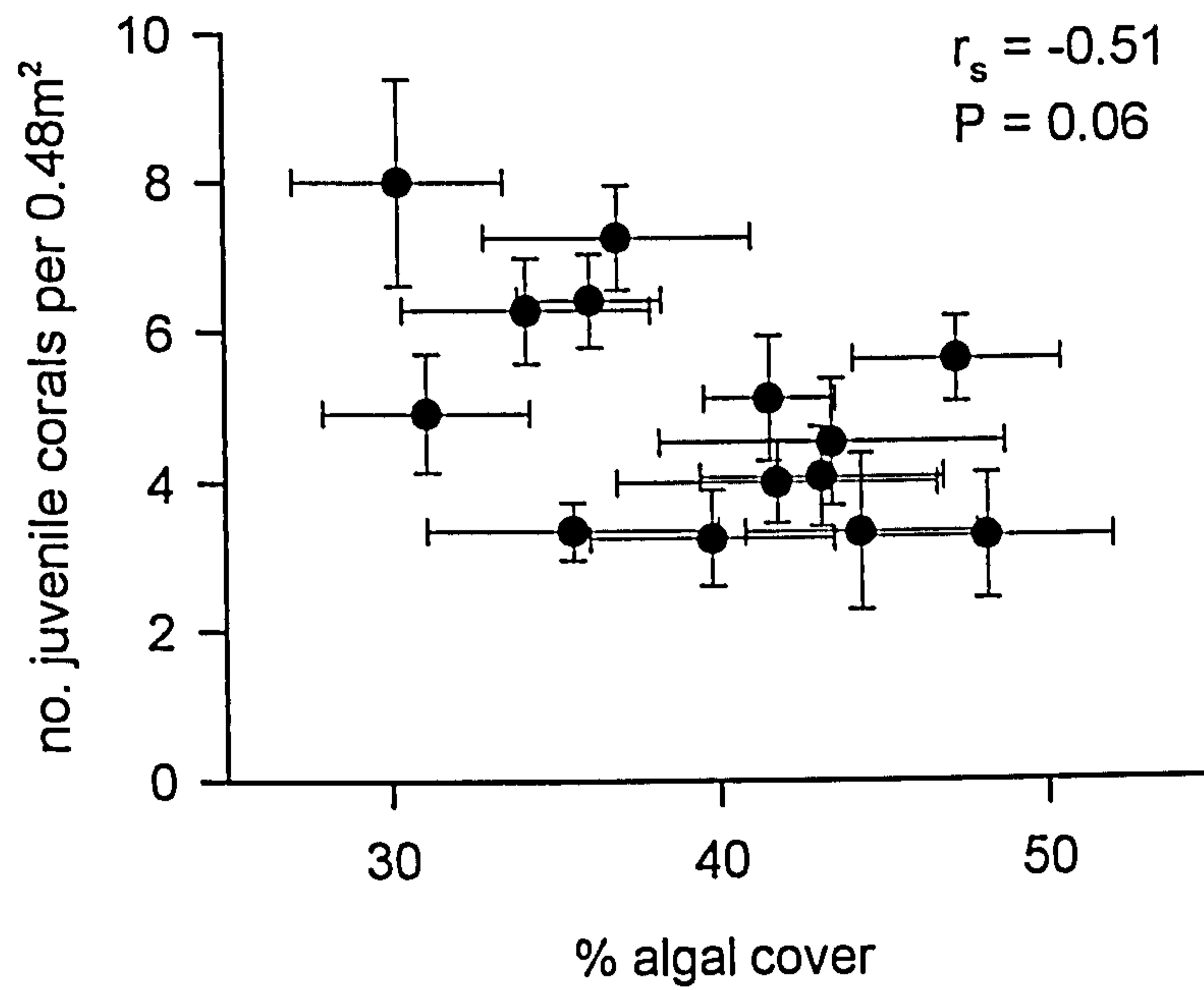


Fig. 10: Relationship between percentage total algal cover and number of juvenile corals (no. per 0.48m²). Spearman correlation coefficient (r_s) is based on mean values per location of each bay ($n = 14$). Error bars represent one standard error.

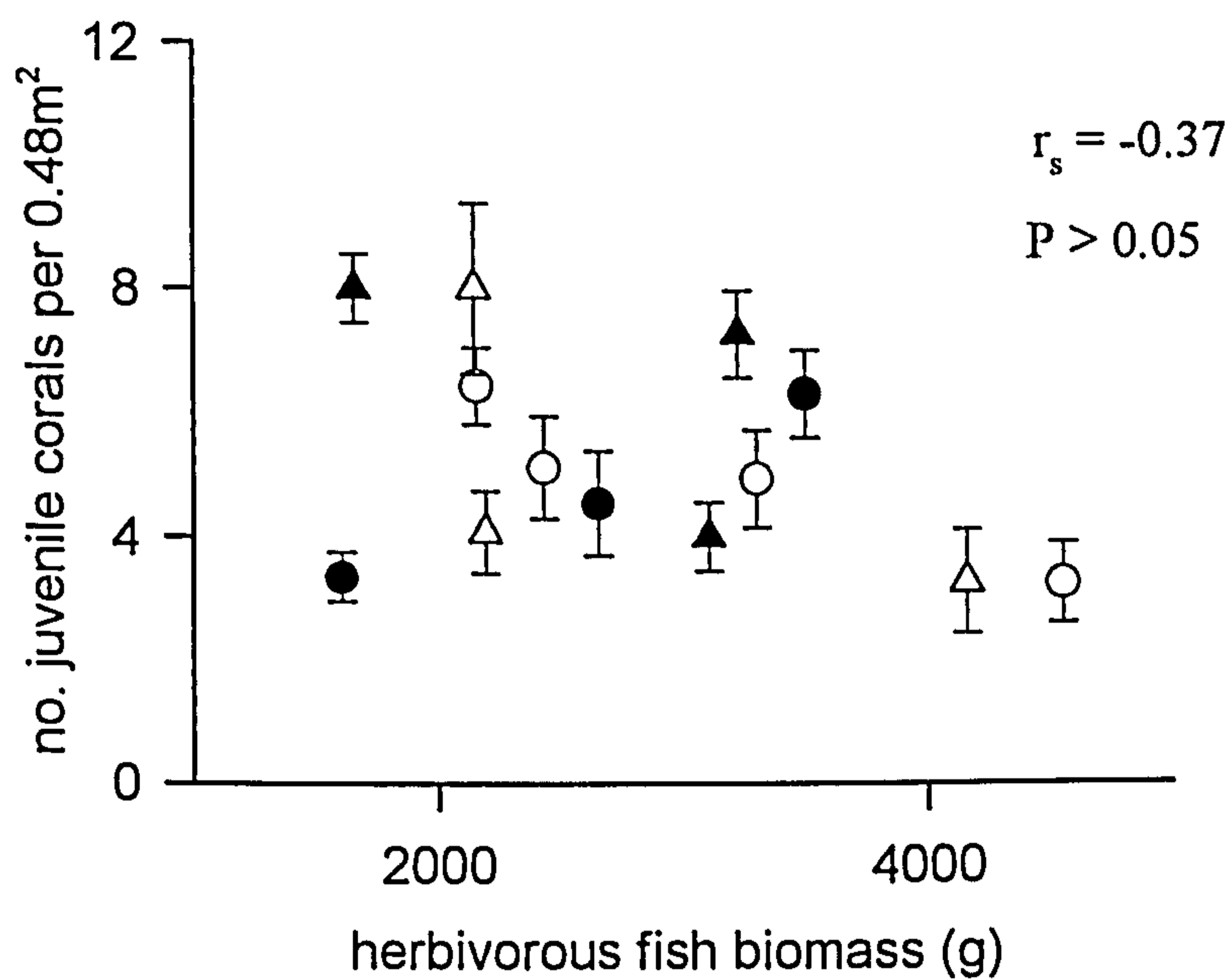


Fig. 11: Relationship between herbivorous fish biomass and mean density of juvenile coral colonies in each location of the high and low sedimentation bays. Data for each location were pooled and plotted \pm SE ($12 < n < 19$). Spearman correlation coefficient is based on mean values per location ($n = 14$). \blacktriangle = low sedimentation bay L1, \triangle = low sedimentation bay L2, \circ = high sedimentation bay H1, \bullet = high sedimentation bay H2.

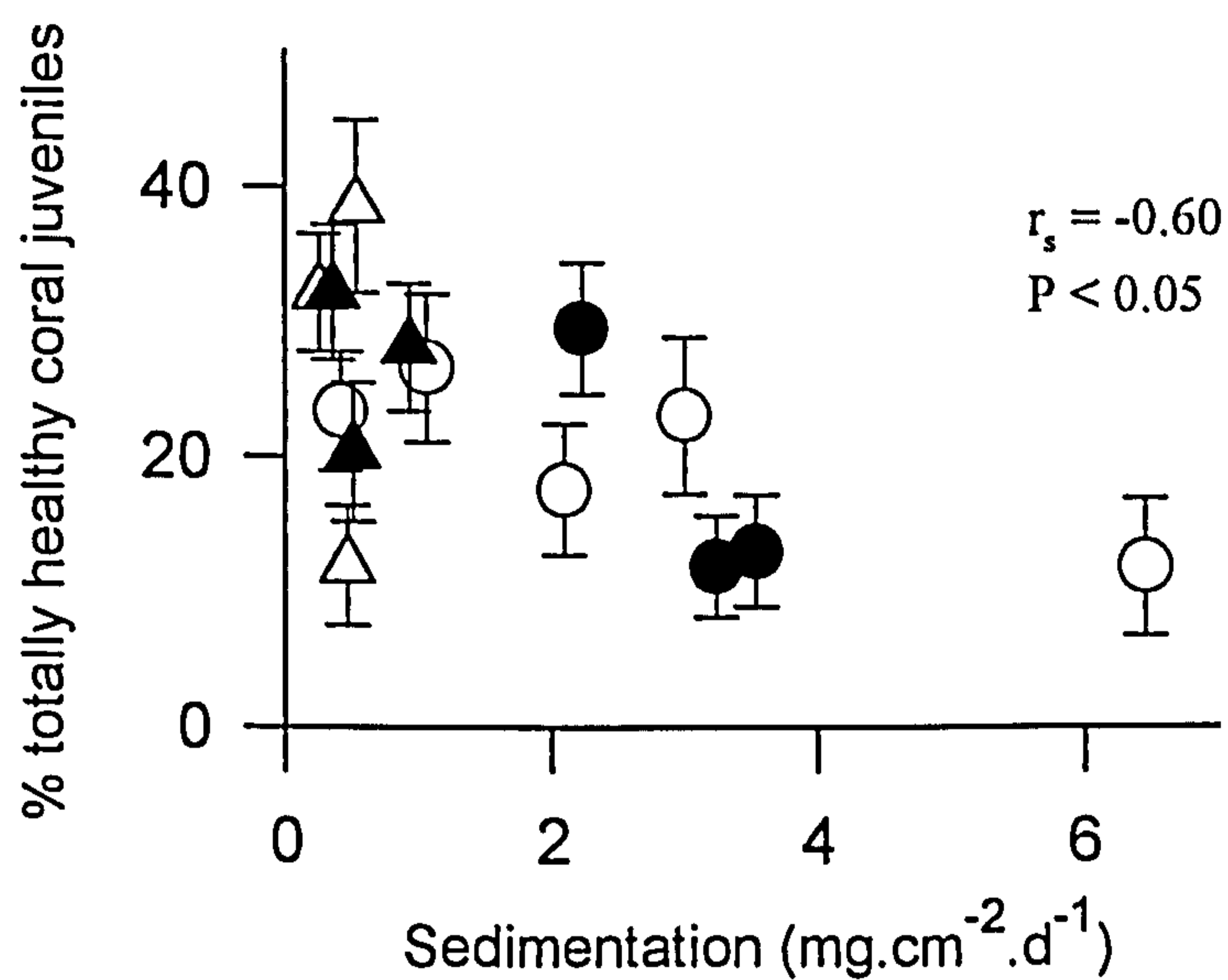


Fig. 12: Relationship between sedimentation rate ($\text{mg.cm}^{-2}.\text{d}^{-1}$) and percentage of totally healthy juvenile corals in each location of each bay (\pm SE). Spearman correlation coefficient (r_s) is based on mean values per location of each bay ($n = 14$). \blacktriangle = low sedimentation bay L1, \triangle = low sedimentation bay L2, \circ = high sedimentation bay H1, \bullet = high sedimentation bay H2.

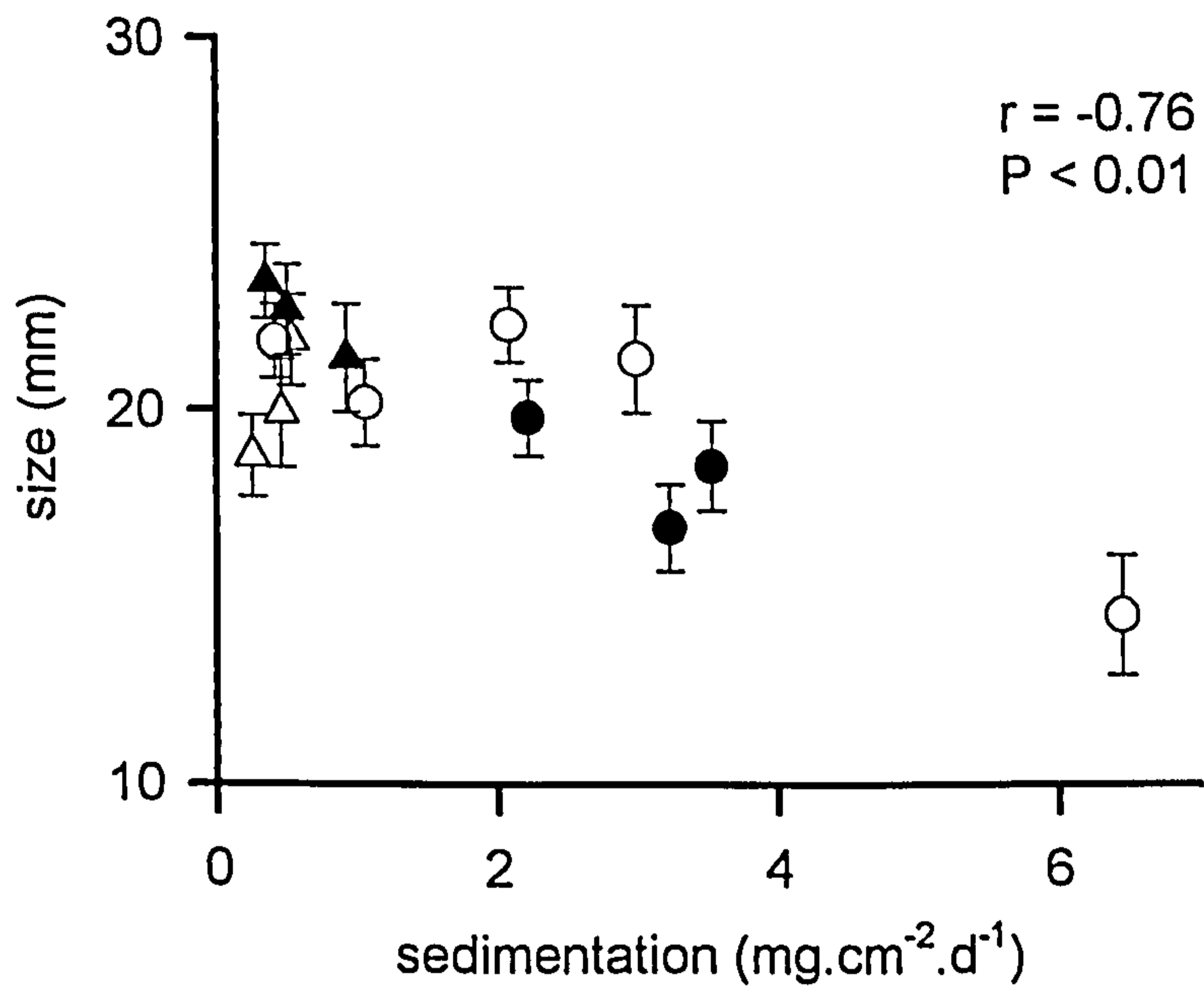


Fig. 13: Pearson correlation analysis between sedimentation rate (mg.cm⁻².d⁻¹) and the size (mm) of juvenile corals for each location of each bay (\pm SE, $n = 14$). \blacktriangle = low sedimentation bay L1, \triangle = low sedimentation bay L2, \circ = high sedimentation bay H1, \bullet = high sedimentation bay H2.

3.3.4 Benthic substrata, herbivores, juvenile coral size and health status

There is a strong positive relationship between the mean number of juvenile corals and coral cover, and a negative relationship with algal cover (Fig.9 and Fig. 10). While herbivorous fish may exert some control over algal cover they did not seem to affect juvenile coral density (Fig. 11). Only one sea urchin per location was found in the in-mid and mid-offbay location of the high sedimentation bay H1 and in the midbay location of the low sedimentation bay L1, and so their numbers were not used for further analyses.

Sediment had a significant impact on the health status of juvenile corals (Fig. 12), decreasing the percentage of totally healthy juvenile corals. Sedimentation also affected the mean size of juvenile corals (Fig. 13). Juvenile corals living in high sedimentation bays were typically smaller than corals growing on reefs of the low sedimentation bays.

3.5 Discussion

The results of this study show clearly that sediment input from two river mouths negatively affected juvenile coral assemblages. Although the analysis of variance did not show a significant difference in abundance of juvenile corals between high and low sedimentation bays, the inbay locations of the high sedimentation gradients were characterised by a significantly higher sediment load compared to mid- and offbay locations, and showed a lower juvenile coral abundance. I found that using correlation analysis increasing sedimentation led to a reduction in the abundance of juvenile corals and in the number of juvenile coral species. It also led to a change in juvenile coral species composition. Sediment pollution negatively affected the health status and size distribution of juvenile coral colonies. Adult coral cover and juvenile coral abundance showed a positive relationship, whereas a negative relationship was found between algal cover and the number of juvenile corals. However, herbivorous fish did not have any clear effect on juvenile coral abundance. Sedimentation thus appears to be a key factor determining juvenile coral assemblages.

In a similar study, Wittenberg and Hunte (1992) found a higher abundance of juvenile corals on less eutrophic and low sedimentation reefs than in more polluted areas of Barbados. They suggested this may be the result of unsuccessful coral larval settlement in eutrophic reef sites due to lower reproduction and reduced availability of substrata for settlement (Tomascik and Sander 1987b, Wittenberg and Hunte 1992). However, my results also show that sedimentation is not the only factor determining juvenile coral density. For example, at the offbay location of the low sedimentation bay L1, the number of juvenile corals was very low compared to the inbay and midbay location (see Fig. 1). There, other factors, for example the degree of wave exposure and currents could also play an important role (Sammarco 1991, Hughes et al. 2002).

There is also evidence from my study that sedimentation causes the health status of juvenile corals to deteriorate. On reefs with very low sedimentation more than half the juvenile corals observed showed signs of overgrowth, partial mortality, bleaching, damages or disease. On reefs with high sedimentation, totally healthy juvenile corals accounted for only 20% or less. The most frequent direct cause of impact was overgrowth by filamentous and fleshy algae (90-95% of cases). Other studies have shown that juvenile corals living on reefs in deeper water are more likely to be buried by sediments or to be overgrown by a combination of benthic organisms such as non-coelenterate encrusting animals, bryozoans, sponges and colonial ascidians (Bak and Engel 1979, Van Moorsel 1985) whereas algal overgrowth is identified as the most significant factor of juvenile coral mortality in shallow water in Curaçao (Van Moorsel 1985). Furthermore, boring sponges and endolithic algae are also responsible for high juvenile coral mortality by weakening the substrate corals settle (Van Moorsel 1985). In these cases mortality is abrupt and the cause difficult to identify.

Juvenile corals identified in this study showed increasing size with decreasing sedimentation. The smaller sizes of juvenile corals on reefs with higher sedimentation may be due to a higher mortality rate. Coral colonies on reefs with high sedimentation experience: (a) a higher risk of smothering by sediment particles (Hodgson 1990a, Rogers 1990, Te 1992), (b) a risk of lesions due to abrasion by sediment particles (Johannes 1975, Loya 1976, Rogers 1983,

Tomascik 1991) and (c) a greater possibility of attack by harmful bacterial populations feeding on the mucus and tissue of these corals (Hodgson 1990b). Consequently, coral juveniles might die younger and at smaller sizes on high sedimentation reefs.

However, smaller-sized juvenile corals may be found with increasing sedimentation because they are more efficient in rejecting sediment. The transport of sediment particles is of short distance which may give smaller-sized corals an advantage in high sedimentation conditions. On the other hand, larger juveniles may be better able to recover from partial mortality (Bak and Meesters 1999). In general, there is little evidence that efficiency of sediment rejection by corals is size dependent (Rogers 1990).

Another explanation for the presence of smaller-sized juvenile corals on high sedimentation reefs is redirection of energy from growth to removal of sediment particles (Edmunds and Davies 1989). Corals experiencing high sediment loads have lower growth rates compared with conspecifics living on low sedimentation reefs (e.g. Bak 1978, Dallmeyer et al. 1982, Cortès and Risk 1985, Tomascik and Sander 1985, Rice and Hunter 1992).

Compounding the energy cost of rejecting sediment, suspended particles in the water column reduce light availability for corals, especially in deeper water. This decreases photosynthesis by symbiotic zooxanthellae in coral tissue. Hence, high water turbidity results in slower growth of corals living in high sedimentation conditions (Chalker 1981, Tomascik 1990, Anthony and Fabricius 2000).

An alternative to the above explanations is that different juvenile coral sizes might also be the result of different periods of successful settlement and low mortality rates of newly settled corals in the different study sites. However, this is unlikely as the sites lie close to each other and it is unlikely that the timing of settlement would differ consistently between replicate high and low sedimentation bays.

Eutrophication may also play a role in determining size structures. Juvenile corals on eutrophic reefs in Barbados were larger than juvenile corals of less eutrophic reefs (Wittenberg and Hunte 1992). Wittenberg and Hunte (1992) explain this result as a combination of higher mortality of smaller individuals,

lower settlement rates and faster growth on eutrophic reefs. Larger coral colonies have a greater chance of long-term survival (Hughes 1985). However, Tomascik and Sander (1985) suggest that suspended particulate matter may be an energy source for corals, increasing growth up to a certain point before suppressing it. This is supported by Rosenfeld et al. (1999) who used fluorescently labelled sediment particles in a laboratory experiment and observed that corals have an ability to digest the sediment's organic fraction. Furthermore, Anthony (2000) tested differences in feeding-response curves, assimilation efficiencies and published records of ambient particle concentrations of coral colonies on turbid inshore and less turbid offshore reefs. He found that corals on turbid inshore reefs were 10-20 times more heterotrophic on suspended sediment than corals of less turbid environments.

However, investigations of growth and mortality rate are important to make further statements because several factors affect the growth rate of corals simultaneously and, consequently, the variation in growth and mortality rates is high (Tomascik and Sander 1985). In addition, growth rate can vary independently not only between different species but also within a single species and even one coral colony (e.g. Barnes 1973, Gladfelter 1982, Dodge and Brass 1984, Babcock 1985, Brown and Howard 1985).

The results of my study showed an obvious decrease in the number of juvenile coral species and in species diversity with increasing sedimentation. This mirrors Wittenberg and Hunte's (1992) study, despite the different depths at which the studies were conducted (1-6m depth in their study). In addition, Chiappone and Sullivan (1996) found in the Florida Reef Tract that the number of coral juveniles of the most abundant species was significantly greater in deeper (> 10m) water and related this to a lower sedimentation load with increasing depth.

I found that the species composition of the juvenile coral assemblages appears to be strongly affected by sedimentation rate. Low sedimentation locations had a similar species composition, which was distinct from the assemblages at the two inbay locations on high-sediment gradients. The most abundant species in my study area were *Agaricia* spp. and *Porites astreoides* followed by *Eusmilia fastigiata*, *Leptoseris cucullata* and *Montastrea decactis* on

the two low-sediment gradients, and *Meandrina meandrites*, *Siderastrea siderea*, *E. fastigiata* and *Madracis decactus* at the two highest sediment locations on the high sediment gradients. Juveniles of large massive coral species such as *M. cavernosa*, *M. annularis*, and *Colpophyllia natans* were rarely present throughout the reefs I studied.

In the present study, I found evidence that coral species show a range of responses to sedimentation. Several species increased in abundance with decreasing sediment input (Table 1). Nevertheless, species such as *M. meandrites* and *S. siderea* showed an increase in abundance with increasing sedimentation. According to Hodgson (1994) who tested tolerance towards sedimentation of 50 coral species, the survival rate of the coral colony is based on morphology, orientation, growth habit and the sediment rejecting behaviour. The general trend with increasing pollution is a higher abundance and dominance of coral species with smaller polyp size (Tomascik and Sander 1987a). The type of sediment is also important (Rogers 1990). *M. cavernosa* and *S. siderea* are defined as species that are relatively tolerant of high levels of sedimentation (Loya 1976, Lasker 1980). *M. cavernosa* is characterised by large calices whereas *S. siderea* has small ones. *M. cavernosa* was the most abundant species and the major frame-builder of reefs in Puerto Rico that were subject to heavy sedimentation (Loya 1976). Other species in Puerto Rico coral communities that seemed to succeed on reefs with heavy sedimentation included *S. radians*, *S. siderea*, *D. strigosa*, and *M. meandrites* (Loya 1976). However, *M. cavernosa* was not found in large numbers in my study area, although slightly more juvenile corals of this species were found in the high sedimentation bays. I found *S. radians*, *S. siderea*, and *M. meandrites* to be increasing in number with increasing sedimentation. These species possess most of the morphological features typical of corals having greater ability to reject sediment (Loya 1976).

M. annularis has been found to be an inefficient sediment rejecter in the laboratory (Bak and Elgershuizen 1976). The abundance of juveniles of this species was very low in St. Lucia, but slightly higher on the less sedimented than on the high-sediment reefs despite its dominance in the adult coral community, especially in areas with low sedimentation (Nugues pers. comm.).

Bak (1978) suggested *P. astreoides* to be an inefficient sediment rejector, and Tomascik and Sander (1987a) described *A. agaricia* as a species being an inferior competitor in high sedimentation conditions. However, in my study corals of these two species dominated juvenile assemblages in both high and low sedimentation bays. Both species appear to sustain high settlement rates. However, in the long term, species with low settlement and mortality rates may be able to out-compete species with high settlement and high mortality rates such as *A. agaricia* and *P. astreoides* (Bak and Engel 1979, Logan 1988, Smith 1992). Furthermore, *A. agaricites* is described as a species that is not easily overgrown because of its growth form (Van Moorsel 1985). Van Moorsel (1985) reported that the borders of all undisturbed *A. agaricites* colonies in Curaçao were at least partly raised above the benthic substratum. This feature may also explain this species dominance in the juvenile assemblages of St. Lucia and on other reefs in the Caribbean (Bak and Engel 1979, Rogers et al. 1984, Chiappone 1996).

Dodge and Vaisnys (1977) observed a change in community structure in response to increased sedimentation due to a shift from *Diploria strigosa* to *D. labyrinthus*. This result was supported by Hubbard and Pocock (1972) who defined *D. labyrinthus* as a species more capable of sediment rejection than *D. strigosa*, at least for particles larger than fine sand. In the present investigation, juveniles of these species were exclusively found in one high sediment location.

Reasons why different studies on the same species show contradictory findings of survival rates under sedimentation stress may be that these studies are done either in the laboratory or *in situ*, with different amounts of sediment, different particle sizes, or on different reefs with different currents and water exposure (Pastorok and Bilyard 1985, Rogers 1990, Van Katwijk et al. 1993). In addition, the nature of the sediments used in experiments (natural vs. anthropogenic source) may have different effects on individual species as well as at the coral community level (Tomascik and Sander 1987a). It also seems that corals can adapt to turbid conditions. Meesters et al. (2002) tested RNA/DNA ratios, a growth estimation, of corals from reefs with different turbidities. Growth and condition are commonly evaluated as direct measures of somatic growth (length and weight) (Bradford and Geen 1992). RNA/DNA ratios (biochemical

index) have been increasingly implicated as viable and sensitive indirect measures of relative growth (Bergeron 1997). Decline in RNA/DNA ratios indicates less-than-optimal conditions. For growth corals depend largely on energy transferred from the symbiotic zooxanthellae and, hence, Meesters et al. (2002) expected changes in RNA/DNA ratio with turbidity disturbance that in turn affects irradiance. They found a negative relationship between RNA/DNA ratio and light that was consistently higher in corals of the highly turbid reefs than of reefs with low turbidity. This revealed a possibly genetic adaptation in the metabolic functioning of corals in turbid environments (Meesters et al. 2002). However, as long as methods differ, comparisons among various studies should be made cautiously.

In this study, juvenile coral abundance was positively related to the percentage of living coral cover. Wallace and Bull (1981) found the highest juvenile coral densities at sites with highest adult coral cover on the Great Barrier Reef. By contrast, Fisk and Harriott (1990) observed highest settlement rates on reefs at Lizard Island (GBR) which had low adult coral populations following predation by the asteroid *Acanthaster planci*. The results of other studies are also equivocal, some finding that juvenile coral abundance is directly related to adult cover (Bak and Engel 1979, Rylaarsdam 1983), while other failed to detect this correlation (Fitzhardinge 1985, Harriott 1985). In Barbados, Hunte and Wittenberg (1992) noted that juvenile coral abundance was not closely associated with adult coral cover. Some sites with high coral cover showed low settlement rates.

The results of my study show a near significant negative relationship between juvenile coral density and algal cover. Several other studies have shown that coral settlement is not only limited by sedimentation but algal growth (e.g. Birkeland et al. 1981, Hodgson 1990a, Te 1992, Chiappone 1996). In addition, filamentous algae could further suppress juvenile coral survival in high sedimentation conditions by trapping sediment particles in the turf (Stafford-Smith and Ormond 1992). Smaller coral colonies are particularly affected by algae as they are more easily overgrown (Bak and Engel 1979). Algae are fast-growing organisms which respond more directly to a rich supply of nutrients and

light (Birkeland et al. 1981). Therefore, increasing nutrient enrichment on coastal reef zones is resulting in more prolific algal growth, reducing coral survival (Hatcher 1984, Littler and Littler 1984, Lapointe 1997).

The influence of herbivorous fish and sea urchins on coral settlement rates is still unclear. By grazing macroalgae and filamentous turf they provide bare substrate for the settlement of coral larvae (Dart 1972, Ogden and Lobel 1978, Sammarco 1980). Overexploitation of herbivorous fish stocks reduces grazing pressure on reefs resulting in increased growth of algae (Rogers et al. 1984, Hughes 1985, Wittenberg and Hunte 1992). This can lead to a shift from coral to algal dominance on reefs that, when severe, could cause degradation of the reef framework (Done 1992). On the other hand, intense herbivory has a direct negative effect on juvenile corals as herbivores damage or scrape juvenile corals from the substrate while foraging unselectively (Bak and Engel 1979, Maida et al. 1994). However, Birkeland (1977) found grazing fish (Acanthurids and *Scarus croicensis*) avoiding corals as little as 3mm in diameter. Rogers et al. (1984) observed herbivorous fish to have a more active grazing behaviour in more shallow water providing a high rate of new coral settlers. In a laboratory experiment where juvenile corals were placed in the same aquarium with *Diadema antillarum* the juvenile coral colonies showed size-dependent mortality (Rylaarsdam 1983). After 5 days, one quarter of corals smaller than 3mm in diameter died due to being grazed, compared with a survival rate of 95% and more of larger colonies. Conflicting results also exist on the effects of damselfish territoriality on the survival of juvenile corals. By guarding their territory from feeding by other herbivorous fishes and sea urchins they prevent grazing of small corals (Done 1992). However, other observers have shown a lower survival of juvenile corals inside damselfish territories than outside (e.g. Kaufman 1977, Potts 1977, Lobel 1980). The effect depends on the level of algal growth that damselfish promote. Some develop dense, high biomass turf, while others develop much shorter lawns.

In my study, herbivorous fish had no clear influence on the number of juvenile corals. Despite increasing herbivorous fish stocks due to the implementation of marine reserves on some of the reefs (Roberts et al. 2001,

Hawkins in prep.) the fish stocks still may not have reached a size to affect the abundance of juvenile corals significantly. The abundance of sea urchins was so low in my investigation that they can be rejected as a factor in determining algal biomass and juvenile coral abundance.

3.6 Conclusion

In conclusion, high rates of sedimentation had marked effects on juvenile assemblages. They included:

- (1) reduction in juvenile coral abundance,
- (2) reduction in coral recruit diversity,
- (3) a change in juvenile coral composition, probably due to a selection of more sediment tolerant species,
- (4) a deterioration in the health status of juvenile coral colonies,
- and (5) a decrease in size compared to juvenile corals of less sedimented reefs.

Additionally, my study showed that juvenile coral abundance is negatively affected by algal cover and that the number of juvenile corals is positively related to adult coral cover. Furthermore, grazing appeared not to affect the abundance and diversity of juvenile corals. While sedimentation is the main stressor affecting juvenile coral settlement, other factors also influence their distribution, such as currents, larval supply, reef topography and wave exposure (Harriott 1983).

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Chapter 4

The effects of sedimentation on coral larval settlement

4.1 Abstract

Sediment pollution has been reported to cause mortality of corals on reefs throughout the world. To counter degradation new juveniles must replace damaged corals. However, there has been little work on the impacts of sedimentation on replenishment of coral assemblages, particularly settlement. Deposition of sediment on suitable settlement substrate and on newly settled coral larvae could impede settlement. Furthermore, levels of sedimentation that may pose no threat to adult corals could harm larvae. This study compares levels of coral larval settlement in four different bays on the west coast of St. Lucia, West Indies. Two bays received low sediment inputs and two bays were subject to high sedimentation. Ceramic tiles were screwed to a PVC-pipe construction at two different heights and different positions to provide artificial substrate for larval settlement. Paired settlement arrays were installed at three locations in each of the low and high sedimentation bays: inbay (closest in the bay), midbay (between the inbay and offbay locations) and offbay (at the headlands of the bay). The tiles were left under water for around six months, then collected and analysed. This process was undertaken twice. There were no significant differences in rates of larval settlement between high and low sedimentation bays. However, settlement rates were lower at the head of bays than at their headlands. There were also

differences in settlement behaviour between the low and high sedimentation bays. More settlers were found on the lower tiles in the low sedimentation bays, whereas more larvae settled on the higher tiles in the high sedimentation bays. There was also an indication that settlement rates differed between the two low sedimentation bays. This may explain why a direct influence of sedimentation on the settlement rate could not be detected. No significant relationship was found between herbivorous fish biomass and settlement rate. Also coral cover was only weakly correlated with the number of settlers. In both study periods, *Agaricia* species were the most common settlers followed by species of *Porites*. *Stephanocoenia intersepta* only settled in the first study period on tiles in high sedimentation bays. Unexpectedly, *Agaricia* spp. settlers were the most abundant in high than low sediment bays. *Porites* spp. abundance appeared unaffected by sedimentation, but lower settlement rates were found in the inbay than offbay locations. These results suggest that sedimentation affects the composition of species settling. The size of all settled corals was not affected by sedimentation or the location in the bays. In summary, this study suggests that sedimentation acts in combination with other factors to affect settlement rates and behaviour of coral larvae, and influencing settlement behaviour.

4.2 Introduction

Coral reefs are dynamic systems that develop through the gradual accretion of calcium carbonate deposited by corals and associated organisms (e.g. Hubbard et al. 1990, Langer et al. 1997). Carbonate lost to bioerosion, dissolution and storms or other natural or human disturbances, must be replaced by new coral growth and successful coral recruitment (e.g. Richmond 1997). Coral recruitment, that is survival of young corals to first reproduction, depends on successful larval settlement but also on post-settlement mortality rates. High settlement rates may balance out high mortality rates of juvenile corals. Bak and Engel (1979) who conducted a study on distribution, abundance and survival of juvenile scleractinian corals in Barbados described three different life history strategies of corals, (1) high recruitment and high mortality rates, (2) low recruitment and low

mortality, and (3) asexual fragmentation as the main reproductive strategy. These observations have been supported by several other workers (Loya 1976, Smith 1992, Wittenberg and Hunte 1992).

In the life history of corals, settlement is a crucial process (Reichelt-Brushett and Harrison 2000). Coral larvae show complex settlement behaviours (Mundy and Babcock 1998, Heyward and Negri 1999, Raimondi and Morse 2000) and successful settlement depends on several abiotic and biotic factors. These include the substrate type and level of irregularity (Carleton and Sammarco 1987), light penetration (Maida et al. 1994, Mundy and Babcock 1998), water temperature, salinity and motion (Richmond 1997), and species-specific chemical cues that invoke settlement mechanisms of coral larvae (Morse and Morse 1984, Heyward and Negri 1999). However, successful settlement does not equate to successful recruitment. Metamorphosis of settled coral larvae is sensitive to chemical signals, perhaps still below levels detectable by human technology (Connell and Miller 1984). Hence, metamorphosis after settlement may fail.

Coral reefs world-wide are subject to growing levels of threat from human activities (Bryant et al. 1998, Hodgson 1999). In particular, sedimentation from land-clearing and soil erosion represents a major threat to coral reefs (Bell 1992, Bryant et al. 1998). While several studies have examined how sedimentation affects adult coral colonies and communities (e.g. Tomascik and Sander 1987, Stafford-Smith and Ormond 1992, Hodgson 1994, Riegl and Branch 1995, Sladek Nowlis et al. 1997, Wesseling et al. 1999), the implications for larval settlement are very poorly known. It could be that sedimentation levels posing little or no threat to adult corals may be detrimental to coral larvae and the settlement process. In controlled laboratory experiments, Babcock and Davies (1991) showed that increasing sedimentation rates changed settlement patterns of coral larvae. In low sediment treatments, settlement rates on the upperside of horizontal plates exceeded settlement rates on the underside. With increasing sediment levels, settlement rates on the undersides increased significantly. Other laboratory work by Hodgson (1990) examined the effects of coral larval settlement on glass partially and fully covered with sand and in treatments without sand. He observed that settlement rates in all sand treatments were significantly lower compared to

control treatments. Experimentations by Te (1992) revealed that settled coral larvae could reverse their metamorphosis (to 'bail out') and were most likely to do so in treatments with high sedimentation rates.

In natural situations, larval settlement may be influenced by a variety of factors such as competition for space, resuspension effects of the accumulated sediments on the reef, and water movements from currents and waves (e.g. Babcock and Davies 1991, Hunte and Wittenberg 1992, Rodriguez et al. 1993, Maida et al. 1994, Dial and Roughgarden 1998, Lugo-Fernandez et al. 2001). Only a few studies have examined impacts of sedimentation on coral larval settlement in the field, and most have been conducted along eutrophication gradients. Eutrophication is often linked to increased sedimentation rates due to suspended particulate matter in the water (Hunte and Wittenberg 1992). Tomascik (1991) and Hunte and Wittenberg (1992) installed artificial settlement plates along a eutrophication gradient on the west coast of Barbados. Tomascik (1991) observed lowest settlement rates on the most eutrophic reef, while Hunte and Wittenberg (1992) showed that settlement rates decreased with increasing sedimentation. However, Hunte and Wittenberg (1992) left settlement tiles submerged for 3 years before analysis. Hence, other factors affecting post-settlement mortality might have influenced their result (Hunte and Wittenberg 1992). Nevertheless, artificial settlement tiles that were checked monthly, also showed lower rates of larval settlement on reefs that were more eutrophic (Hunte and Wittenberg 1992).

Corals exhibit different mechanisms to get rid of sediment (Stafford-Smith and Ormond 1992). These include increased tentacular activity, mucus production and tissue expansion by active uptake of water (see Rogers 1990, Stafford-Smith and Ormond 1992). These efforts all require energy which could otherwise be used for reproduction and growth, and so sedimentation imposes a metabolic cost on corals (Tomascik and Sander 1985, Edmunds and Davies 1989).

Globally coral reefs have undergone shifts from coral to algal dominated benthic communities (Done 1992, Hughes 1994, McCook 1999, Nyström 2001) (Done 1992, Hughes 1994, McCook 1999, Nyström et al. 2001). This may be linked to increased nutrient inputs fertilising algal production (Bell and Elmetri

1995, Lapointe 1997) and/or over-exploitation of herbivorous fish leading to increased algal cover due to reduced grazing pressure (see Chapter 2, Sammarco 1983, McClanahan 1997). Algae represent a threat to coral larval settlement by competing with settlers for space (Birkeland 1977, Harriott 1985, Hunte and Wittenberg 1992, Miller and Hay 1996). Algae with canopy growth forms prevent corals from receiving enough light to undertake photosynthesis and frondose algae are reported to actively damage corals when swept around by water motion (Coyer et al. 1993). It is also suggested that some algae produce chemical substances which may prevent coral settlement (De Nys et al. 1991).

Marine reserves are reported to rebuild overexploited fish stocks (Roberts et al. 2001). Grazing by reef fish may enhance the opportunities for coral to settle, and may also provide more light to newly settled corals by keeping algae cropped short. This could also prevent tissue damage by frondose algae. However, the impacts of grazing fish on newly settled corals are poorly understood. Authors have reported fish feeding on algae leaving corals as small as 3 mm undamaged (Birkeland 1977), whereas others believe that herbivorous fish graze unselectively and scrape off small coral settlers (Fitzhardinge 1988, Gleason 1996).

There is a real need for field studies to understand the effects of human-induced pollution, including sediment runoff, on coral larval settlement. In this study I examine coral settlement patterns on coral reefs on the west coast of St. Lucia in the Caribbean Sea. At this location it was possible to look at the degrading effects of sedimentation on coral settlement at a large-scale. Studies using this approach are much needed. I sought answers to the following questions: (1) Do coral larval settlement rates differ among reefs with different sedimentation input? (2) Does sedimentation affect the growth rate of newly settled corals? (3) Does coral cover on the reef and herbivorous fish biomass have any effect on coral larval settlement?

I hypothesise that sedimentation reduces coral larval settlement by reducing water quality and smothering newly settled corals. I also predict that newly settled corals which survive on high sedimentation reefs will grow slower because they transfer more energy to sediment removing mechanisms than to metabolic processes such as growth. Finally, I predict that coral larval settlement

is higher in areas with high adult coral cover that are sources of larval production and/or attractive to settling larvae, and that herbivorous fish reduce algal growth on the tiles when grazing and, in doing so, create more suitable space for coral larval settlement.

4.3 Materials and methods

4.3.1 Location

This study was conducted in the same bays and locations as the previous study in Chapter 3 (see Fig. 1 in Chapter 3). Hence, for detailed description of the study area, see section 3.3.1 in Chapter 3.

4.3.2 Sedimentation rates

At each location, I installed two pairs of sediment traps. Sedimentation rates were collected over seven different periods from 1997 to 2001 (Table 1). The sediment traps are described in detail in section 3.3.2 in Chapter 3, where I also explain the methods I used to measure sedimentation rates.

In 1999, sand accumulated around traps that were established at the offbay location in the high sedimentation bay H1 because of a major storm (Hurricane Lenny, see also Chapter 2). If currents and/or waves were strong, this sand could stir up and was caught in the traps. This could bias the results because sand is heavier than sediment. In this analysis only sedimentation measurements without sand were used.

4.3.3 Artificial settlement plates

At each location, I established two arrays (I and II) of artificial coral settlement plates (see Figure 1, Rogers et al. 2001). The frame for each array was constructed from PVC pipes by gluing a T-fitting (width 20cm, length 10cm) to one end of a 60cm long pipe (diameter 4cm). Into each end of the T-fitting I glued a 20cm long

Table 1: Sedimentation measurements taken at two week intervals from 1997 to 2001 on 7 different trips by two collectors.

Interval	Trip	Observer
Period 1 (23/8-6/9/97)	I	M. Nugues
Period 2 (6/9-20/9/97)	I	M. Nugues
Period 3 (20/9-4/10/97)	I	M. Nugues
Period 4 (17/1-31/1/98)	II	M. Nugues
Period 5 (31/1-14/2/98)	II	M. Nugues
Period 6 (14/2-28/2/98)	II	M. Nugues
Period 7 (28/6-12/7/98)	III	M. Nugues
Period 8 (12/7-26/7/98)	III	M. Nugues
Period 9 (26/7-9/8/98)	III	M. Nugues
Period 10 (9/11-23/11/98)	IV	M. Nugues
Period 11 (23/11-7/12/98)	IV	M. Nugues
Period 12 (13/5-1/6/00)	V	C.K. Schelten
Period 13 (1/6-15/6/00)	V	C.K. Schelten
Period 14(15/6-29/6/00)	V	C.K. Schelten
Period 15 (29/6-14/7/00)	V	C.K. Schelten
Period 16 (14/7-30/7/00)	V	C.K. Schelten
Period 17 (30/7-14/8/00)	V	C.K. Schelten
Period 18 (14/8-29/8/00)	V	C.K. Schelten
Period 19 (18/1-1/2/01)	VI	C.K. Schelten
Period 20 (1/2-15/2/01)	VI	C.K. Schelten
Period 21 (15/2-1/3/01)	VII	C.K. Schelten
Period 22 (16/07-28/07/01)	VII	C.K. Schelten
Period 23 (28/07-11/08/01)	VII	C.K. Schelten
Period 24 (11/08-25/08/01)	VII	C.K. Schelten

PVC-pipe (diameter 4cm). A further PVC-pipe (50cm long and 4cm diameter) was screwed horizontally and at right angles 30cm under the T-fitting using stainless steel bolts. Plastic rectangles (Perspex, 10cm x 3.8cm x 0.6cm) were glued into each open end of the cross pipes at vertical and horizontal positions, so that half of the rectangle extended beyond the end of the pipe. For more stability, holes were drilled through the ends of the pipes and the plastic rectangles and a stainless bolt was screwed through them. All bolts were secured with two locking nuts. Four pairs of ceramic tiles (15cm x 15cm) per rack were bolted to the plastic rectangles protruding from the ends of the pipes so that the glazed sides faced inwards and the unglazed surfaces were exposed. On each cross pipe one pair of tiles was fixed horizontally and one vertically. The constructions were secured to the reef at 15m depth using a quick-setting mixture of cement and plaster of Paris (3:1 concentration). A few tiles broke in the first month (for unknown reasons) but were replaced immediately.

Tiles were sampled twice. Sample period I extended from July 2000 to February 2001 and is termed the winter period. It included the mass coral spawning event which occurred in August 2000 (pers. obs.). Sample period II was the summer period and extended from February 2001 until August 2001. Sample period II was shorter than period I (46 to 118 days). In both periods, I installed a total of 224 tiles.

After tiles were collected and replaced, I photographed the exposed side of each using a Nikon 60D with Fuji Sensia 100 ISO film. The percentage cover of benthic components that grew on the exposed sides was estimated visually. The benthic parameters I considered included cover of different functional groups of algae including filamentous, fleshy, macro-, encrusting and coralline algae (adapted from Steneck 1994), sponge, hydroids, bryozoa, sand and mud. Areas of tiles lacking benthic overgrowth were described as empty. After this procedure, tiles were put into bleach for at least 12 hours, then rinsed and carefully checked to ensure all organic material had been removed. They were then sun dried and further examined for coral skeletons using a loupe (8x) magnifying glass and a microscope (Motic S/N 10x).

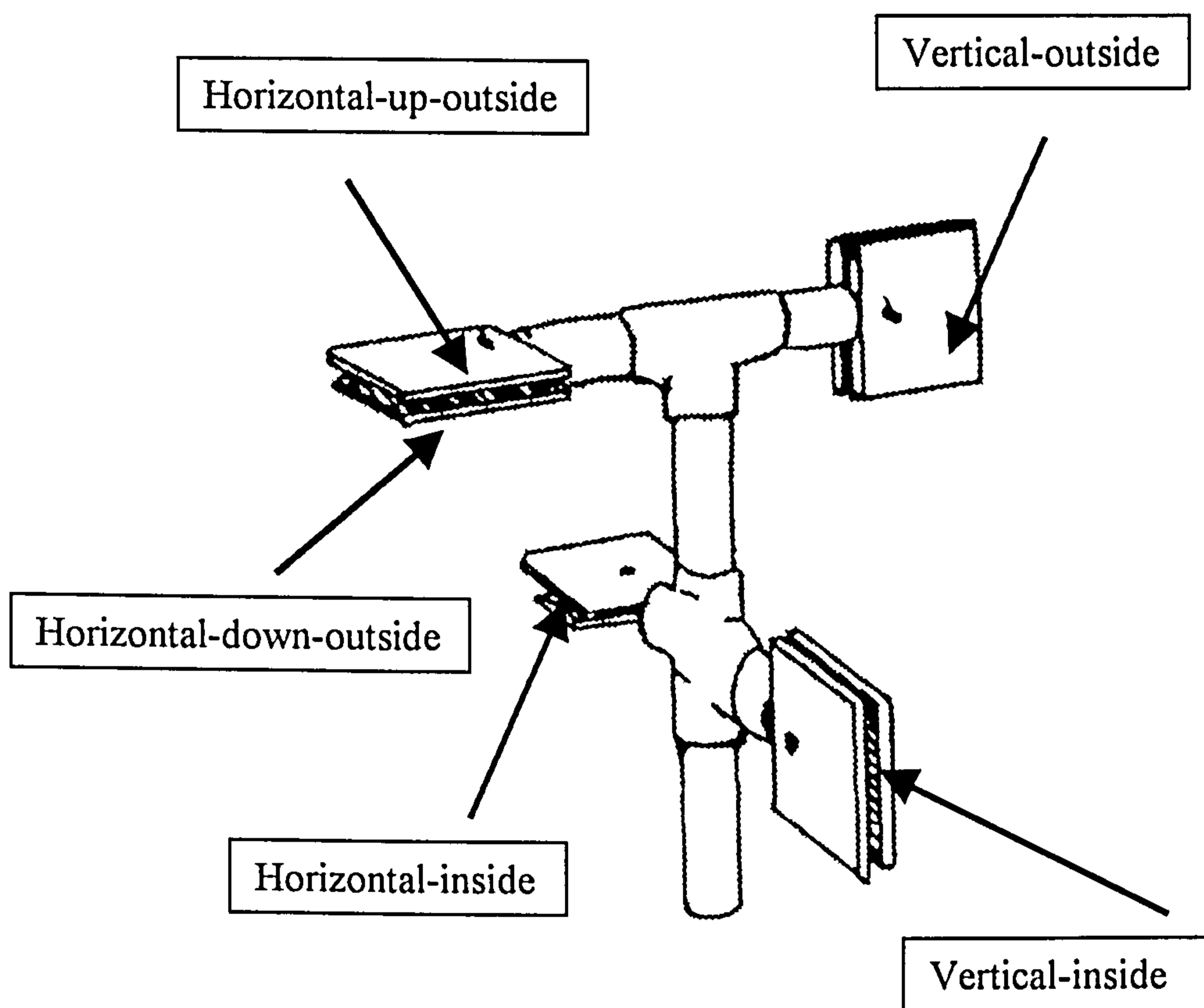


Fig. 1: Construction of artificial settlement plates used to assess coral larval settlement. The upper tiles are 65 cm above the reef substrata, the lower tiles are installed at 25cm height. Boxes indicate the positions in which coral larvae could settle. Method and picture adapted from Rogers et al. (2001).

Each coral skeleton found was identified to species level if possible, and measured to the nearest millimetre. I also noted the position on the tile (horizontal-up-outside, horizontal-down-outside, horizontal-inside, vertical-outside, vertical-inside) on which an individual settler was found (Fig. 1).

4.3.4 Herbivorous fish biomass

Herbivorous fish including surgeonfish (Acanthuridae) and parrotfish (Scaridae) species were counted at depths of 15m at each location once each year from 1995 to 2001, except in 1999. Methods used are described in section 3.3.5 in Chapter 3.

4.3.5 Coral cover

Massive coral cover was monitored once in 2000 and in 2001 at depth of 15m using SCUBA. I estimated percentage massive coral cover visually using a 1m²-quadrat placed at random intervals spaced between 1 m and 5 m along the reef. A minimum of 9 quadrats was sampled on each survey at each location. Three different observers (J. Sladek Nowlis, M. Nugues and myself) performed this monitoring and standardised methods to ensure comparable results.

4.3.6 Data analysis

4.3.6.1 Sedimentation rates

Sedimentation rate (mg.cm⁻².d⁻¹) was analysed using a four-way ANOVA (analysis of variance). The independent factors tested were sedimentation level (high and low), location in bay (inbay, midbay, offbay), time (seven different periods of sedimentation measurements, see also Table 1) and trap height (25cm and 65cm). An incomplete design was used and all interactions among more than two factors were omitted. Sedimentation rate was log_e transformed to approximate the residuals to a normal and homogeneous distribution. Differences in sedimentation rate between the low sedimentation bays and between the high sedimentation bays were analysed using two separate one-way ANOVAs.

4.3.6.2 Coral larval settlement rates

Only tiles remaining fixed to the arrays were analysed. Any tiles or broken pieces found on the reef were not included in the analyses. Settlement rates were estimated for 225cm² which represents the area of an unbroken tile. Settlement rates were calculated for 100 days of exposure in the water. This was necessary because tiles were put in the water and replaced at different times.

An ANOVA with six factors including period (I and II), sedimentation level (high and low), location in bay (inbay, midbay, offbay), stack (I, II), height (25 and 65cm) and the position of the tile (horizontal-up-outside, horizontal-down-outside, horizontal-inside, vertical-outside, vertical-inside) was used with coral larval settlement rate (no of settled corals.225cm⁻².100d⁻¹) as the independent variable. The factor bay was nested within sedimentation level. The ANOVA was incomplete (only two-way interactions were analysed) and a stepwise exclusion of the interactions and factors (only if they were not included in anymore interaction) with the least significant P-value was performed (C. Dytham, pers comm., Quinn and Kojis 2002). All variables that had more than two groups were tested for significance with Tukey's *post-hoc* test (Zar 1996). Residuals were tested for normality and heteroscedasticity (Pallant 2001). Pearson's correlation analyses were used to look at the relationships between coral larval settlement and sedimentation rate, coral cover and herbivorous fish biomass.

The differences in settlement rates between the two low sedimentation bays L1 and L2, and between the two high sedimentation bays H1 and H2 were tested with two separate Mann-Whitney tests to see if bays of the same sedimentation levels receive equal amounts of settlers and if it was legitimate to pool their data.

Finally, I analysed settlement rates of the two commonest species *Porites* spp. and *Agaricia* spp. for the effects of period (I, II), sedimentation level (low, high) and location (inbay, midbay, offbay) using a three-way ANOVA. I did not test for bay as a factor due to very small sample sizes. Performing both tests, I stepwise excluded the most non-significant interactions.

4.3.6.3 Size

Since time of settlement is unknown, the size of settled corals cannot be pooled across periods I and II. Analyses of size needs cautious consideration since the day of settlement for each coral is unknown.

A non-parametric test (Mann-Whitney test) was used to analyse differences in coral sizes between period I and period II. Additionally, two separate non-parametric tests were used for the data set of period I and period II to examine differences in size according to sedimentation level and location in the bay, as well as their interaction (Scheirer-Ray-Hare test).

For each period, differences in size of settled coral species were tested with a Mann-Whitney test due to non-normal and heteroscedastic residuals. Finally, Pearson's correlation analysis was used to test the relationship between the size of settled corals and sedimentation rates.

4.4 Results

4.3.1 Sedimentation rate

A nested fractional factorial ANOVA was used to test differences in sedimentation rate (independent variable) between time (seven different periods of sedimentation measurements), sedimentation level (high, low), location (inbay, midbay offbay) and trap height (25cm, 65cm). Table 2 shows results of the ANOVA model after the stepwise removal of all non-significant interactions. All main factors and two interactions were significant. Sedimentation rate differed significantly over time, varying as a result of seasonal changes in rainfall and events such as coastal and inland construction works (Fig. 2a). Sedimentation was significantly greater in high sedimentation bays (mean: $2.19 \text{ mg.cm}^{-2}.\text{d}^{-1} \pm 0.16 \text{ SE}$) compared to low sedimentation bays ($0.68 \text{ mg.cm}^{-2}.\text{d}^{-1} \pm 0.03 \text{ SE}$) (Fig. 2a-c). In all locations sedimentation rates in the low sedimentation bays were consistently lower compared to those in the high sedimentation bays (Fig. 2b). The high sedimentation bays showed greater fluctuations in sediment load than did the low sedimentation bays (Fig. 2a-c). On all trips, sediment input was greater in the high than in the low sedimentation bays (Fig. 2a).

Table 2: Results of the 4-factor nested ANOVA with time (7 different periods of sedimentation rate measurements from 1997 to 2001 (see Table 1), sedimentation level (low, high), location (inbay, midbay, offbay) and trap height (25cm and 65cm). All significant main factors and interactions after all non-significant interactions were stepwise removed are shown.

Source	df	F-value	P-value
Time	6	30.241	< 0.001
Sedimentation	1	305.446	< 0.001
Location	2	41.651	< 0.001
Trap height	1	5.150	0.023
Sedimentation*Location	2	13.514	< 0.001
Sedimentation*Time	6	12.750	< 0.001
error	1307		
total	1326		

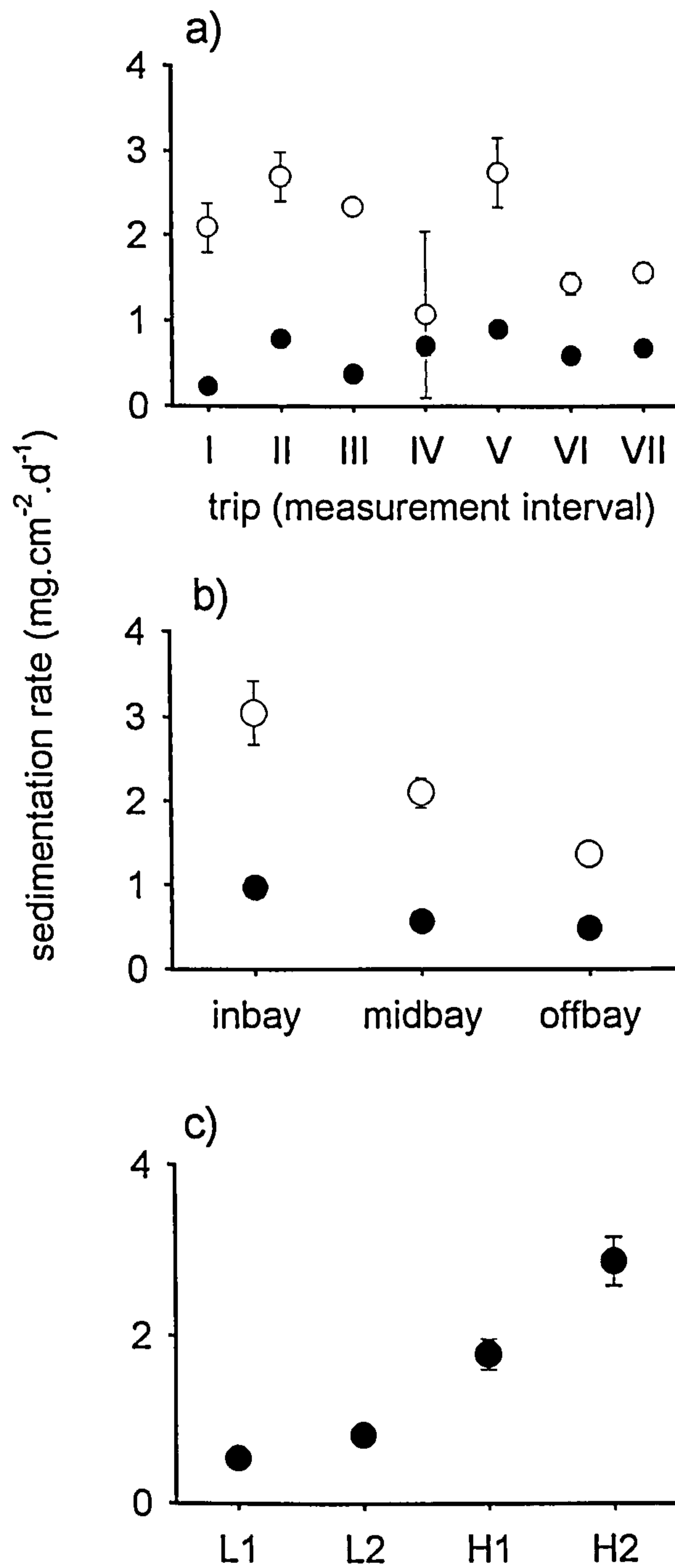


Fig. 2: Patterns of variation in sedimentation rate (mg.cm⁻².d⁻¹) in a) the low and high sedimentation bays (●=low, ○=high) for the different periods from 1997 to 2001 in which sedimentation rate was measured, b) in the different locations (inbay, midbay, offbay) of the low and high sedimentation bays (●=low, ○=high), and c) in the different bays (L1, L2, H1, H2). All points have one standard error bars.

Sedimentation rates differed significantly according to location in bays (Table 2, Fig.2b). The high sedimentation bays represent a gradient of sediment input. Sedimentation was lowest in the offbay and highest in the inbay locations (Fig. 2b). By contrast, sedimentation differed little between locations in low sediment bays (Fig. 2b). However, the inbay location also showed highest sedimentation rate (Fig. 2b).

There was more sediment in the 25cm sediment traps than in the 65cm traps (Table 2). Mean sedimentation rate in the 25cm traps was $1.71 (\pm 0.15 \text{ SE}) \text{ mg.cm}^{-2}.\text{d}^{-1}$, and $1.35 (\pm 0.10 \text{ SE}) \text{ mg.cm}^{-2}.\text{d}^{-1}$ in the 65cm sediment traps. Low traps received greater input from resuspended sediment than high traps.

There was a significant difference in sedimentation rate between the high sedimentation bays and also between the low sedimentation bays. The high sedimentation bay H2 received higher levels of sediment than the high sedimentation bay H1 ($df = 1, F = 14.891, P < 0.001$) and the low sedimentation bay L2 had higher sedimentation rates than the low sedimentation bay L1 ($df = 1, F = 37.058, P < 0.001$) (Fig. 2c).

4.3.2 Coral larval settlement rates

176 of 224 tiles from period I and 183 of 224 tiles from period II were suitable for analysis. The rest were broken, probably by fish pots and anchors. On the unbroken tiles, I counted 119 settled corals in period I and 74 corals in period II. In period I, I found three coral species settled on the tiles, whereas in period II I recorded only two species. Settled corals were identified as *Porites* spp., *Agaricia* spp. and *Stephanocoenia intersepta* (Fig. 3 and 4). Species distribution differed between bays with high and low sedimentation (Fig. 4).

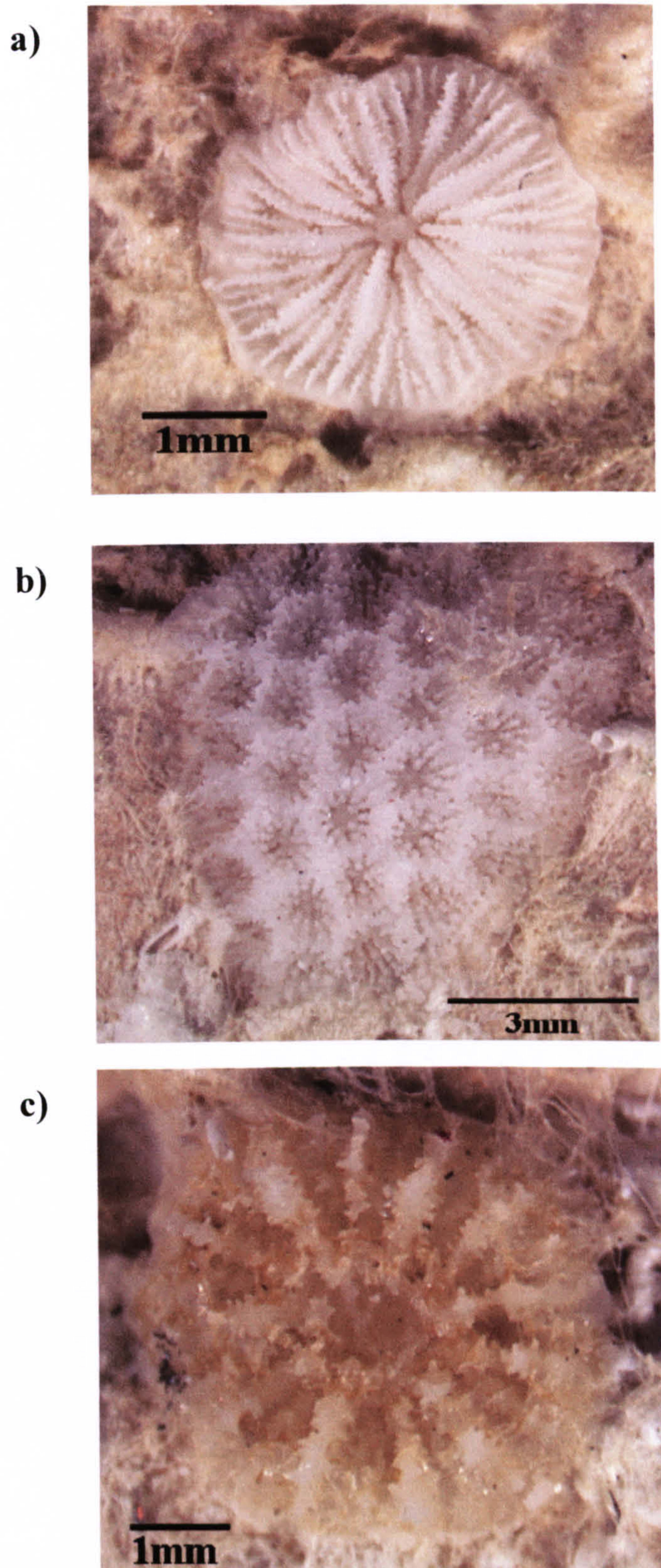


Fig. 3: Coral skeletons found on the tiles were identified as a) *Agaricia* spp., b) *Porites* spp., c) *Stephanocoenia intersepta*.

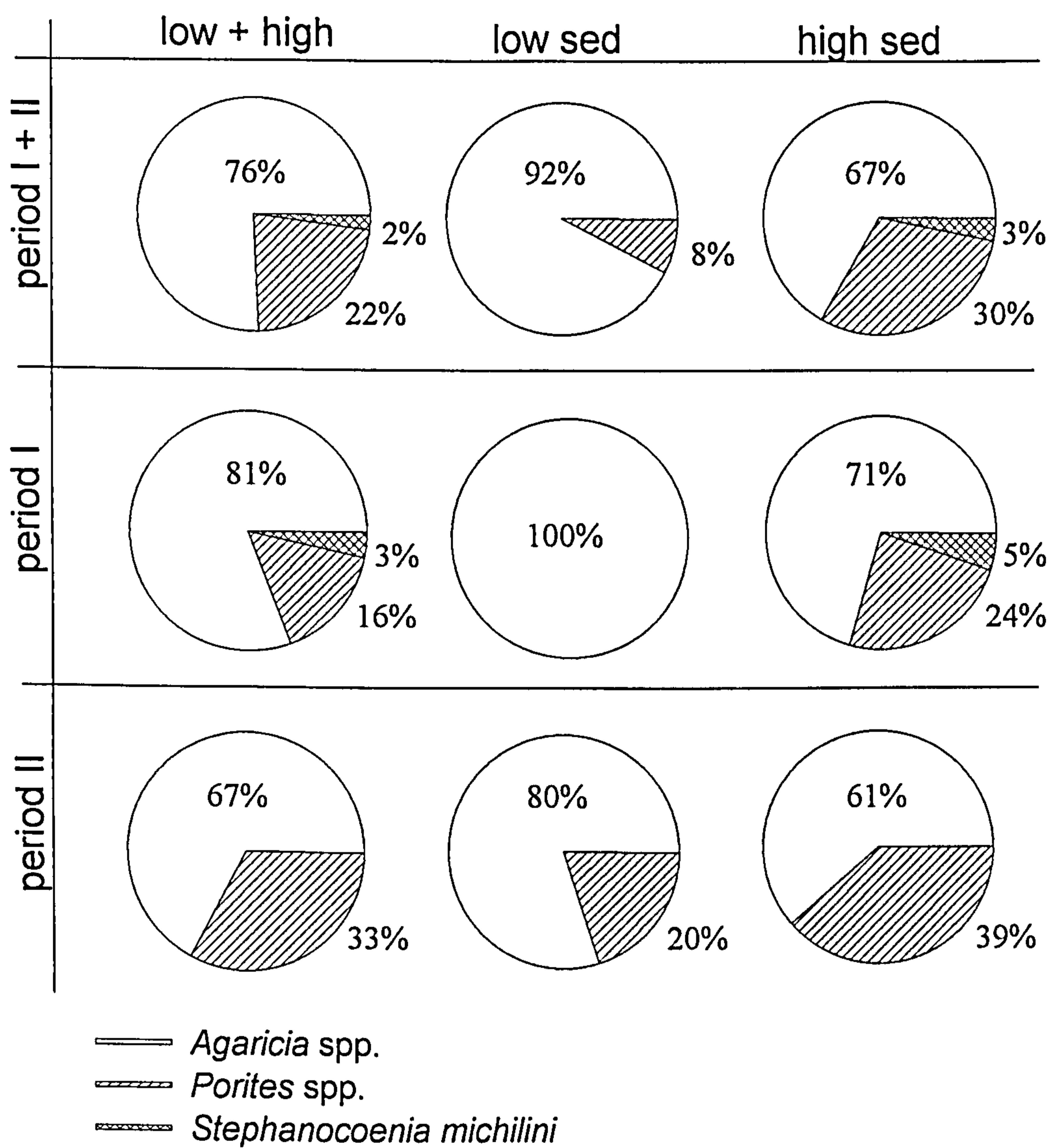


Fig. 4: Pie charts of species distribution showing percentage of total abundance for high sedimentation sites, low sedimentation sites and low and high sedimentation sites combined for period I, period II and period I and II combined. Abundance values are percentage of all settled corals found in one combination.

Table 3: Results of a six-way ANOVA with period (I and II), sedimentation level (high and low), location (inbay, midbay, offbay), height (25cm and 65cm), stack (I, II) and position of the tile (horizontal-up-outside, horizontal-inside, horizontal-down-outside, vertical-inside, vertical-outside). The number of settled coral larvae (number of settled corals. $225\text{cm}^{-2} \cdot 100\text{d}^{-1}$) was the dependent variable. Only two-way interactions were included (incomplete design). The final model shows the results after stepwise exclusion of interactions and variables (only if not present in any interaction) with highest non-significant P-value. Sed = sedimentation level, Loc = location.

source	First Model			Final Model		
	df	F	P	df	F	P
Period	1	0.063	0.802	-	-	-
Sed	1	0.020	0.888	1	0.091	0.763
Loc	2	2.819	0.061	2	3.007	= 0.05
Stack	1	0.369	0.544	-	-	-
Height	1	0.172	0.679	1	0.211	0.646
Position	4	12.037	< 0.001	1	13.384	< 0.001
Period*Sed	1	0.000	1.000	-	-	-
Period*Loc	2	0.926	0.397	-	-	-
Period*Height	1	0.169	0.682	-	-	-
Period*Stack	1	1.417	0.235	-	-	-
Period*Position	4	1.070	0.371	-	-	-
Sed*Loc	2	0.314	0.730	-	-	-
Sed*Height	1	5.193	0.023	1	4.405	0.036
Sed*Stack	1	1.566	0.211	-	-	-
Period*Position	4	0.575	0.681	-	-	-
Loc*Height	2	0.137	0.872	-	-	-
Loc*Stack	2	0.363	0.696	-	-	-
Loc*Position	8	1.504	0.154	-	-	-
Height*Stack	1	0.145	0.703	-	-	-
Height*Position	4	0.167	0.955	-	-	-
Stack*Position	4	0.047	0.996	-	-	-
error	410			449		
total	459			459		

Results of the fractional factorial designed ANOVA including only two-way interactions showed that location (inbay, midbay, offbay) and position of the tile (horizontal-up-outside, horizontal-inside, horizontal-down-outside, vertical-inside, vertical-outside) were factors with significant influences on coral larval settlement rate (Table 3). The interaction between sedimentation level and height (25cm, 65cm) was also significant (Table 3). Table 3 shows all variables and interactions tested (First Model) and also gives results after interactions and variables with the highest P-values were stepwise excluded (Final Model). Variables were only taken out if they were not part of any interaction.

Settlement rates differed significantly according to location within bays (Table 3, Fig. 5). Lowest settlement rates were observed at the inbay location and highest at the offbay location (Fig. 5). I also found a significant effect of tile position on settlement (Table 3, Fig. 6). Settlement was observed on both exposed and covered sides of the differently positioned tiles, except for the upper horizontal tile. Here, settlers were only found on the covered sides. Tukey's *post hoc* test showed that settlement rate was greatest on the vertical-outside tiles compared to all other tile positions (Fig. 6). Although the interaction between sedimentation and settlement position is not significant, it is interesting that slightly more corals settled on the horizontal-down-outside tiles of the high sedimentation bay than on the horizontal-down-outside tiles of the low sedimentation bays (Fig. 6).

Finally, the interaction of the factors sedimentation and height was significant (Table 3). In the low sedimentation bays, settlement rate was higher on tiles 25cm above the reef substrate compared to tiles 65cm above the substrate, whereas settlement rate of the high sedimentation bays was higher on the 65cm high tiles (Fig. 7).

To look at the difference in settlement rate between the two low sedimentation bays and between the two high sedimentation bays, two separate non-parametric Mann-Whitney tests were used. The low sedimentation bays just failed significance ($P = 0.057$), whereas it was clear that there was no significant difference in settlement rates between the high sedimentation bays ($P = 0.221$) (Fig. 8).

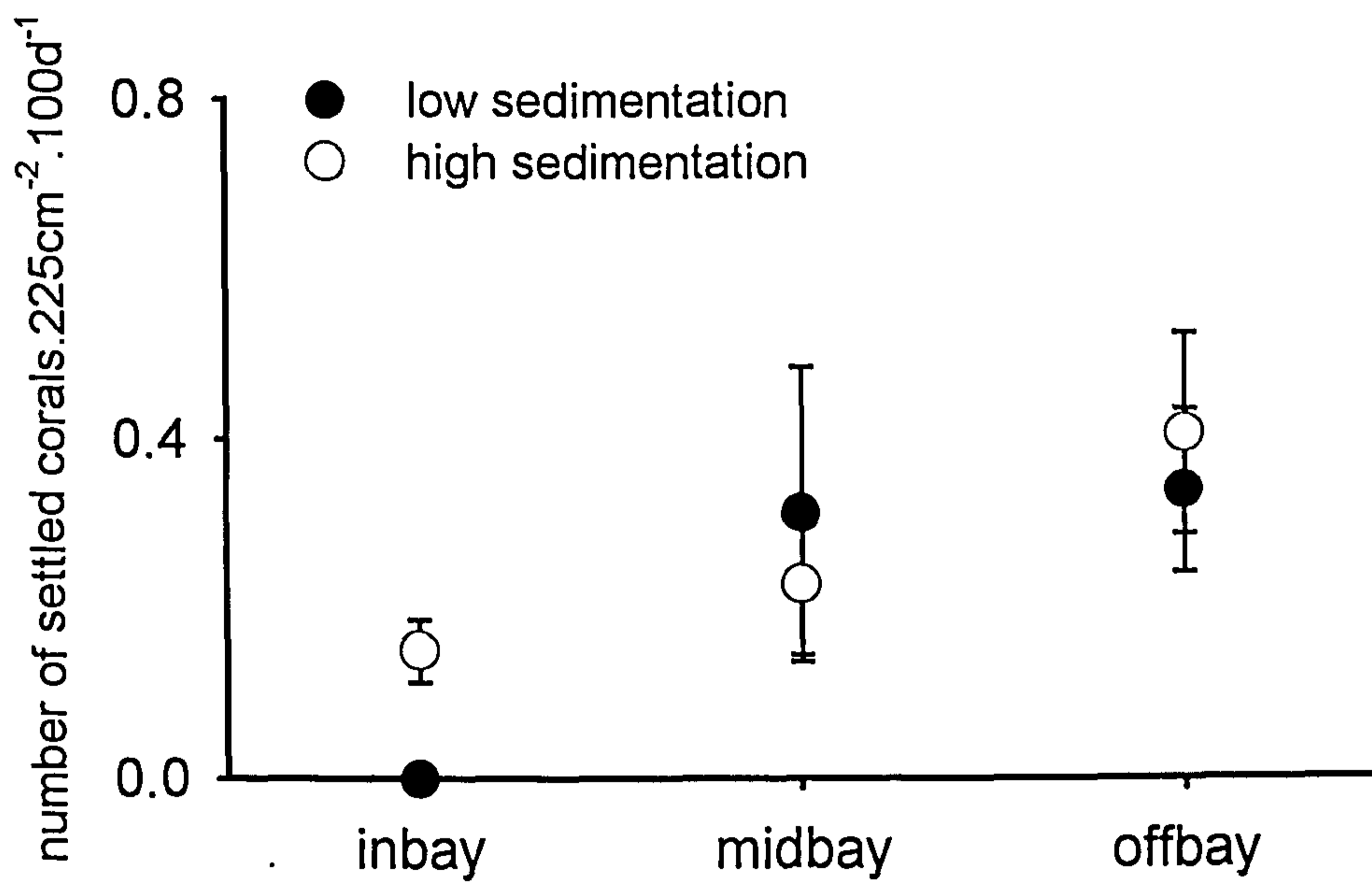


Fig. 5: Patterns of variation in coral larval settlement (number of settled corals.225cm⁻².100d⁻¹) in inbay to offbay locations for high and low sedimentation level. Years are pooled together. Error bars represent one standard error.

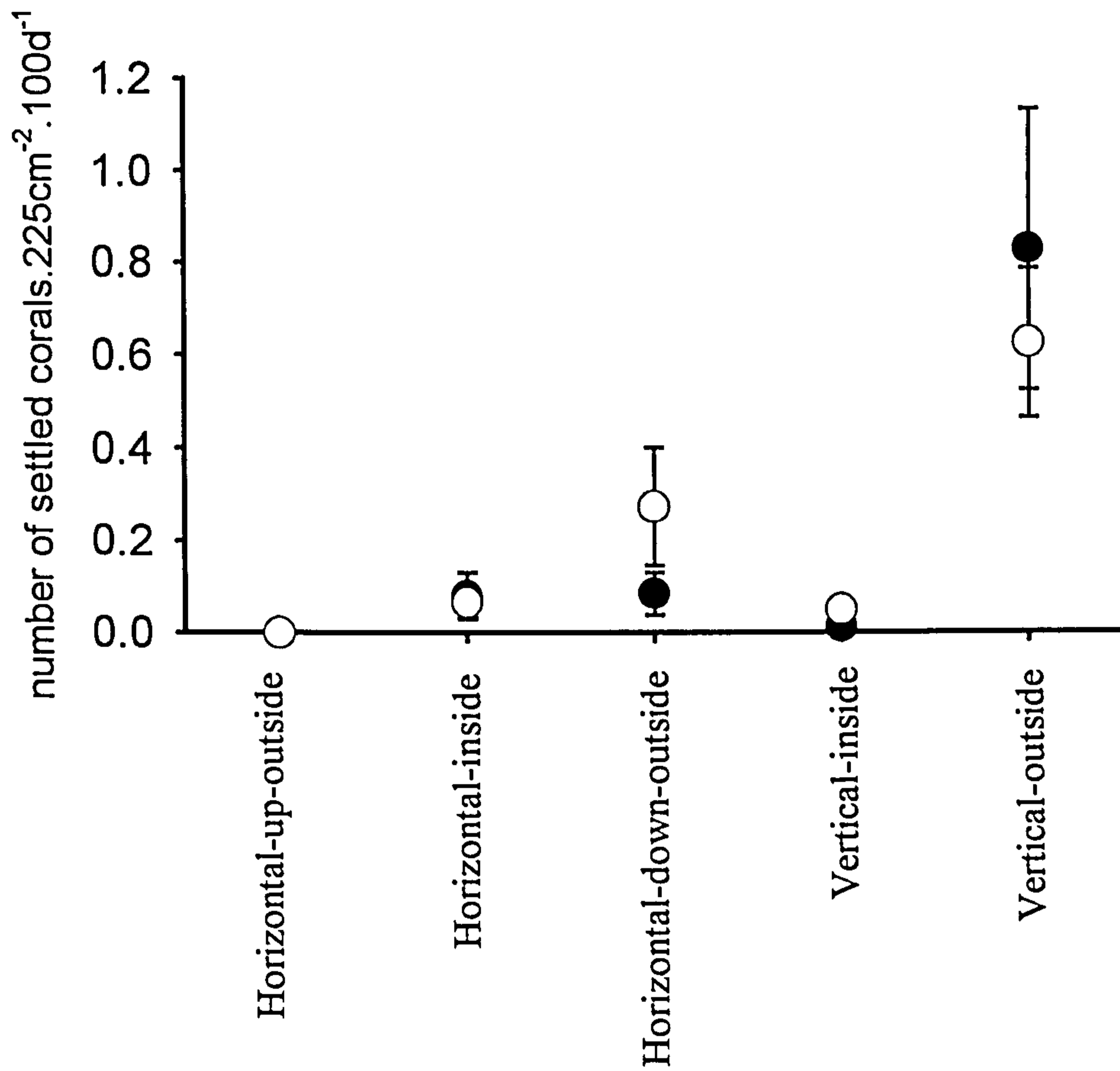


Fig. 6: Patterns of variation in coral larval settlement rate (number of settled corals. $225\text{cm}^{-2} \cdot 100\text{d}^{-1}$) for the differently positioned tiles (horizontal-up-outside, horizontal-inside, horizontal-down-outside, vertical-outside, vertical-inside). Period (I and II) and height (25cm and 65cm) are pooled ($31 \leq n \leq 62$). Error bars represent one standard error. ● = low sedimentation bays, ○ = high sedimentation bays

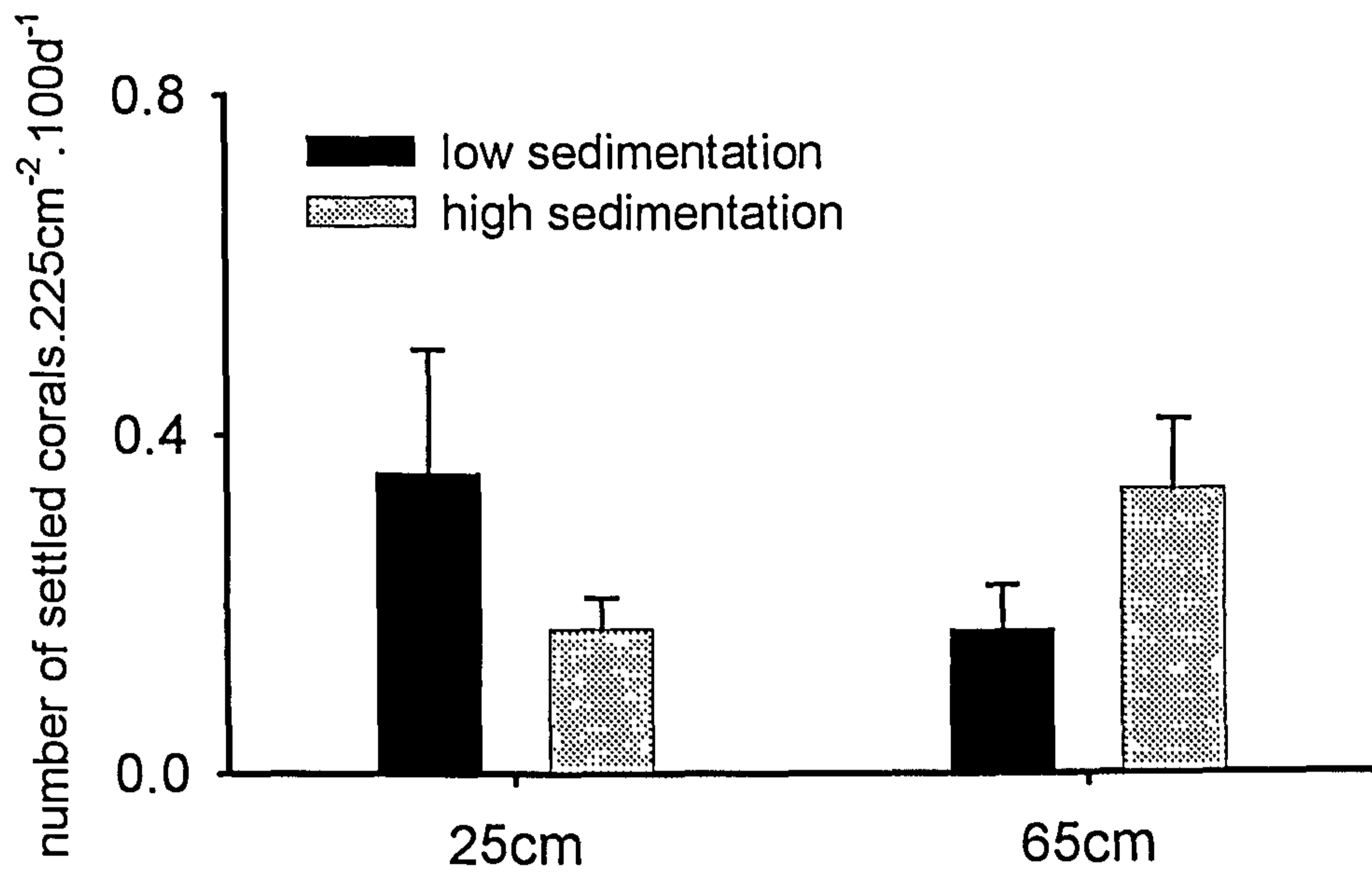


Fig. 7: Number of settled corals (means \pm SE) on tiles ($225\text{cm}^2 \cdot 100\text{d}^{-1}$) that were installed 25cm and 65cm above the reef substrata for low and high sedimentation level.

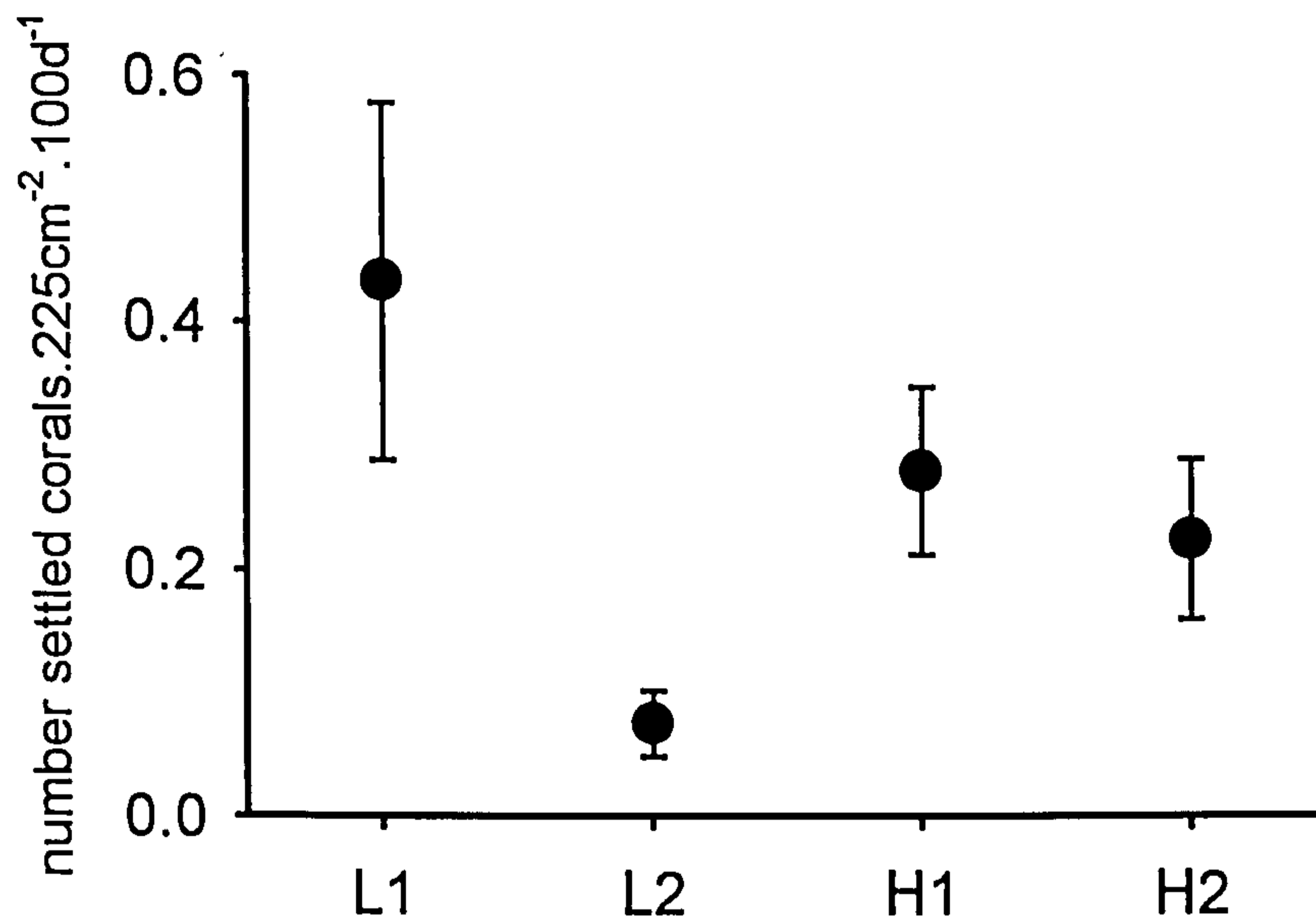


Fig. 8: Coral larval settlement rate (number of settled corals.225cm⁻².100d⁻¹) for each bay (L1, L2, H1, H2) with sample periods pooled together. Error bars represent one standard error. Sample sizes were $n(L1) = 67$, $n(L2) = 65$, $n(H1) = 146$, $n(H2) = 81$.

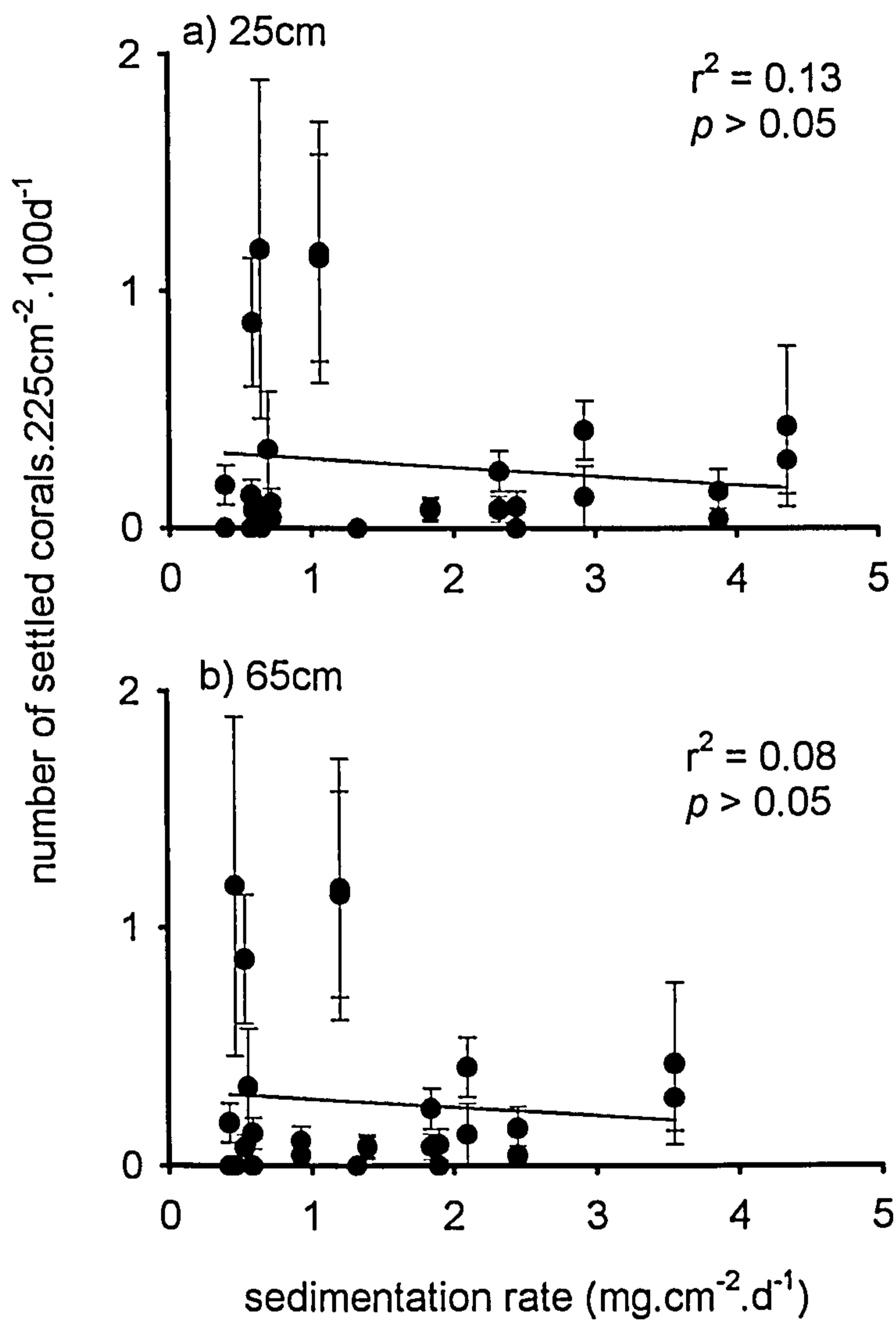


Fig. 9: Relationship between coral larval settlement rate (number of settled corals.225cm⁻².100d⁻¹) and a) sedimentation rate (mg.cm⁻².d⁻¹) of 25cm sediment trap, and b) sedimentation rate (mg.cm⁻².d⁻¹) of 65cm trap. Sedimentation data has been collected from 1997 to 2001. Data for the number of settlers from each site during period I and II have been plotted \pm SE ($4 \leq n \leq 16$). Pearson coefficients are based on mean values per site ($n = 27$). ● = settlement in period I, ○ = settlement in period II.

Pearson's correlation analysis was used to consider the relationship between coral larval settlement rates and actual sedimentation rates from 25cm and 65cm sediment traps measured from 1997 to 2001. Correlations were very weak and relationships non-significant (Fig. 9). However, it is notable that highest settlement rates occurred in the locations with very low sedimentation. I also analysed settlement versus sedimentation rate using sedimentation data only for the period tiles were in the water. The highest settlement rates are still found in locations with low sedimentation input, but the results of this analysis were even weaker compared to the analysis using sedimentation rates from 1997 to 2001. This is probably because the sedimentation rate sample sizes of both periods were very small (period I: n=3, period II: n=4).

Using Pearson's correlation, I analysed relationships between settlement rates and massive coral cover and herbivorous fish biomass on the reef (Fig. 10a and 10b). Coral cover was positively associated with the number of settled corals (Fig. 10a). Coral larval settlement tended to increase with increasing coral cover. Herbivorous fish biomass did not show any clear relationship with the settlement rate (Fig. 10b).

Finally, I analysed settlement rates separately for the two most common species (*Porites* spp. and *Agaricia* spp.) to see if both reacted similarly to sedimentation and location in the bay. *Porites* spp. settlers were around two-thirds more common than *Agaricia* spp. (Fig. 4 and Fig. 11). The factor bay nested within sedimentation as well as all independent factors describing the position of the settled corals were omitted due to low sample sizes. The results show that location in the bay had a strong effect on *Porites* spp. but not on *Agaricia* spp., with settlement rates increasing from inbay to offbay (Table 4, Fig. 11). By contrast, *Agaricia* spp. was significantly affected by sedimentation but *Porites* spp. was not (Table 4). More *Agaricia* spp. larvae settled to the high compared to the low sedimentation bays (Fig. 11).

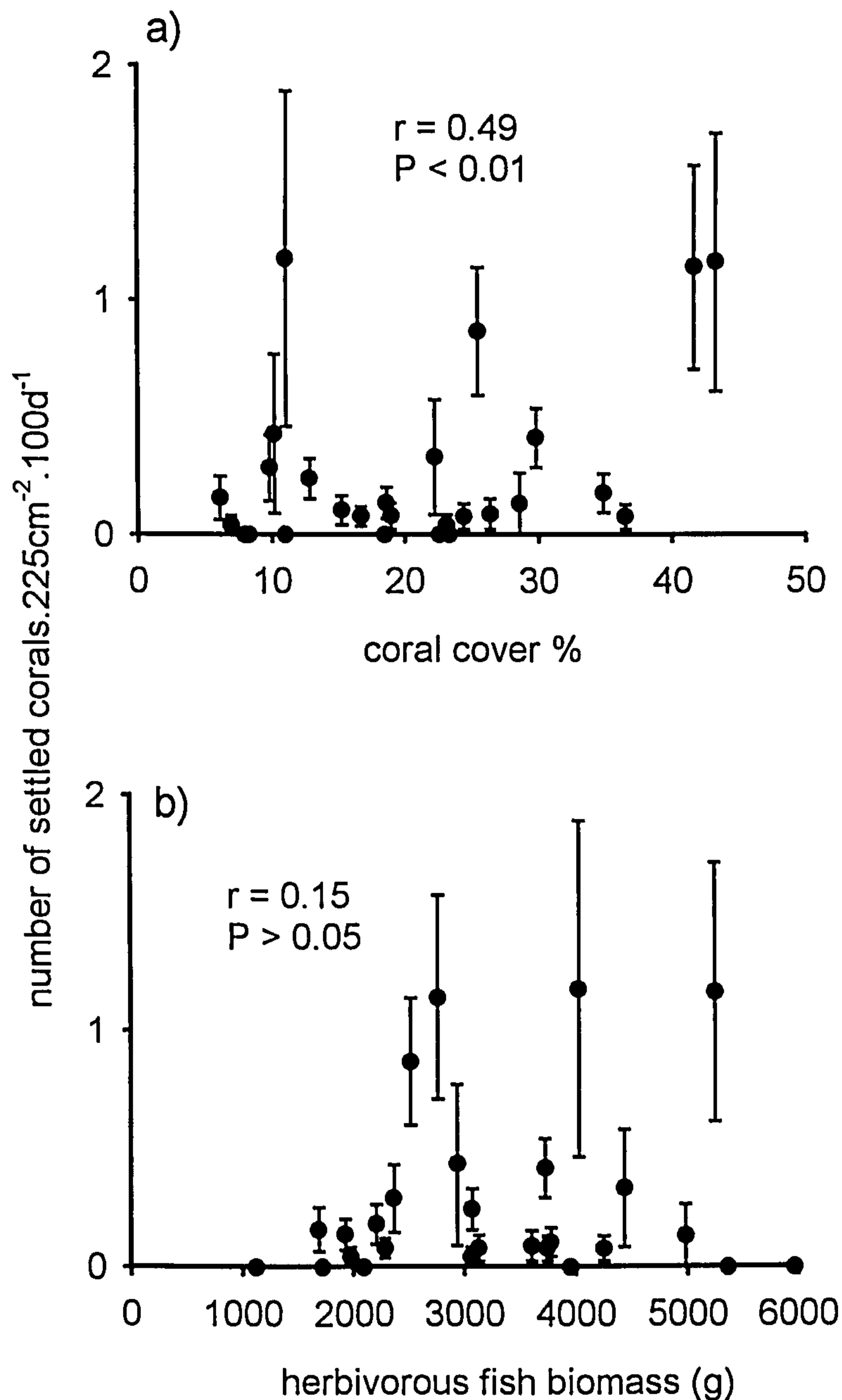


Fig. 10: Relationship between coral larval settlement rate (number of settled corals.225cm².100d⁻¹) and a) percentage coral cover and b) herbivorous fish biomass (g). Data from each site for period I and period II is plotted. Error bars represent one standard error. Sample size for coral cover was $12 < n < 16$ 1m²-quadrats per location and herbivorous fish biomass $n = 6$ counts per location. Pearson coefficients are based on mean values per site ($n = 27$).

Table 5: Results of 3-factor ANOVA with period (I, II), sedimentation level (low, high) and location (inbay, midbay, offbay) as factors and with 1) *Porites* spp. and 2) *Agaricia* spp. the as the independent variables. For *Porites* spp. the first ANOVA model is shown and for *Agaricia* spp. the final model after stepwise removal of all non-significant interactions. Sed = sedimentation, Loc = location

Source	1) <i>Porites</i> spp.			2) <i>Agaricia</i> spp.		
	df	F	P	df	F	P
Period	1	0.377	0.540	1	1.933	0.165
Sed	1	0.048	0.826	1	4.640	0.032
Loc	2	4.399	0.013	2	1.043	0.353
Period*Sed	1	0.020	0.889	-	-	-
Period*Loc	2	1.316	0.270	2	2.582	0.077
Sed*Loc	2	0.423	0.655	-	-	-
Period*Sed*Loc	2	2.792	0.063	-	-	-
error	347			347		
total	359			359		

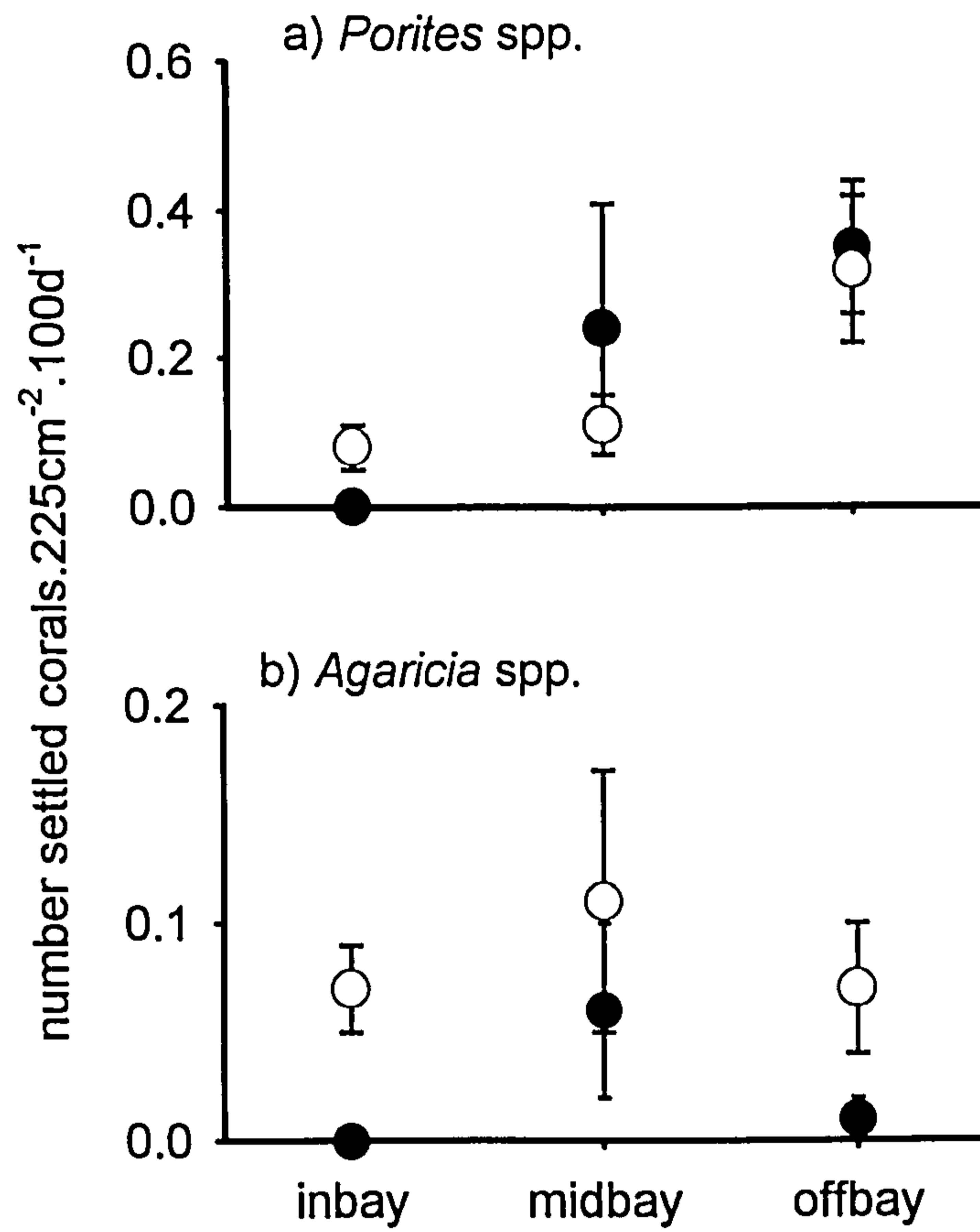


Fig. 11: Pattern of variation in settlement rate (number of settled corals.225cm².100d⁻¹) for the coral species a) *Porites* spp. and b) *Agaricia* spp. in low and high sedimentation bays. Periods I and II are pooled. Error bars represent one standard error. ● = low sedimentation, ○ = high sedimentation.

4.3.3 Size

Since time of settlement is unknown, the size of settled corals cannot be pooled across periods I and II. Settlers measured at the end of period II were the same size as settlers from period I (Mann-Whitney test: $P > 0.05$, period I: mean = $2.3\text{mm} \pm 0.2 \text{ SE}$; period II: mean = $2.2\text{mm} \pm 0.1 \text{ SE}$) despite period II being around 70 days shorter than period I.

For each period (I and II) and for the main coral species (*Agaricia* spp. and *Porites* spp.), I tested whether size was affected by sedimentation level (high, low) and/or the location in the bay using two separate Scheirer-Ray-Hare tests for period I and II. For both periods, neither of the factors nor their interaction were significant ($P > 0.05$ for sedimentation level, location and their interaction for both periods) (Fig. 12).

In period I, there was a significant difference in size among the three species (Kruskal-Willis test: $P < 0.001$), with *Agaricia* spp. corals being bigger than *Porites* spp. In period II, the coral species also differed in size from each other (Fig. 13). Since *S. intersepta* only settled in period I, only the size between *Porites* spp. and *Agaricia* spp. could be compared. The Kruskal-Willis test gave a significant result ($P < 0.001$). Again, *Agaricia* spp. settlers were bigger than *Porites* spp. (Fig. 13b).

To further examine whether sedimentation rate influences settlement rates, I plotted larval settlement against sedimentation rates of 25cm and 65cm sediment traps using sedimentation rates measured from 1997 to 2001 (Fig. 14a). All correlations were not significant and no relationship between settlement rate and sedimentation rate (25cm and 65cm) could be found (Fig. 14a). I also tested the relationship between size and sedimentation of each trap that was measured in period I and period II while tiles were exposed. Results of this analysis did not show any relationship either, probably also because only a small sample size of sedimentation measurements for each period was present (period I: $n = 3$, period II: $n = 4$).

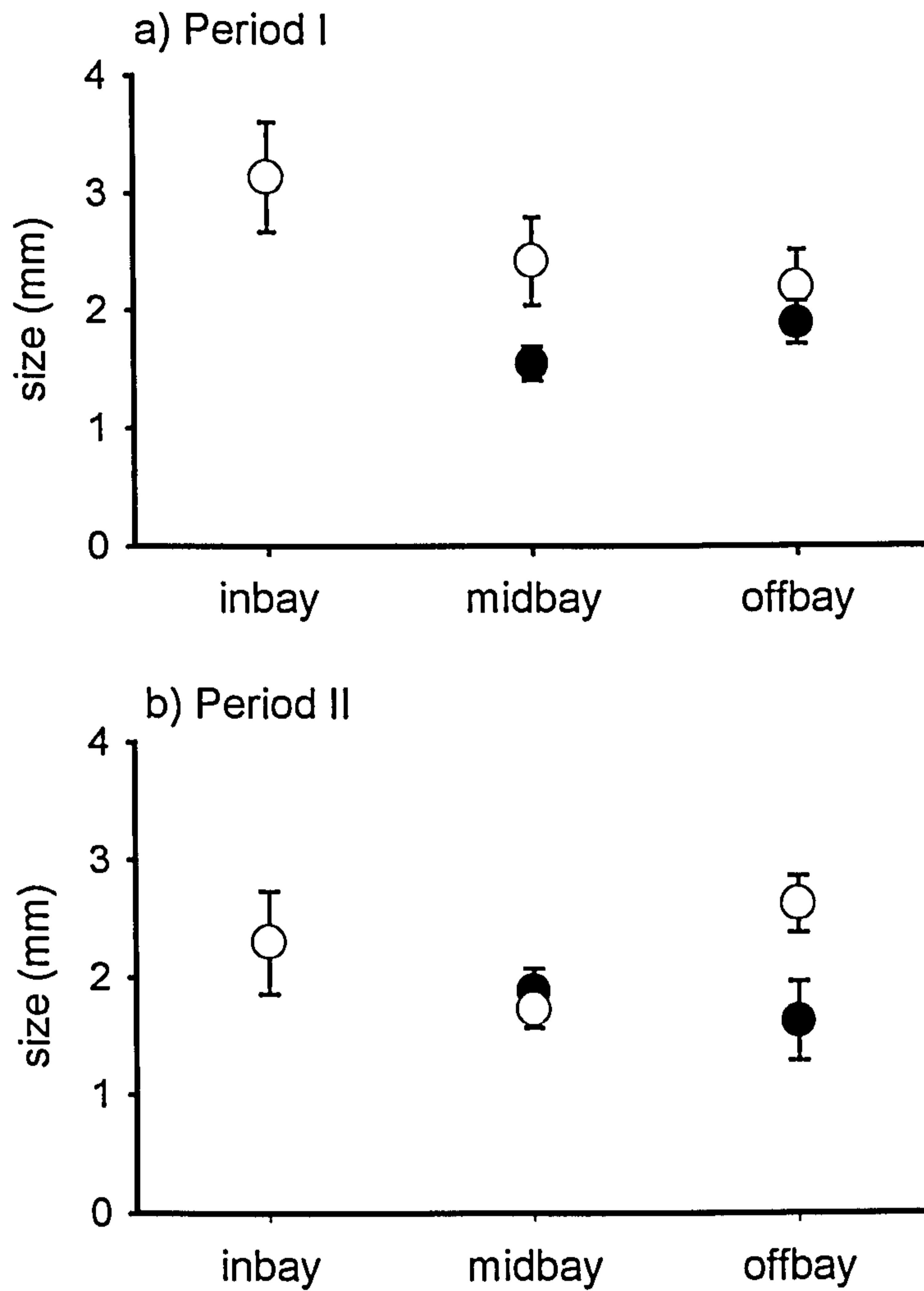


Fig. 12: Patterns of differences in size (mm) of settled corals (● = low sedimentation bays, ○ = high sedimentation bays) found in period I and period II (mean \pm SE). No corals were found in the inbay locations of the low sedimentation bays in both periods.

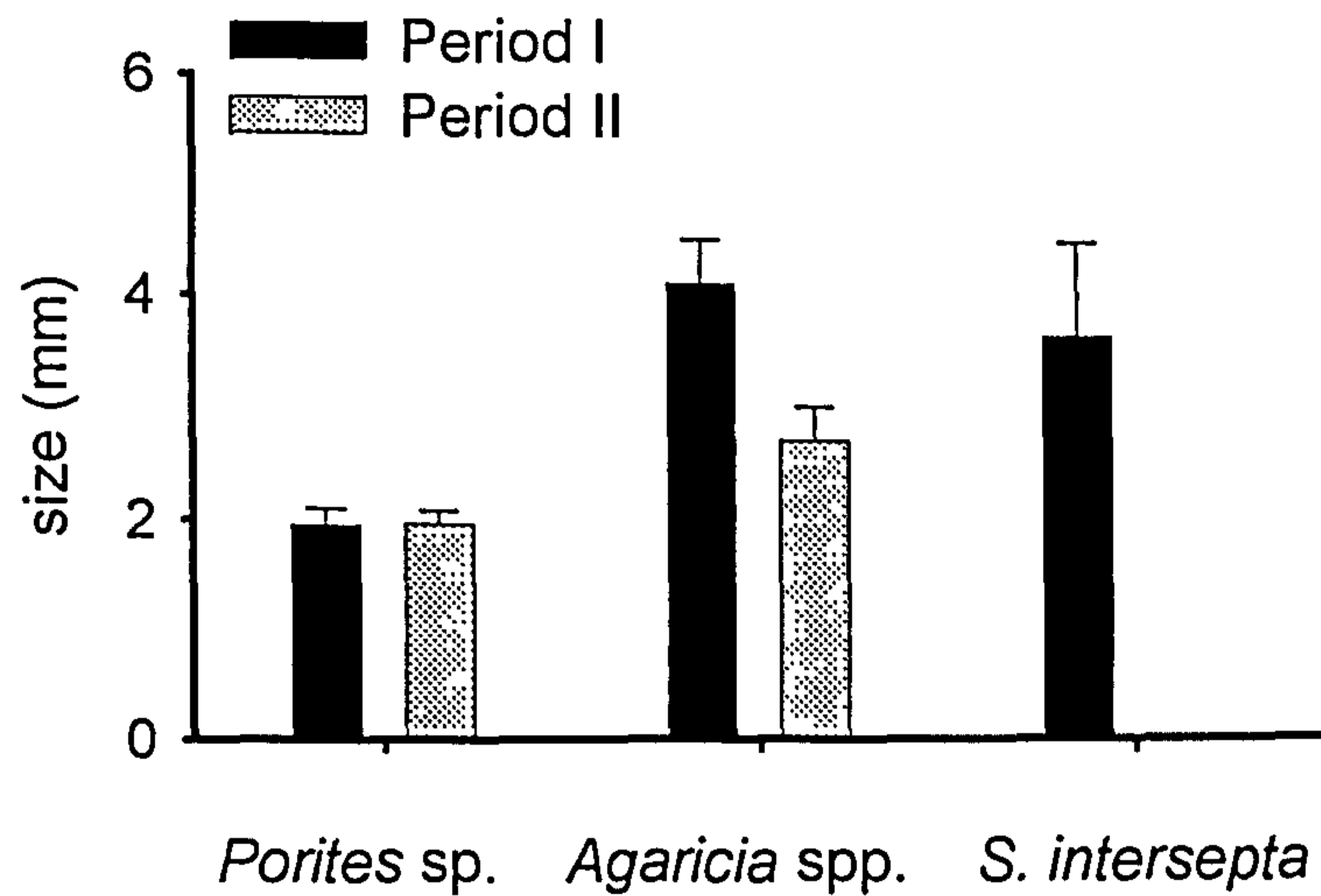


Fig. 13: Patterns of difference in size (mm) of corals found settling on tiles in period I and period II. *Stephanoeceania intersepta* (*S. intersepta*) was only found in period I. Error bars represent one standard error. Sample sizes for period I: *Porites* spp.: $n = 97$, *Agaricia* spp.: $n = 18$, *S. intersepta*: $n = 4$; period II: *Porites* spp.: $n = 49$, *Agaricia* spp.: $n = 24$).

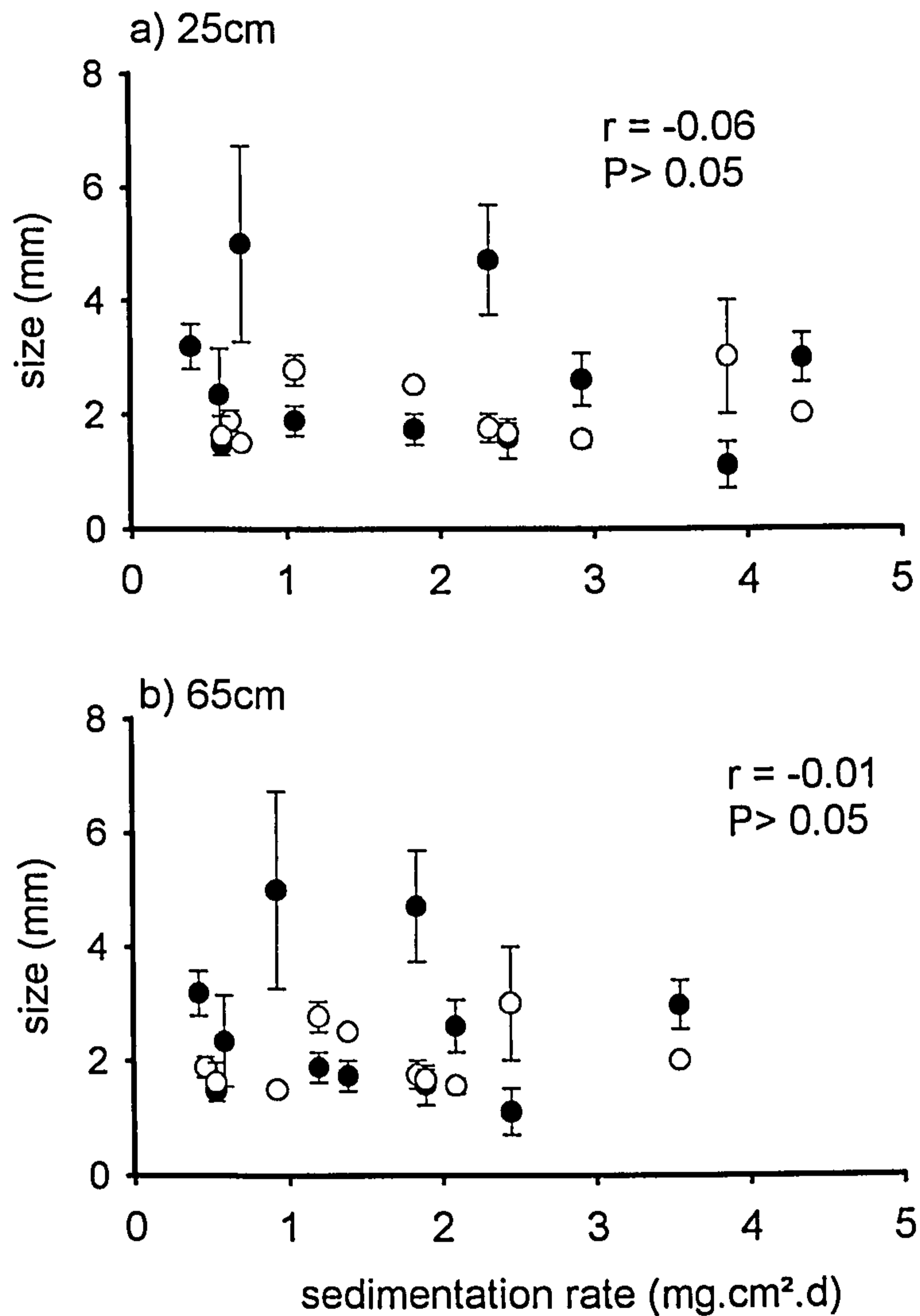


Fig. 14: Relationship between the size (mm) of settled corals and a) sedimentation rate (mg.cm⁻².d⁻¹) measured in 25cm traps from 1997 to 2001, and b) sedimentation rate (mg.cm⁻².d⁻¹) measured in 65cm traps from 1997 to 2001. Data from each site during period I and II is plotted. Error bars represent one standard error. Sample size for each site was $1 \leq n \leq 30$. Pearson coefficients are based on mean values per site ($n = 21$). ● = period I, ○ = period II.

4.5 Discussion

My study showed no direct effect of sedimentation on total coral larval settlement rate. There was no difference in the number of settlers between bays with low and high sedimentation level, but it seems that different coral species react differently to sediment inputs. However, total settlement rate increased with increasing distance from the head of bays to their headlands. Furthermore, I observed changes in the settlement behaviour of coral larvae when different quantities of sediment were present. In the low sedimentation bays, coral larvae preferred to settle on tiles that were closer to the reef, whereas in the high sedimentation bays more settlers were found on tiles that were further above the reef. Biomass of herbivorous fish did not show a significant effect on the number of settlers, whereas adult coral cover was weakly related to larval settlement. Sedimentation input did not affect the size of the settled corals. Size differences were species-specific.

Despite observing highest settlement rates in locations receiving very low levels of sediment, a major difference in settlement rates between the two different levels of sediment input could not be found. This might be because even if the low sedimentation bays have much lower sediment input than the high sedimentation bays, the two low sedimentation bays differed in their quantities of sediment. The low sedimentation bay L2 had significantly higher sediment input than the low sediment bay L1. The higher sedimentation rate of L2 may be enough to reduce settlement. In a laboratory experiment using high and low sedimentation treatments and a control treatment without sediment, Gillmour (1999) observed that coral larval settlement was reduced not only by high sediment input (ca. 100 mg.l⁻¹), but even larvae exposed to low sedimentation levels (ca. 50 mg.l⁻¹) underwent significantly less settlement. However, Babcock and Davies (1991) also failed to find a significant difference in settlement rate under different sediment treatments (0.5 to 325 mg.cm⁻².d⁻¹) in a laboratory experiment. It is notable that the high sedimentation bay H1 had higher settlement rates than L2 indicating that reef variables other than sedimentation act separately in each bay and that such factors may have played an important role in

determining settlement rates. For instance, the locations in each bay (inbay, midbay, offbay) also represent an exposure gradient and differ in coral cover and herbivorous fish biomass (see Chapter 2). Sedimentation rates were lowest in the offbay locations, whereas coral cover and herbivorous fish biomass were lowest in the inbay locations and highest in the offbay locations (Chapter 2). Moreover, other factors such as currents, wave activity and predation on planktonic larvae might be important in determining number of larval settlers (Gaines and Bertness 1992, Holmes et al. 1997, Hughes et al. 2000, Lugo-Fernandez et al. 2001).

Although a direct relationship between sedimentation and coral larval settlement was not found, my results indicate that sedimentation influences settlement behaviour. The low sedimentation bays showed high coral settlement rates on tiles 25cm above the reef substrata and lower settlement rates on 65cm high tiles whereas the reverse was true in the high sedimentation bays. Conditions on the high sedimentation reefs could be worse closer to the reef due to greater resuspension of sediment. Hence, coral larvae may avoid settling on lower substrata even though lower settlement positions may be preferred. In the low sedimentation bays, coral larvae might be able to exercise any preference for lower lying substrata due to better water quality. My finding is supported by other studies where 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). However, it is worth noting that artificial settlement substrata were used in all these studies and settlement rates to natural benthic substrata might differ. For example, more sediment accumulation may occur on natural substrata due to increased algal growth that captures sediment particles (Walker and Ormond 1982).

My study shows that coral larval settlement was lowest on horizontal tiles. Not a single coral was observed settling on the exposed sides of the horizontal-up tiles. This may be because such corals died at an early stage before I examined the tiles and their skeleton was eroded beyond recognition. Several other researchers who did not find settlers on horizontal upper artificial substrata suggested that it may be because settlement is prevented by increased sediment particle

accumulation in filamentous algae in this position (Birkeland et al. 1981, Baggett and Bright 1985, Oren and Benayahu 1997). Hence, even at the low sedimentation locations of my study area, sedimentation accumulation on the upper side of horizontal tiles might have been sufficient to prevent coral settlement.

In this study, highest settlement rates occurred on the outside of the vertical tiles, a finding common to other studies (Rogers et al. 1984, Carleton and Sammarco 1987, Babcock and Mundy 1996). I observed very high settlement rates of other benthic organisms (e.g. sponges, ascidians, bryozoans) especially on the outside of horizontal-down-tiles and they probably competed with coral larvae for space (Baggett and Bright 1985, Fitzhardinge 1988, Harriott 1995, Dunstan and Johnson 1998). Furthermore, it is notable that on the horizontal-down-outside tiles settlement was slightly higher in the high sedimentation bays than in the low sedimentation bays. It seems that under high sediment conditions more larvae choose the usually unfavourable settlement site underneath the tile, perhaps to avoid sediment, whereas under low sediment conditions, they seem to prefer the outside of the vertical tiles (see Fig. 7). Another explanation is that spatial competition with other benthic organisms may be lower on reefs with high sediment input due to worse water quality and substrate conditions caused by sediment (e.g. Maida et al. 1994) and, hence, less larvae are able to settle on the outside of horizontal-down-tiles in low sediment conditions. In the study area I found that dry-weight of benthic biomass was reduced with increasing sedimentation (see Chapter 2).

Herbivorous fish may affect corals by grazing algae and opening up free space for coral larvae to settle (Birkeland 1977, Brock 1979, Birkeland 1988). They may also reduce densities of newly settled corals by unintentionally scraping them off when feeding on algae (Sammarco 1980, Sammarco and Carleton 1981, Harriott 1985, Miller and Hay 1996, Miller and Hay 1998). In this study, no clear relationship between grazing fish and larval settlement was found. However, apart from one point, there is a suggestion in Figure 10b of higher settlement at intermediate herbivore fish biomass. This would suggest that low grazing pressure enhances algal growth and prevents coral larvae from settling, and too much grazing pressure decreases settlement rates, probably because fish scrape off small

corals when feeding on the algae. On some of the tiles, I found deep bite marks and marks of scraping teeth. This seemed to occur at random indicating that grazing was unselective. However, there is a slight possibility that fish grazing on the tiles might have influenced my results.

Coral cover shows a weak relationship with coral larval settlement. Since I do not have data on the species distribution of adult corals, I can only hypothesise that high coral cover also means high cover of the species that settled on the tiles. All settlers in my study (*Agaricia* spp., *Porites* spp.) are brooders (see Fadlallah 1983) and, hence, their larvae might settle close to the parental colony (Harrison and Wallace 1990, Harriott 1992, Harriott and Banks 1995, Fabricius and De'ath 2001). If a location has a low coral cover, low coral settlement might be due to lack of parental brooders. Several studies have shown a positive relationship between adult coral cover and juvenile coral abundance (Neudecker 1981, Chiappone 1996, Nzali et al. 1998, Reyes and Yap 2001), whereas others have failed to show a relationship (Bak and Engel 1979, Edmunds 2000, Hughes et al. 2000). However, another possibility is that high coral cover represents 'good' conditions for growth and survival of settled corals and, consequently, larvae might use presence of adults as a settlement cue (Allee effect) (Courchamp 1999).

In the Caribbean, the most common coral species found in settlement studies belong to the genus *Agaricia* and *Porites* (Bak and Engel 1979, Rogers et al. 1984, Baggett and Bright 1985). This was also true in my study. *S. intersepta* is a gonochoric spawner (Hagman et al. 1998, De Graaf et al. 1999) and, hence, was only found on tiles in period I that included the spawning event. *Agaricia* spp. only settled on tiles installed on reefs with high sedimentation rates in period I. I did not expect to find *Agaricia* spp. in higher numbers in the bays with high sedimentation rates because *Agaricia* spp. is known as a species that is normally rare in high sediment conditions due to its low resistance towards smothering by sediment (see Rogers 1990). Hence, it could be hypothesised that corals in high sediment conditions are adapted to survive in these conditions (Bak and Elgershuizen 1976, Chou 1988, McClanahan and Obura 1997).

I expected corals in high sedimentation locations to have lower growth rates because of the energy required to remove sediment and/or reduced light

penetration and photosynthesis (Edmunds and Davies 1989). This was not the case and growth rates even appeared to be higher in high sedimentation bays. Perhaps corals were growing fast to escape being smothered by sediment (Wittenberg and Hunte 1992, Babcock and Mundy 1996). However, they could only do this if they had sufficient energy. Tomascik and Sanders (1985) who measured growth rates of *Montastrea annularis* along a eutrophication gradient in Barbados found that growth was highest with moderate eutrophication levels. They speculate that corals may use nutrients as an energy source and increase growth rates up to the point where eutrophication levels have negative impacts on corals including smothering and reduced photosynthetic output due to decreased light penetration. Rosenfeld et al. (1999) provided direct evidence for the ability of a coral to digest the sediment's organic fraction and suggest sediment as possible food source for corals.

In conclusion, my study showed that coral larval settlement does take place on reefs with high sedimentation rates. In the high sedimentation location of my study area, larvae occur in the water column and readily settle on artificial substrata. However, even if coral larvae settle on reefs with high sedimentation rates, mortality rates of juvenile corals might be higher due to smothering by sediment and reduced health status (Chapter 3, Tomascik 1991, Babcock and Mundy 1996, Gilmour 1999). Coral larval settlement is reported to be very variable in space and time (Birkeland 1977, Fisk and Harriott 1990, Smith 1992, Dunstan and Johnson 1998, Hughes et al. 1999) and my study confirms this. It seems that longer monitoring projects will be necessary to fully understand the forces affecting coral larval settlement. For example, the two periods over which I collected data might have been good or bad ones for coral settlement. Long-term studies may also help extract the impacts of sedimentation from the background of other factors acting on reefs and confounding the results, such as eutrophication (Tomascik 1991, Wittenberg and Hunte 1992). High sedimentation rates generally also mean greater eutrophication since nutrients and organic matter accompany sediment (Tomascik and Sander 1985, Tomascik and Sander 1987, Wittenberg and Hunte 1992, Gabric and Bell 1993, Sladek Nowlis et al. 1997). However, my study does suggest that sedimentation affects settlement in subtle ways and can be a chronic reef degrading factor.

4.6 References

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Chapter 5

Impacts of sedimentation on mortality, settlement and growth of juvenile coral

5.1 Abstract

Sedimentation is caused by run-off from rivers, mainly after heavy rainfall and is one of the major threats to coral reefs world-wide. I studied sediment impacts on reefs of the west coast of St. Lucia in four different bays. Two bays had low sedimentation inputs and two bays had high sedimentation input from rivers that opened into them. In each bay, three to five locations were selected for monitoring between the head of the bays and their headlands. This study focuses on the effects of sedimentation on the replenishment of coral communities by coral larval settlement and examines survival and growth of settled corals on natural reef substrata using permanent photoquadrats. Observations were repeated twice over a one year period. The results show that settlement, mortality and growth rates of juvenile corals were very variable over time. Mortality rates of juvenile corals did not differ between bays with different sedimentation levels, nor did the location in the bay play an important role. A close to significant ($P = 0.073$) correlation showed that with increasing sedimentation mortality rates decreased. Settlement rates on natural substrata did not differ between the low and high sedimentation

bays either, but were significantly higher at the mouths of the bays ($0.5 \text{ settlers} \cdot 600\text{cm}^{-2} \cdot 100\text{d}^{-1} \pm 0.07 \text{ SE}$) than at their heads ($0.23 \text{ settlers} \cdot 600\text{cm}^{-2} \cdot 100\text{d}^{-1} \pm 0.06 \text{ SE}$). Juvenile coral growth rates were higher on reefs with low sedimentation ($0.15\text{cm} \cdot 100\text{d}^{-1} \pm 0.02 \text{ SE}$) than with high sedimentation ($0.09\text{cm} \cdot 100\text{d}^{-1} \pm 0.01 \text{ SE}$). A correlation between sedimentation and settlement rates showed that with increasing sedimentation settlement decreased significantly. Growth rate of all corals was higher in the low sedimentation than in the high sedimentation bays. However, I did not find any difference in growth of different species between the low and high sedimentation reefs. Irrespective of coral species, degradation rate did not differ between low and high sedimentation reefs. The total mortality rate for all locations for the one year study was 40.7%, and the settlement rate to natural substrata was equivalent to 18.8% of the original coral numbers. These settlement rates are comparable with rates reported from other studies in the Caribbean. However, mortality rates encountered in this study seem to be very high and are unlikely to be representative over the long-term. If they were such, in several years time no juvenile corals would be found on these reefs. In summary, this study showed that sedimentation has a negative effect on the replenishment of coral reefs by reducing settlement and growth. Long-term observations are necessary to determine juvenile coral mortality rates over several years to reveal whether or not new settlers can replace the loss of coral cover seen on St. Lucia's reefs.

5.2 Introduction

Coral reefs occupy only 0.09% of the total area of the world's oceans (Spalding et al. 2001), but they are among the most productive and diverse ecosystems on earth (Paulay 1997, Reaka-Kudla 1997). Reefs are built as a result of calcium carbonate deposition by scleractinian corals and coralline algae (Hubbard et al. 1990, Langer et al. 1997). Scleractinian corals are, despite their low living biomass, essential for the existence of other reef organisms in tropical coral reef

environments because they provide habitat structure, hard substrate and food (e.g. Paulay 1997, Reaka-Kudla 1997).

Coral reef fisheries contribute approximately one-quarter of the total global fish catches (Jameson et al. 1995, Hinrichsen 1997). On many coral reefs, herbivorous fish suffer overexploitation leading to reduced grazing pressure on algae (Done 1992, Roberts 1993, Roberts 1995). In the Caribbean, grazing pressure decreased subsequent to the mass mortality of the herbivorous sea urchin *Diadema antillarum* due to an epidemic disease outbreak in 1983/4 (Lessios et al. 1984, Van Steveninck and Bak 1986, Lessios 1988). Hence, many Caribbean reefs have been reported to undergo phase shifts from coral to algal dominance (e.g. Hughes 1994, Hughes and Connell 1999, Scheffer et al. 2001).

Due to an expanding world population, increased agriculture, deforestation, diseases and pollution additionally threaten the vitality of coral reef communities (Bryant et al. 1998, Hodgson 1999, Spalding et al. 2001). Major human-induced stresses to coral reefs besides overfishing include sedimentation and eutrophication (Ginsburg 1994). Global warming also poses a serious threat (Brown 1996, Wilkinson and Hodgson 1999). These threats have led to a dramatic decrease in coral cover world-wide (Bryant et al. 1998, Wilkinson 2000, Spalding et al. 2001).

Recruitment (additions to the adult coral community as a result of reproductive activity) is critical to the replenishment of coral populations. Recruitment rates depend on settlement rates and post-settlement survival. A healthy and vital coral reef is likely to be characterised by high settlement rates and low post-settlement mortality rates resulting in replacement of lost adult corals.

The life history of corals can be very complex (Raimondi and Morse 2000). Corals with different life history strategies may respond differently to biotic and abiotic environmental changes (Wittenberg and Hunte 1992). In addition, these changes may act in several ways on different life stages of corals (Richmond 1997). It is possible that new recruits could be more vulnerable to human stresses than adults (Pearson 1981, Hughes 1989, Richmond 1997). However to date, most studies of reef degradation have focused on the effects of

stress on adult coral colonies (e.g. Rogers 1983, McClanahan and Obura 1997, Sladek Nowlis et al. 1997). Those studies that have examined settlement rates and mortality rates of settled larvae have been on either artificial substrata such as ceramic tiles and concrete blocks (e.g. Rogers et al. 1984, Babcock 1985, Van Moorsel 1988, Porter and Meier 1992, Wittenberg and Hunte 1992) or on natural substrata (e.g. Bak and Engel 1979, Rylaarsdam 1983, Chiappone 1996, Edmunds 2000, Miller et al. 2000). However, juvenile coral mortality and recruitment rates seem to differ between artificial and natural substrata (Rylaarsdam 1983, Cortès and Risk 1985, Fisk and Harriott 1989, Porter and Meier 1992), so cautious interpretation of results from artificial substrata is advisable.

Few investigations have focused on human-induced impacts such as sedimentation and eutrophication on juvenile coral communities. Wittenberg and Hunte (1992) found that mortality rates of juvenile corals appeared higher under eutrophication stress compared to unpolluted reefs in Barbados, but the difference was not statistically significant. Hunte and Wittenberg (1992) investigated settlement rates on the same reefs on cement blocks exposed for three years. They reported decreasing numbers of settled corals with increasing eutrophication pollution. They suggested that this may be due to decreased coral larval supply or higher post-settlement mortality on reefs with higher eutrophication. Artificial substrata that were checked monthly also showed decreased settlement rates with increasing eutrophication suggesting that eutrophic reefs have lower reproductive output and/or larval supply rather than higher post-settlement mortality (Hunte and Wittenberg 1992). Similarly, Tomascik (1991) also observed coral larval settlement along the same eutrophication gradients in Barbados and found that settlement rates on artificial substrate were higher on the least eutrophic reefs and lower on the most eutrophic.

It has been suggested that coral cover determines coral larval settlement rates because adult colonies are responsible for larval production (e.g. Bak and Engel 1979, Hughes et al. 2000, see also Chapter 4). However, several authors have failed to find such a relationship (e.g. Chiappone 1996, Nzali et al. 1998).

This study focuses on the effects of sedimentation on juvenile corals. The harmful effects of sedimentation on adult corals are well known (e.g. Rogers et al.

1984, Abdel-Salam and Porter 1988, Stafford-Smith and Ormond 1992, Riegl and Branch 1995, Lewis 1997, Wesseling et al. 1999, Torres 2001), but effects on juveniles have been studied little in the field. In a laboratory experiment, Te (1992) found that sedimentation decreased settlement rates of coral larvae by covering available hard substrate with loose particles. In the field, sediment also gets trapped in filamentous algae and may prevent coral larvae from settling (Walker and Ormond 1982). Depositing sediment particles can smother settled larvae and abrade their tissue (Rogers 1983, Maida et al. 1994, Wesseling et al. 1999). Smaller coral colonies are more likely to be smothered than large colonies and so will have a greater risk of total mortality (Wittenberg and Hunte 1992). Hence, juvenile corals may suffer more from sedimentation than adult coral colonies do.

This study examines the effects of sedimentation caused by river run-off on mortality, settlement and growth rates of juvenile stages of common Caribbean corals on the west coast of St. Lucia, West Indies. The questions I address in the study are:

- (1) Are mortality rates of juvenile corals influenced by sedimentation rate?
- (2) Are settlement rates to natural substrata affected by sedimentation?
- (3) Does sedimentation have an impact on the growth rates of juvenile corals?
- (4) Does the abundance of herbivorous fish influence settlement, mortality or growth rates of juvenile corals?
- (5) Is coral larval settlement related to adult coral cover?

My hypotheses are that juvenile corals on reefs stressed by high sediment loads will experience higher mortality, lower settlement and lower growth rates than on less sediment polluted reefs. By reducing algal cover, increased grazing by fish could promote coral settlement, survival and growth by exposing suitable substrata. In a separate study conducted on the same reefs, I quantified settlement rates using artificial substrata (see Chapter 4). I found a weak relationship between adult coral cover and settlement rates. This study aimed to assess whether settlement rates on natural substrata behave differently.

5.3 Materials and methods

5.3.1 Study site

This study was conducted on coral reefs off the west coast of St. Lucia, West Indies. I worked in two regions, (1) in the Soufrière Marine Management Area (SMMA) established in 1995 and consisting of marine reserves (reefs protected from fishing), fishing priority zones (fishing grounds where other users are allowed but do not interfere with fishing activities) and multiple use zones where all activities are allowed, and (2) on reefs south of the town Anse La Raye which is 7km further north of the SMMA and mainly used for fishing (Fig. 1 in Chapter 3). For further detailed description of the study area see section 3.3.1 of Chapter 3.

5.3.2 Sedimentation rates

Sediment traps were established at all locations ($n = 14$) at 15m depth (see Fig. 1 in Chapter 3). The methods I used to built and install the traps, and how I measured sedimentation rates are explained in section 3.3.2 in Chapter 3. For analysis of sedimentation data see section 4.3.1 including Table 2 and Figure 2a-c in Chapter 4.

The results presented in Chapter 4 confirm that sedimentation is significantly greater in the high sedimentation compared to the low sedimentation bays and significantly higher in all locations of the high sedimentation bays than in the low sedimentation locations (see Chapter 4: Table 2, Fig. 2b-c). Even if sedimentation differed significantly over time as a results of changes in rainfall and coastal construction works, the low sedimentation bays received constantly lower sediment input than the high sedimentation bays on all trips (Table 2 and Fig. 3a in Chapter 4).

5.3.3 Benthic substrate monitoring

Monitoring of benthic substrate was carried out in 2000 and 2001 at the same locations where the sediment traps are installed (see Fig. 1 in Chapter 3). I describe the method I used in section 2.3.3 in Chapter 2. In contrast to Chapter 2, in this study I differentiated between fleshy algae and macroalgae (see Table 1).

5.3.4 Fish census

Since the establishment of the marine reserves in the SMMA in 1995, the population of herbivorous fish including parrotfish (Scaridae) and surgeonfish (Acanthuridae) was surveyed annually. For this study, data from the 2000 and 2001 survey were used only. Methods are described in section 3.3.5 in Chapter 3.

5.3.5 Permanent photo quadrats

In June 2000, at each of the 14 study locations, nine permanent photoquadrats (20cm x 30cm) were established at depths of between 12m and 18m. Each quadrat was marked at two opposite corners with plastic tags and an identification number nailed to the reef. Quadrats were located in places with at least three juvenile corals present. A juvenile coral was defined as a coral of 4cm or less in diameter (Bak and Engel 1979). Colonies of this size that were formerly larger but had suffered partial mortality were not included. Each quadrat was observed three times, at the start of the study, after around eight months (period I) and 14 months after the start of the study (period II). The diameter at its largest point was measured to the nearest mm for each juvenile coral in each quadrat. Growth rates were then calculated combining size increases and/or decreases (degradation rate) of an individual coral colony present between measurement intervals. Quadrats were surveyed by parting algae and wafting away sediment to enable corals of up to a minimum of 2mm diameter to be measured. The location of all measured corals was mapped onto a diagram of the quadrat. If a coral disappeared between the surveys, it was referred to as dead.

Table 1: Functional algal groups and the characteristics used to distinguish them (adapted from Steneck and Dethier 1994).

Functional groups	Characteristics	Size ranges
Filamentous algae	Multispecies assemblages of diminutive green filaments	0.1 - 1cm
Fleshy algae	Thick algal species with few ramifications	> 1 - 5cm
Macroalgae	Corticated and leathery marcophytes, articulated calcareous algae; anatomically complex	> 5cm
Coralline Algae	Thin, hard, highly calcified encrusting, overgrowing rocky, limestone substrate; take on surface texture substrate	no size-restrictions
Encrusting algae	Same characteristics as coralline algae, but less calcified.	no size-restrictions
Blue-green algae	Long blue-green to red-brown filaments; superficially attached to the substrate; forming mats over substrate	0.1 - 10cm

Field observations and sketches were supported by photographs taken of each quadrat at each visit to ensure accuracy (Nikonos V with 20mm lens, from 40cm distance, on Fujichrome Velvia 50 ISO film). The photographs were used to help identify juvenile corals that were missed in earlier surveys, or to determine whether larger corals had degraded into smaller parts in between the monitoring intervals. If a coral was not present in photographs taken on previous surveys, it was identified as a new settler.

5.3.6 Statistical analysis

The effects of period (I and II), sedimentation level (low, high), bay nested within sedimentation level and location in the bay (inbay, midbay, offbay) on mortality, settlement and growth rates of juvenile corals were investigated using a nested four-way analysis of variance (ANOVA) with a fractional, factorial design (only two-way interactions included). This design was chosen to limit the numbers of interactions and to focus on the important effects (Miller and Miller 1993). The assumption of this analysis is that that the most important effects are the main effects and their two-way interactions (Quinn and Koijs 2002). Interactions and main factors with non-significant values were removed in a stepwise manner to avoid significant interactions and main factors being missed due to correlations with each other (C. Dytham pers. comm.). Differences between more than two groups were tested with Tukey's *post hoc* test (Zar 1996). Prior to each ANOVA, the residuals of the data were tested for normality by plotting them against the predicted values and for homogeneity by plotting the residuals into a histogram (Pallant 2001).

Pearson's correlation analyses were used to look for relationships between mortality, settlement, growth and degradation rates of juvenile corals and measured reef variables (components of the benthic substrate, herbivorous fish biomass, sedimentation rates, distance from the head of the bays). For correlation analysis, growth and degradation rates were estimated per year (only including juveniles that were present throughout), whereas for the ANOVA growth was calculated for 100 days (included also juveniles present only at period I or II).

All statistical analyses were performed using the SPSS 10.0 package.

5.4 Results

At the beginning of the study, 798 juvenile corals were recorded in 121 permanent photo quadrats (20cm x 30cm) spread across the 14 locations (5 quadrats were lost due to lost markers). After eight months (period I), 169 corals had disappeared or died and 47 new settlers were found. Hence, after period I, 676 corals were counted. After around five more months (period II), 156 of them had died and 103 new corals settled.

5.4.1 Mortality rates of juvenile corals

Total mortality rate in the whole area over the entire study period (around 400 days) was 40.7%. A four-way nested ANOVA showed that the main factors period (I and II) and location (inbay, midbay, offbay) were significant (Table 2). Higher mortality rates were measured in period II (12.3% mortality.100d⁻¹) compared to period I (8.4% mortality.100d⁻¹) (Fig. 1). The midbay location had significantly lower mortality rates than the offbay location (Tukey's test, $P < 0.05$). No difference in mortality rates of juvenile corals was found between the low and high sedimentation bays, and between the inbay and midbay location and the inbay and offbay location (Fig. 2).

There was no significant difference in mortality rate of juvenile corals between the different bays (L1, L2, H1, H2) (see Fig. 2 in Chapter 3). However, there was a trend for juvenile corals in high sedimentation bays to have lower mortality rates compared to bays with low sedimentation input. Interactions between the factors tested did not show significance. The interactions with non-significant results were stepwise excluded (interactions with highest P-values first), but the results did not differ from those of the first ANOVA model including all main factors and interactions and, hence, only the first model is shown (Table 2).

Correlations were used to look at the relationships between the mortality rate of juvenile corals and other reef factors. The results show that mortality rates were significantly affected by filamentous and total algal cover (the latter mainly because of the contribution of filamentous algae) (Table 3).

Table 2: Result of four-way nested ANOVA (fractional factorial design) with period (I, II), sedimentation level (low, high), location (inbay, midbay, offbay) and bay (L1, L2, H1, H2) nested within sedimentation level as dependent variables and mortality rate (percentage.100d⁻¹) of juvenile corals as independent variable. (Sed = sedimentation level, Loc = location)

Sources	df	F	P
Period	1	6.193	0.014
Sed	1	2.798	0.096
Loc	2	3.215	0.042
Bay (Sed)	2	0.569	0.567
Period*Sed	1	1.069	0.302
Period*Loc	2	0.873	0.419
Period*Bay (Sed)	2	0.127	0.881
Sed*Loc	2	0.012	0.988
Loc*Bay (Sed)	4	0.493	0.741
error	224		
total	242		

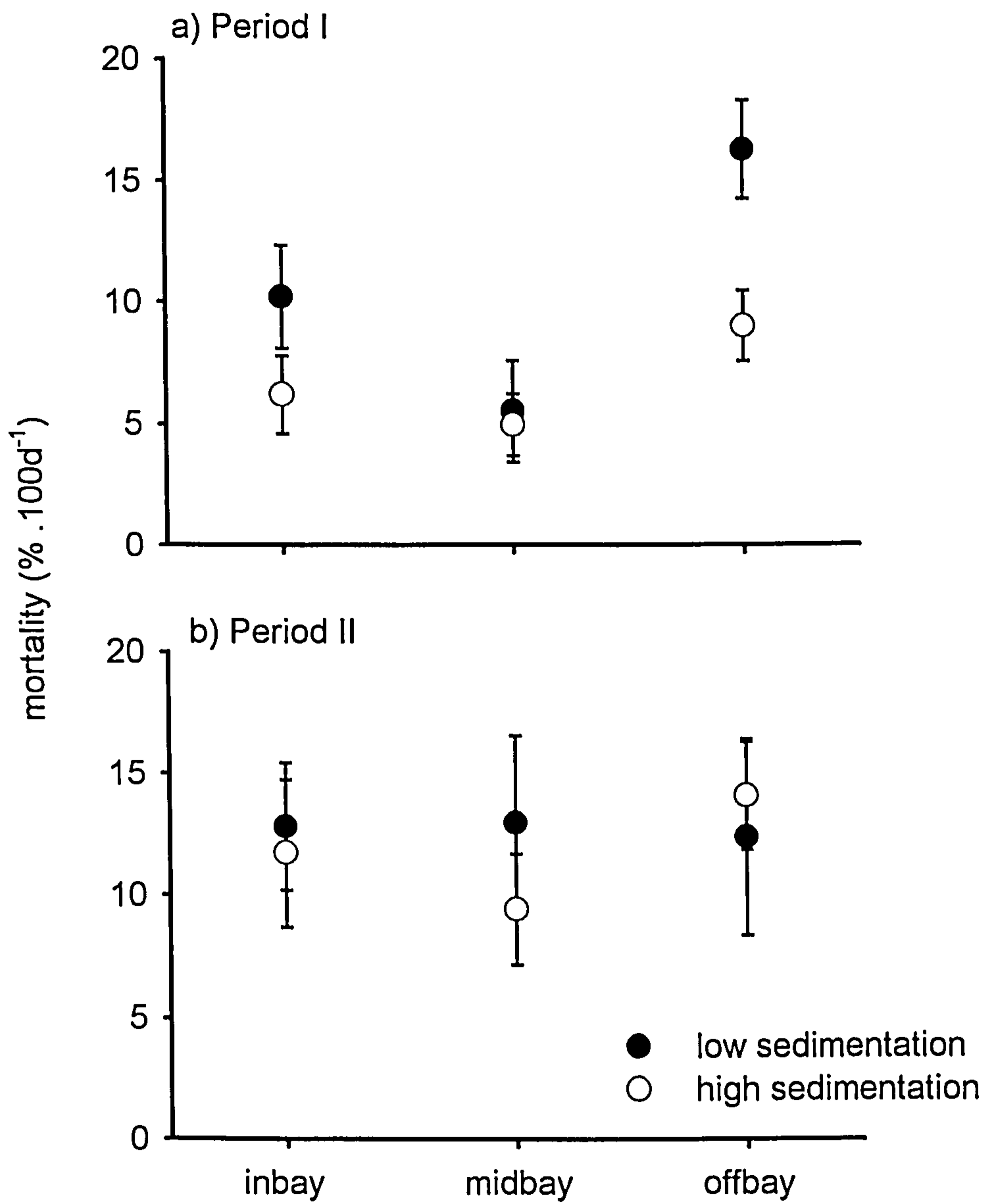


Fig. 1: Pattern of variation in percentage mortality of juvenile corals per 100 days in the different locations in the bay (inbay, midbay, offbay) of high and low sedimentation bays. The error bars represent one standard error.

Table 3: Relationship between the mortality rate ($\%.100d^{-1}$) of juvenile corals and benthic cover of different functional algal groups, coral cover and sedimentation rates. Pearson coefficients are based on mean values per site in period I and II ($n = 14$).

Reef variables	Mortality rates ($\%.100d^{-1}$) Period I		Mortality rates ($\%.100d^{-1}$) Period II	
	r	P	r	P
Filamentous algae	- 0.54	0.048	- 0.53	0.051
Fleshy algae	- 0.31	0.227	0.18	0.549
Macroalgae	0.20	0.488	0.05	0.876
Blue-green algae	0.09	0.769	0.12	0.675
Encrusting algae	- 0.33	0.250	- 0.39	0.173
Coralline algae	0.33	0.248	- 0.39	0.164
Total algal cover	- 0.50	0.070	- 0.58	0.03
Massive coral cover	0.39	0.165	0.33	0.248
Total coral cover	0.44	0.117	0.36	0.206
Herbivorous fish biomass	0.07	0.809	0.34	0.231
Distance from head of bay	0.27	0.355	0.35	0.225
Sedimentation 25cm	- 0.45	0.110	- 0.36	0.201
Sedimentation 65cm	- 0.40	0.151	- 0.29	0.320

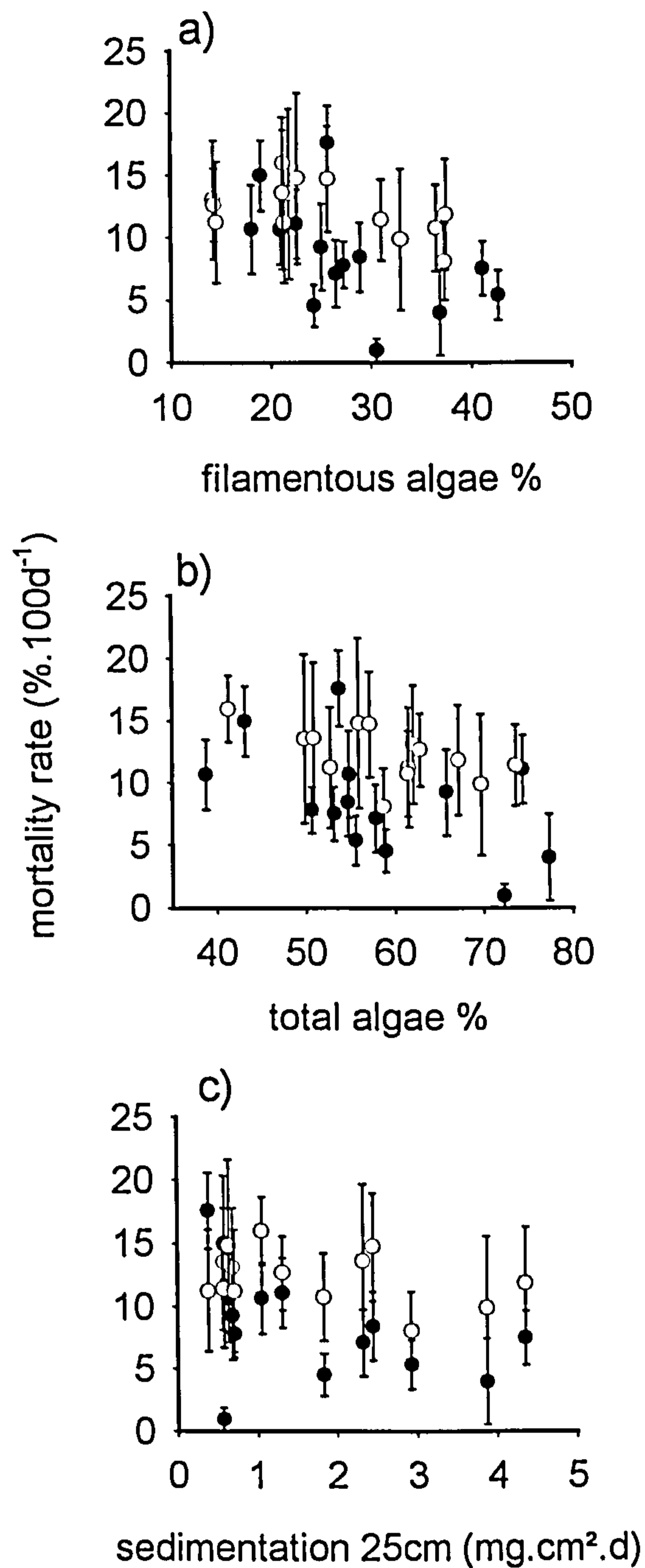


Fig. 2: Relationship between juvenile coral mortality rate (%.100d⁻¹) and a) filamentous algae (%), b) total algal cover (%), and c) sedimentation rate measured (mg.cm⁻².d⁻¹) between 1997 and 2001 for 25cm sediment traps. Data are plotted for low and high sedimentation locations for period I and period II \pm SE (n = 14). ● = period I, ○ = period II.

With increasing filamentous algal cover and increasing total algal cover mortality rates decreased (Fig. 2a-b). Effects of sedimentation rate on mortality rates for 25cm traps measured between 1997 and 2001 were statistically insignificant (Table 3). However, there was a trend showing that increasing sedimentation rates were associated with lower mortality rates of juvenile corals (Fig. 2c).

5.3.2 Settlement rates

The results of the four-way ANOVA show that the main factors period, location and bay nested within sedimentation, and the interaction period and bay nested within sedimentation were significant (Table 4). Settlement rates are higher in period II (mean = 0.50 ± 0.07 SE) than period I (mean = 0.16 ± 0.03 SE) (Fig. 3 and 4). The inbay location had significantly lower settlement rates compared to the offshore location (Fig. 3). Furthermore, settlement in the high sedimentation bay H2 was significantly different from the high sedimentation bay H1 and from the low sedimentation bay L2 (Fig. 4). Differences in settlement rates were not found between the low sedimentation bays L1, L2 and the high sedimentation bay H1 ($P > 0.05$). The interaction between period (I and II) and bay was significant because all bays, except the low sedimentation bay H2, had much higher settlement rates in period II (Fig. 5).

Correlation tests were used to look at the relationships between coral settlement rate (for period I and II separately) and cover of different functional algal groups, coral cover, herbivorous fish biomass, distance from the head of the bays towards their headlands and sedimentation rates (Table 5, Fig. 6a-f).

There were only significant results for period II. There, a negative relationship exists between coral settlement rates and filamentous algal cover and settlement rates and sedimentation rate of the 25cm sediment traps measured from 1997 to 2001 (Table 5, Fig. 6a and 6b). The relationship between settlement rates and total coral cover were just statistically insignificant (Table 5). With increasing total coral cover, coral larval settlement also increased (Fig. 6f).

Table 4: Results of the nested four-way ANOVA with period (I, II), sedimentation level (low, high), location (inbay, midbay, offbay) and bay (L1, L2, H1, H2) nested within sedimentation level as the dependent variables and settlement rates of corals ($\text{no.600cm}^{-2} \cdot 100\text{d}^{-1}$) as independent variable. The first model shows all main factors and all two-way interactions (fractional factorial design), the 2nd step shows the model after removing the highest non-significant interaction, the 3rd step shows the results after removing the interaction between location and bay nested within sedimentation (note that the factor locations becomes significant now) and the final column shows the model after all non-significant interactions were removed. (Sed = sedimentation level, Loc = location)

Sources	df	First Model		2 nd step		3 rd step		Final Model	
		F	P	F	P	F	P	F	P
Period	1	21.472	<0.001	21.472	<0.001	21.832	<0.001	21.859	<0.001
Sed	1	0.975	0.325	0.975	0.325	1.039	0.309	1.039	0.309
Loc	2	1.950	0.145	1.950	0.145	3.227	0.041	3.227	0.041
Bay(Sed)	2	8.437	<0.001	8.437	<0.001	8.773	<0.001	8.775	<0.001
Period*Sed	1	2.375	0.125	2.375	0.125	2.415	0.122	-	-
Period*Loc	2	0.957	0.386	0.975	0.386	0.973	0.380	-	-
Period*Bay(Sed)	2	4.299	0.015	4.299	0.015	4.371	0.014	4.300	0.019
Sed*Loc	2	0.095	0.909	-	-	-	-	-	-
Loc*Bay(Sed)	4	0.422	0.793	0.367	0.793	-	-	-	-
error	df=224			df= 224		df= 230		df= 232	
total	df= 242			df= 242		df= 242		df= 242	

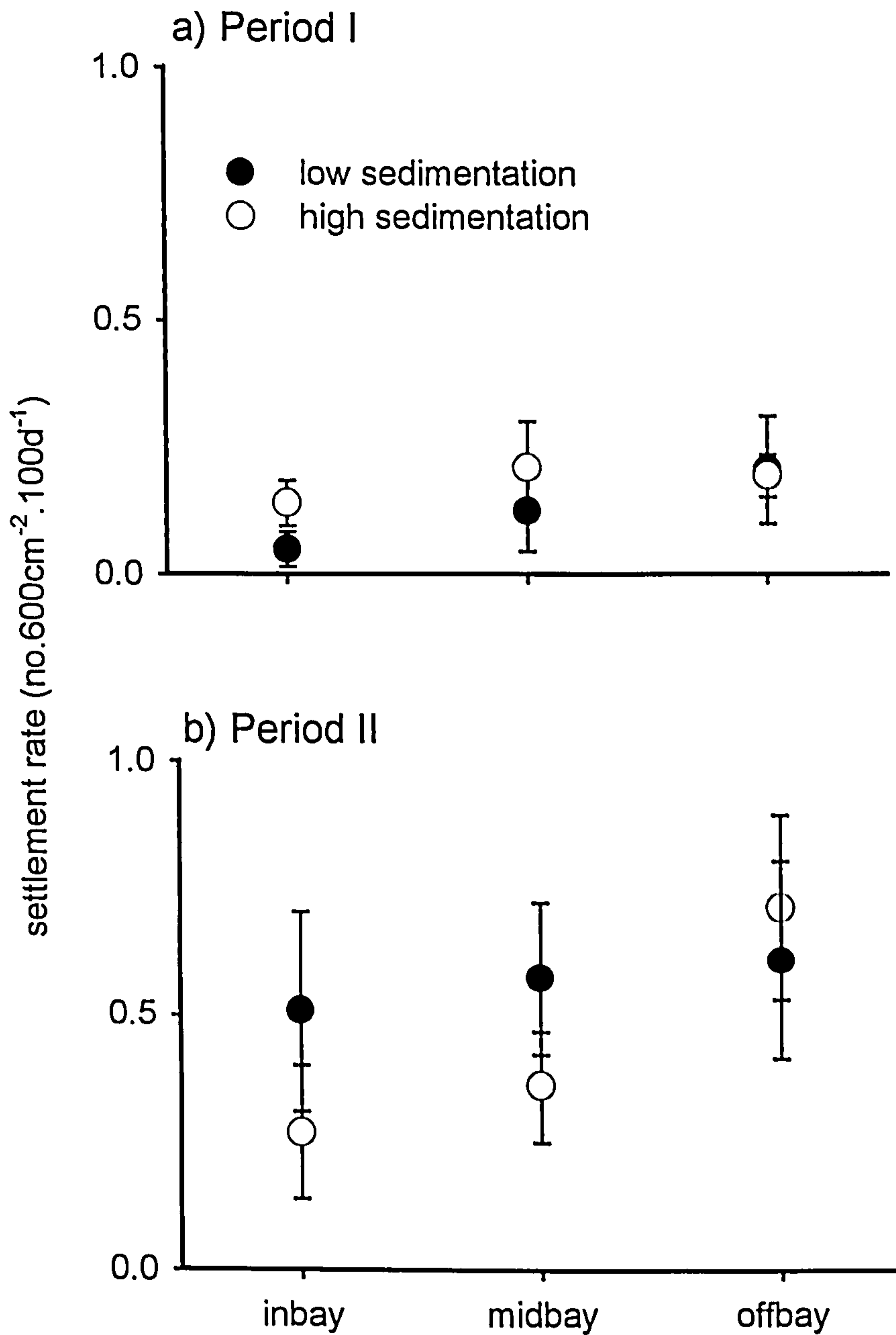


Fig. 4: Patterns of variation in coral settlement rates (no.600cm⁻².100d⁻¹) in the inbay, midbay and offbay location of the low and high sedimentation bays in a) period I and b) period II. Error bars represent one standard error.

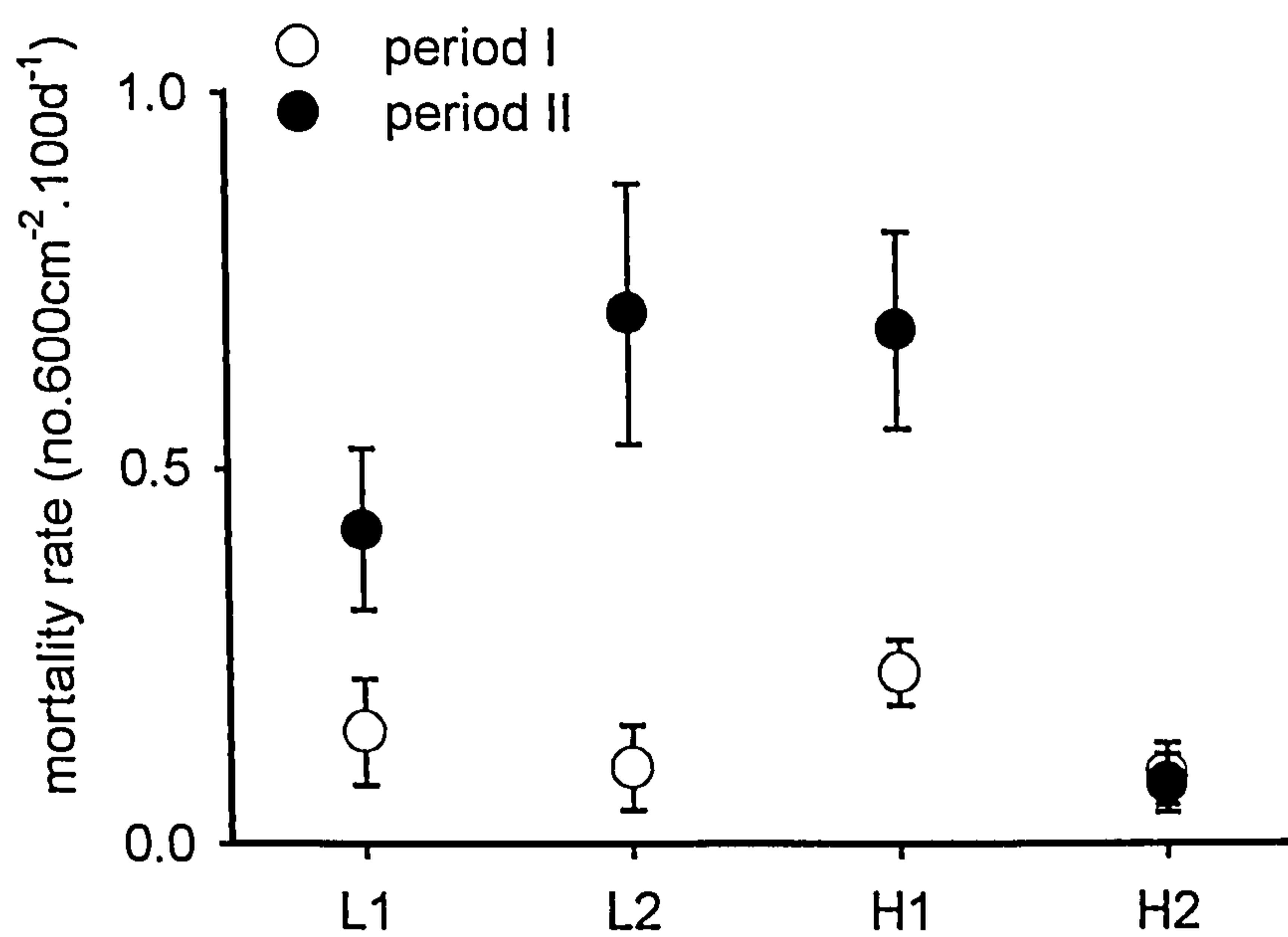


Fig. 5: Patterns of variation in settlement rate ($\text{no.600cm}^{-2} \cdot 100\text{d}^{-1}$) in the different bays with low sedimentation (L1 and L2) and high sedimentation (H1 and H2) in period I and period II. Error bars represent one standard error.

Table 5: Relationship between the settlement rate ($\text{no.600cm}^{-2} \cdot 100\text{d}^{-1}$) and benthic cover of different functional algal groups, coral cover and sedimentation rates. Pearson coefficients are based on mean values per site for each period ($n = 14$).

Reef variables	Settlement rates ($\text{no.600cm}^{-2} \cdot 100\text{d}^{-1}$) Period I		Settlement rates ($\text{no.600cm}^{-2} \cdot 100\text{d}^{-1}$) Period II	
	r	P	r	P
Filamentous algae	- 0.28	0.239	- 0.45	0.044
Fleshy algae	0.33	0.255	- 0.23	0.433
Macroalgae	0.07	0.805	0.41	0.155
Blue-green algae	- 0.38	0.184	- 0.08	0.786
Encrusting algae	- 0.22	0.443	- 0.44	0.122
Coralline algae	- 0.20	0.494	- 0.13	0.654
Total algal cover	- 0.38	0.179	- 0.65	0.013
Massive coral cover	0.47	0.092	0.43	0.122
Total coral cover	0.45	0.106	0.50	0.067
Herbivorous fish biomass	0.21	0.483	0.28	0.924
Distance from head of bay	0.30	0.293	0.56	0.038
Sedimentation 25cm	- 0.20	0.493	- 0.66	0.010
Sedimentation 65cm	- 0.19	0.509	- 0.59	0.027

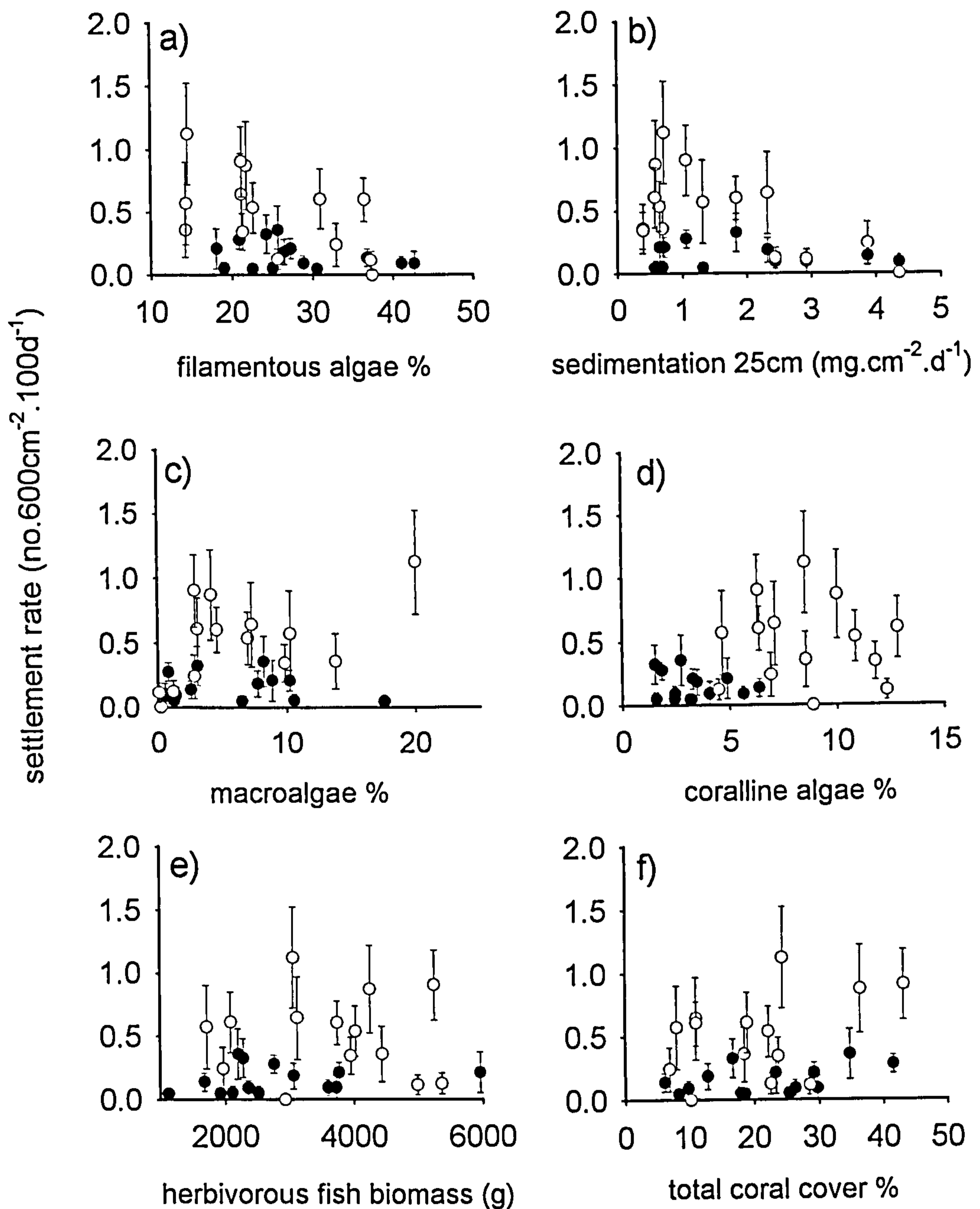


Fig. 6: Relationship between settlement rate (no.600cm⁻².d⁻¹) and a) filamentous algae (%), b) sedimentation rates (mg.cm⁻².d⁻¹) measured from 1997 to 2001 of 25cm traps, c) macroalgae (%), d) coralline algae (%), e) herbivorous fish biomass (g) and f) total coral cover (%). Data are plotted for low and high sedimentation locations of period I and II \pm SE (n = 14). ● = period I, ○ = period II.

I also tested relationships between settlement and sedimentation rates measured only in the periods during which I conducted the permanent photoquadrat study. However, significant results were not found, probably indicating that juvenile corals are affected by long-term sediment inputs because of accumulation of sediment onto the reef.

5.3.3 Growth rates

The results of the four-way nested ANOVA show that the main factors of period, sedimentation level, bay nested within sedimentation, and the interaction between period and sedimentation was significant (Table 7). Greater growth rates were observed in period I ($0.14\text{cm}\cdot 100\text{d}^{-1} \pm 0.01 \text{ SE}$) compared to period II ($0.07\text{cm}\cdot 100\text{d}^{-1} \pm 0.02 \text{ SE}$) (Fig. 7). Juvenile coral growth rate was greater on reefs with low sedimentation ($0.15\text{cm}\cdot 100\text{d}^{-1} \pm 0.02 \text{ SE}$) than on reefs with high sedimentation level ($0.09\text{cm}\cdot 100\text{d}^{-1} \pm 0.01 \text{ SE}$) (Fig. 7). Growth rate of juvenile corals differed between the four bays (Fig. 8). Growth rate in the high sedimentation bay H2 was significantly lower than in the low sedimentation bay L1, the low sedimentation bay L2 and the high sedimentation bay H1 (Fig. 8). There was no difference in juvenile coral growth rates between the other bays. However, it is worth noting that growth rates in the low sedimentation bays did not show a difference between the two periods, whereas the high sedimentation bays showed a higher growth rate in period I and much lower growth in period II (see Fig. 8).

Correlation tests performed with juvenile coral growth and other reef factors (functional algal groups, coral cover, herbivorous fish biomass and distance from the head of the bays towards their headlands) did not show any significant relationships.

Relationships with the same reef factors were also tested for growth rates calculated only including size changes of juvenile corals that have been present throughout the entire study period, with size measured from the beginning until the end of the study (i.e. skipping measurements conducted at the end of period I). The results were qualitatively similar to the ones shown here.

Table 7: Results of four-way nested ANOVA (fractional factorial design) with period (I, II), sedimentation level (low, high), location (inbay, midbay, offbay) and bay (L1, L2, H1, H2) nested within sedimentation level as independent variables and growth rate ($\text{cm} \cdot 100\text{d}^{-1}$) of juvenile corals (estimated from size increases and degradation rates) as dependent variable. Analysis includes growth rates of recruits counted in period I and period II (period I: $n=630$, period II: $n=520$).

Source	df	F	P
Period	1	6.675	<0.01
Sed	1	12.635	<0.001
Loc	2	0.483	0.617
Bay (Sed)	2	10.150	<0.001
Period*Sed	1	3.781	0.052
Period*Loc	2	0.500	0.607
Period*Bay (Sed)	2	0.098	0.907
Sed*Loc	2	0.615	0.541
Loc*Bay (Sed)	4	0.924	0.449
error	1132		
total	1150		

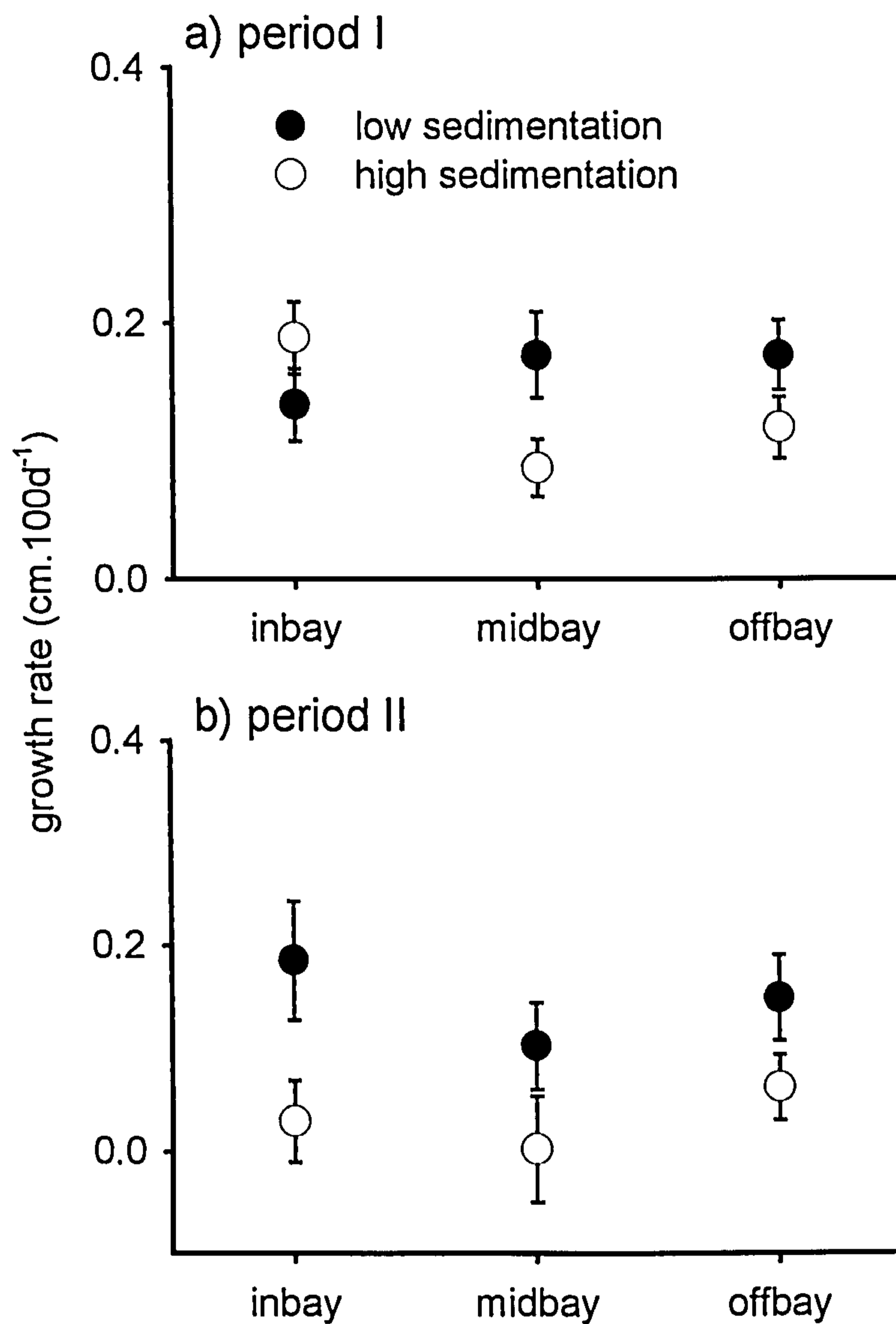


Fig. 7: Pattern of variation of juvenile coral growth rate (cm.100d) in the different locations in the bay (inbay, midbay, offbay) of low and high sedimentation levels. Error bars represent one standard error. Analysis was performed on data set including coral recruits counted in period I and juvenile corals that died between the start of the study and the end of period II. Growth rate includes measured degradation rates (period I: $n = 630$, period II: $n = 520$).

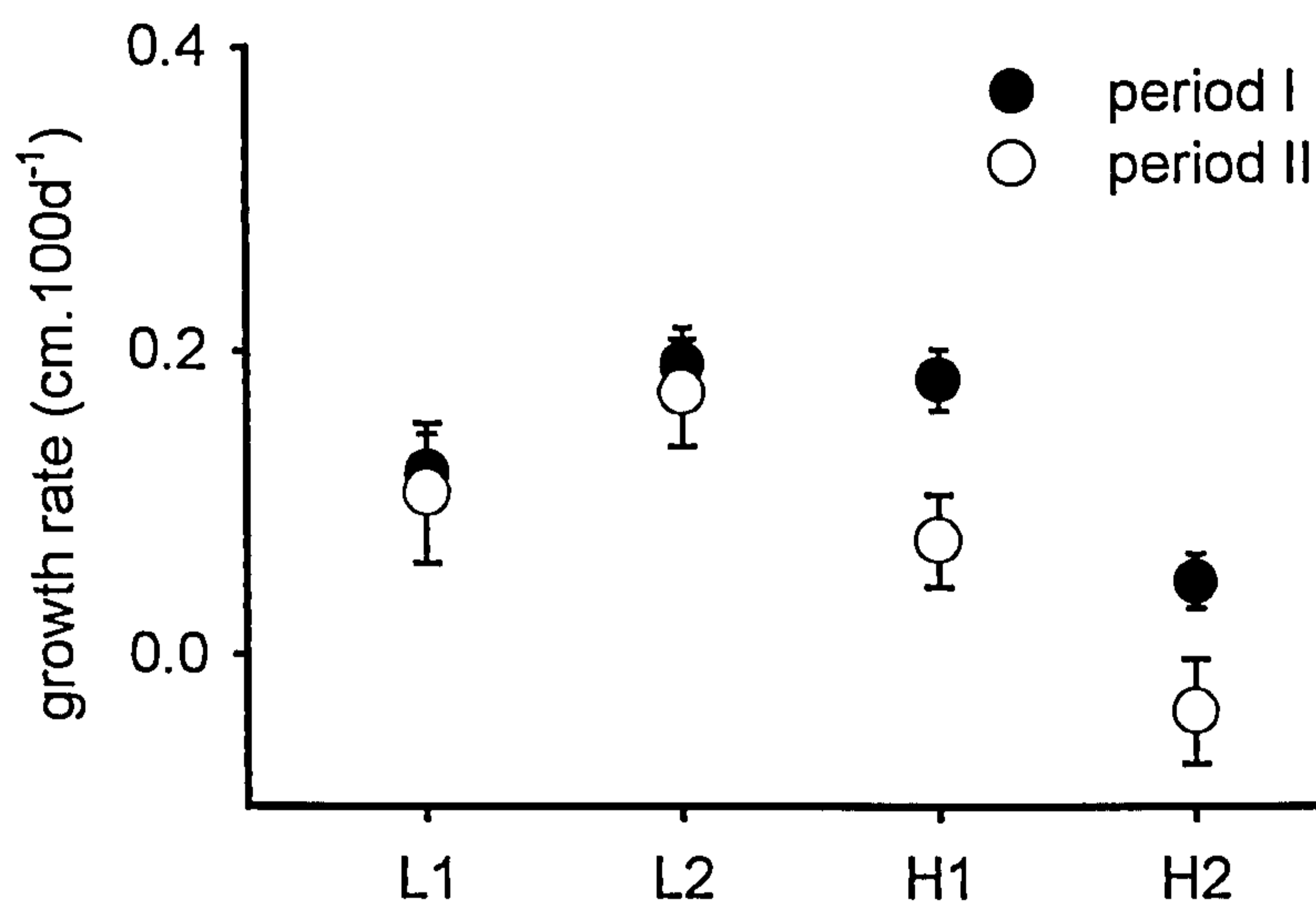


Fig. 8: Pattern of variation in growth rate (cm.yr⁻¹) of juvenile corals in the low sedimentation bays (L1 and L2) and high sedimentation bays (H1 and H2) of period I and period II. Data includes recruits and juvenile corals that disappeared between the beginning of the study and the end of period II. Error bars represent standard error.

Table 8: Relationships between (1) growth rate (cm.yr^{-1}) excluding degradation rates and sedimentation rate (25cm traps and 65cm traps) measured from 1997 to 2001 ($\text{mg.cm}^{-2}.\text{d}^{-1}$) and distance from the head of the bays (km), and relationships between (2) degradation rate only (mm lost.yr^{-1}), sedimentation rates (25cm and 65cm traps) measured from 1997 to 2001 ($\text{mg.cm}^{-2}.\text{d}^{-1}$) and distance from the head of the bay to the headlands (km).

		1) Growth rate	2) Degradation rate
Sedimentation 25cm	r	-0.35	-0.15
	P	0.226	0.607
Sedimentation 65cm	r	-0.37	-0.24
	P	0.194	0.417
Distance	r	0.06	0.67
	P	0.838	0.009

Finally, relationships between total growth rates (cm.yr^{-1}), respectively, total degradation rates (cm.yr^{-1}), sedimentation rates for 25cm and 65cm sediment traps measured from 1997 to 2001 and distance from the head to the bay were tested (Table 8, Fig. 9). The only significant relationship found was between total degradation rate and distance from the head of the bay (Table 8). With increasing distance from the head of the bay, degradation increased (Fig. 9).

Results of the ANOVA with the same factors used as before, but growth rate calculated only from measured size increases were qualitatively similar to the results of the calculation including degradation rates. Applying the same ANOVA model to test differences in degradation rates only showed only significant effects of the independent variables period and bay. Degradation rate was greater in period I compared to period II ($P < 0.05$). The high sedimentation bay H2 showed highest degradation rate compared to all other bays.

5.3.4 Species – mortality and settlement

The results show that mortality exceeded settlement for the most common species (*Agaricia* spp., *Porites astreoides*, *Siderastrea siderea*) during the study periods (Table 9 and Table 10). However, some species that were present only in small numbers such as *Mycetophyllia* spp., *Diploria strigosa* and *Colpophyllia natans*, known as species with low mortality and low settlement rates, showed zero mortality of the juveniles that were observed from the beginning, and I did not find any new settlement of these species either (Table 9). Results show clearly that *Agaricia* spp. and *Porites astreoides* are species with high mortality and high settlement rates when compared with other species present in my quadrats (Table 9 and 10).

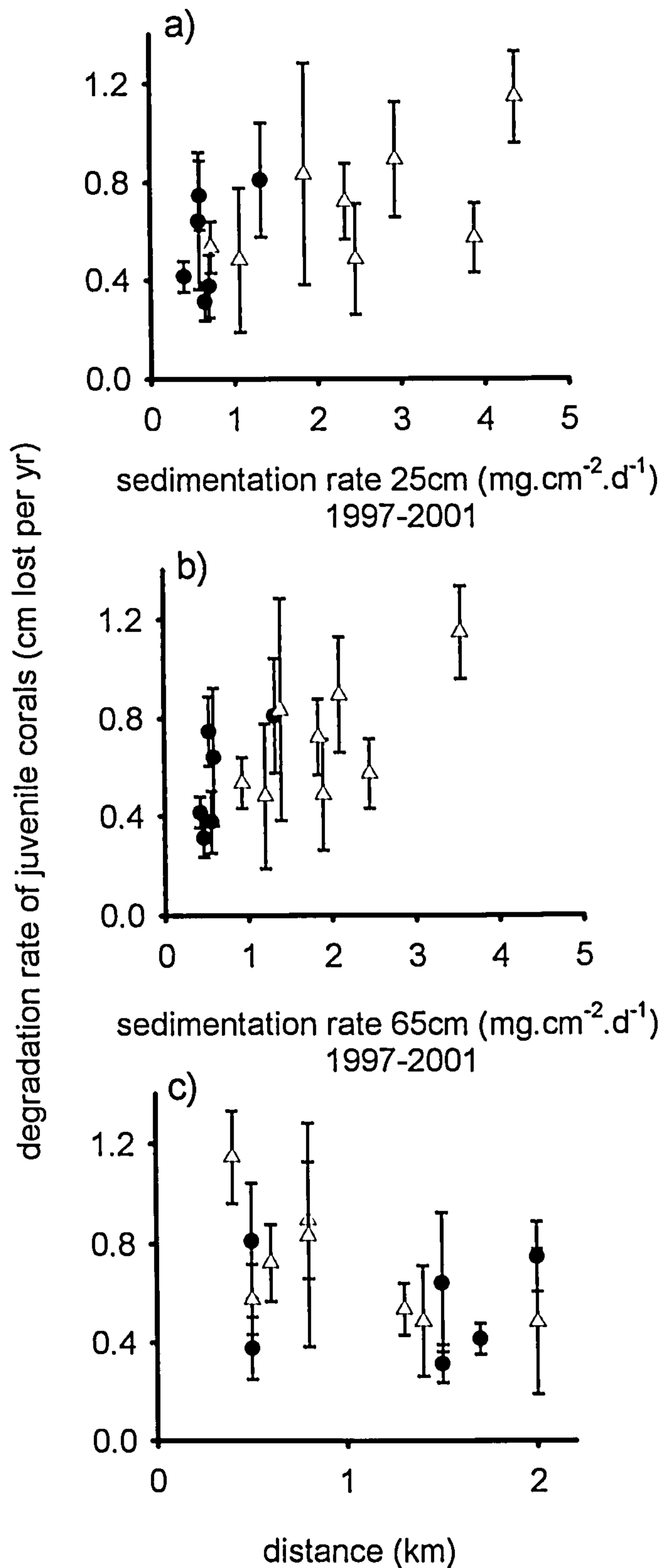


Fig. 9: Relationship between degradation rate (cm lost.yr⁻¹) of juvenile corals and a) sedimentation rate (25cm traps) measured from 1997 to 2001, b) sedimentation rate (65cm traps) measured from 1997 to 2001, and c) distance from the head of the bay to the headland (\pm SE). ● = low sedimentation, Δ = high sedimentation.

Table 9: Number of juvenile corals that disappeared and were assumed dead and number of new settlers for each period for each species. Start = first marking, I = period I, II = period II.

Species	start	I	II
<i>Agaricia spp.</i>			
settler	-	25	68
dead	-	86	79
total	363	302	291
<i>P. astreoides</i>			
settler	-	10	18
dead	-	29	28
total	109	90	80
<i>S. siderea</i>			
settler	-	3	0
dead	-	10	15
total	107	100	291
<i>M. decactis</i>			
settler	-	0	2
dead	-	5	8
total	44	39	33
<i>E. fastigiata</i>			
settler	-	13	0
dead	-	4	6
total	33	29	23
<i>F. fragum</i>			
settler	-	1	2
dead	-	5	10
total	27	23	15
<i>M. meandrites</i>			
settler	-	2	2
dead	-	5	1
total	24	21	22
<i>S. intersepta</i>			
settler	-	0	0
dead	-	5	1
total	23	18	17
<i>L. cucullata</i>			
settler	-	2	2
dead	-	6	3
total	21	17	16

Species	start	I	II
<i>P. porites</i>			
settler	-	1	2
dead	-	7	0
total	13	7	9
<i>Scolymnia spp.</i>			
settler	-	2	3
dead	-	5	2
total	20	17	18
<i>M. annularis</i>			
settler	-	0	0
dead	-	2	0
total	2	0	0
<i>C. natans</i>			
settler	-	0	0
dead	-	0	0
total	2	2	2
<i>M. cavernosa</i>			
settler	-	0	0
dead	-	2	0
total	2	0	0
<i>M. mirabilis</i>			
settler	-	02	0
dead	-	0	1
total	1	3	2
<i>Mycetophyllia spp.</i>			
settler	-	0	0
dead	-	0	0
total	1	1	1
<i>D. strigosa</i>			
settler	-	0	0
dead	-	0	0
total	1	1	1
<i>D. stokesii</i>			
settler	-	0	0
dead	-	0	0
total	1	1	1

Table 10: Mortality (no.period⁻¹ and in %) and settlement (n.period⁻¹ and in % from original) for the most common species in the study sites for low and high sedimentation levels in period I and II.

a)	<i>Agaricia spp.</i>	start	Period I	% I	Period II	% II
low sedimentation	settler	-	11	7.9	29	25.4
	dead	-	37	26.4	33	28.9
	total	140	114	—	110	—
high sedimentation	settler	-	14	6.3	39	33.1
	dead	-	49	22.0	46	24.5
	total	223	188	—	181	—

b)	<i>P.astreoides</i>	start	Period I	% I	Period II	% II
low sedimentation	settler	-	2	3.7	11	26.2
	dead	-	14	25.9	11	26.2
	total	54	42	—	42	—
high sedimentation	settler	-	7	12.7	7	14.6
	dead	-	15	27.3	17	35.4
	total	55	48	—	38	—

c)	<i>S.siderea</i>	start	Period I	% I	Period II	% II
low sedimentation	settler	-	0	0	0	0
	dead	-	3	11.1	4	16.7
	total	27	24	—	20	—
high sedimentation	settler	-	2	2.5	0	0
	dead	-	7	8.8	11	14.5
	total	80	76	—	65	—

Table 11: Growth rate (cm.yr⁻¹) for each species (only individuals that were present throughout the study) in low and high sedimentation conditions and in total (growth rates of low and high sedimentation conditions combined). SE = one standard error, n = number of observations

Species	low sedimentation			high sedimentation			total		
	mean	SE	n	mean	SE	n	mean	SE	n
<i>Agaricia spp.</i>	0.81	0.06	62	0.80	0.06	96	0.80	0.04	158
<i>C. natans</i>	1.46	-	1	0.26	0	1	0.86	0.60	2
<i>E. fastigiata</i>	1.11	0.22	15	0.74	0.22	5	1.02	0.18	20
<i>F. fragum</i>	0.62	-	1	0.39	0.14	9	0.38	0.13	10
<i>L. cucullata</i>	1.65	-	7	2.88	0.64	5	2.16	0.38	12
<i>M. decactis</i>	0.25	0.39	6	0.27	0.06	17	0.26	0.06	23
<i>M. meandrites</i>	1.65	0.06	5	1.05	9.15	12	1.23	0.21	17
<i>M. mirabilis</i>	0.34	-	1	-	-	-	0.34	-	1
<i>Mycetophyllia spp.</i>	1.89	-	1	-	-	-	1.89	-	1
<i>P. astreoides</i>	0.92	0.12	26	0.91	0.11	25	0.92	0.08	51
<i>P. porites</i>	2.17	0.23	2	1.00	0.30	3	1.47	0.34	5
<i>S. siderea</i>	0.31	0.06	18	0.22	0.04	36	0.25	0.03	54
<i>Scolymia spp.</i>	0.90	0.39	4	0.80	0.18	7	0.84	0.17	1
<i>D. stockesii</i>	-	-	-	0.78	-	1	0.78	-	1
<i>D. strigosa</i>	-	-	-	2.11	-	1	2.11	-	1
<i>M. cavernosa</i>	-	-	-	0.27	0.15	4	0.27	0.15	4
<i>S. intersepta</i>	-	-	-	0.77	0.23	15	0.77	0.23	15
total	0.87	0.06	139	0.72	0.05	237	0.78	0.04	376

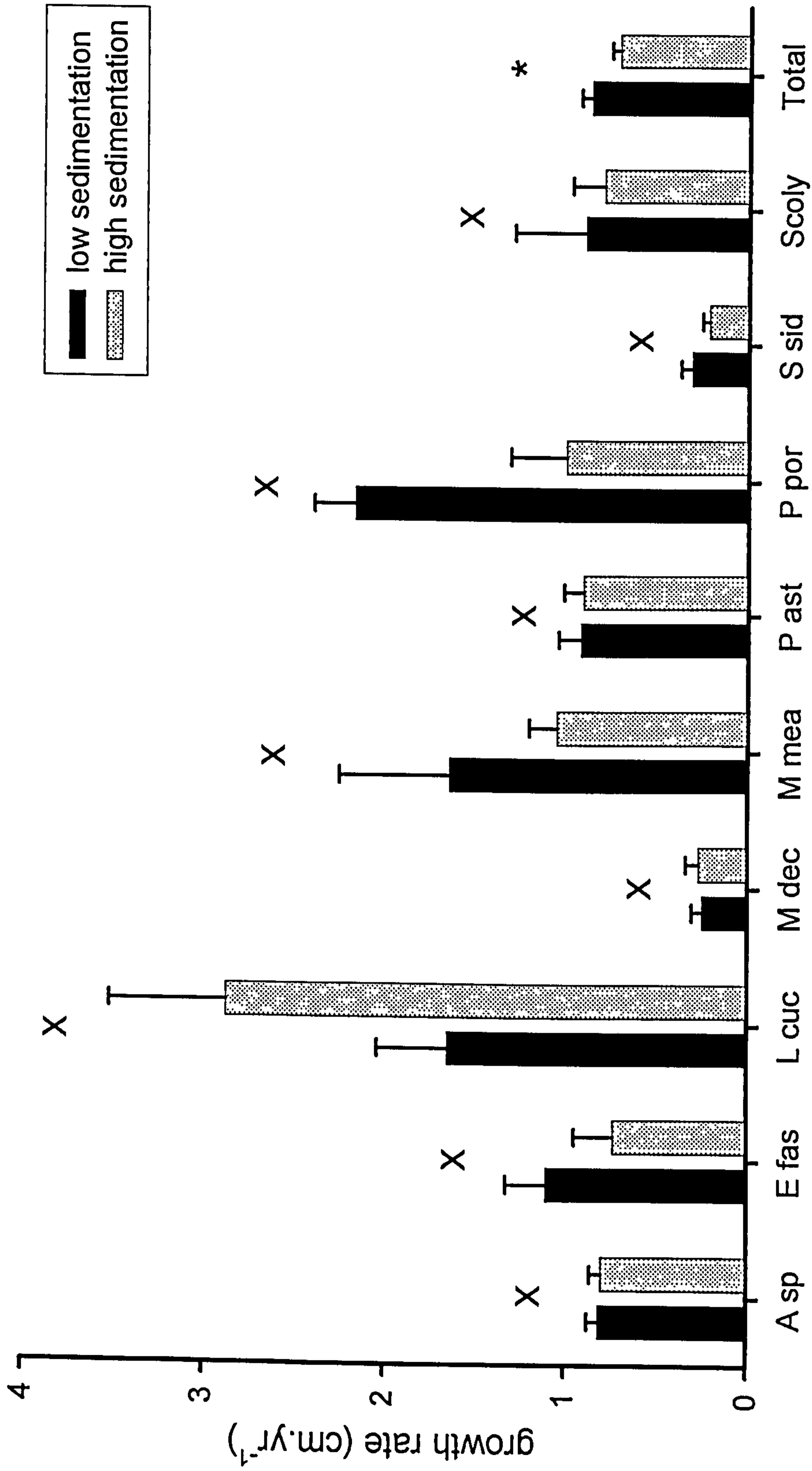


Fig. 10: Growth rate (cm.yr⁻¹) of different species in high and low sedimentation levels and total growth rate including all species. Error bars represent one standard error. X = P > 0.05, * = P < 0.05 (one-way ANOVA tests). Sample sizes see Table 12.

Table 12: Degradation rate (cm.yr^{-1}) for each species (only individuals that were present throughout the study) in low and high sedimentation conditions and in total (degradation rates of low and high sedimentation conditions combined). SE = one standard error, n = number of observations

Species	low sedimentation			high sedimentation			total		
	mean	SE	n	mean	SE	n	mean	SE	n
<i>Agaricia spp.</i>	-0.65	0.13	14	-0.70	0.10	33	-0.69	0.08	47
<i>C.natans</i>	-	-	-	-	-	-	-	-	-
<i>E.fastigiata</i>	-0.54	0.03	3	-	-	-	-0.54	0.03	3
<i>F.fragum</i>	-0.97	0.35	2	-	-	-	-0.97	0.35	2
<i>L.cucullata</i>	-0.87	-	1	-	-	-	-0.87	-	1
<i>M.decactis</i>	-1.50	-	1	-0.49	0.19	6	-0.64	0.22	7
<i>M.meandrites</i>	-	-	-	-0.25	-	1	-0.25	-	1
<i>M.mirabilis</i>	-	-	-	-	-	-	-	-	-
<i>Mycetophyllia spp.</i>	-	-	-	-	-	-	-	-	-
<i>P.astreoides</i>	-0.42	0.14	5	-0.87	0.41	4	-0.62	0.20	9
<i>P.porites</i>	-	-	-	-0.08	-	1	-0.08	-	1
<i>S.siderea</i>	-0.62	0.23	2	-0.60	0.02	27	-0.60	0.11	29
<i>Scolymnia spp.</i>	-0.43	-	1	-0.18	0.09	2	-0.26	0.10	3
<i>D.stockasii</i>	-	-	-	-	-	-	-	-	-
<i>D.strigosa</i>	-	-	-	-	-	-	-	-	-
<i>M.cavernosa</i>	-	-	-	-2.17	-	1	-2.17	-	1
<i>S.intersepta</i>	-	-	-	-0.81	0.29	2	-0.81	0.29	2
total	-0.65	0.08	29	-0.65	0.09	77	-0.65	0.05	106

5.3.5 Species – growth rates and degradation rates

Table 11 shows the growth rates (degradation values excluded) of the different species in high and low sedimentation conditions and in total (average of low and high sedimentation combined). There was much variability among species in response to sedimentation, although at the species level, none of the differences between high and low sedimentation conditions were significant (Fig. 10). However, combining all species together, growth rates under low sedimentation conditions were higher than under high sedimentation (Fig. 10).

There was no significant difference in degradation rates of the species observed between the low and high sedimentation conditions either separately or when pooled (Table 12).

5.5 Discussion

The results show that settlement, mortality and growth rates of juvenile corals were very variable over time. Sedimentation could not be identified as a main factor determining mortality rates of juvenile corals. However, I found a nearly significant relationship showing increasing mortality rates with increasing sedimentation. Coral larval settlement rates did not differ between the low and high sedimentation bays, although there was a significant negative relationship between actual sedimentation rates and settlement rates. Nevertheless, the location in the bays had an effect on both early life history processes of corals. Mortality rates were lowest at the midbay location, whereas the number of settlers was lowest at the inbay location and highest at the offbay location. Settlement rates differed among the four bays with the high sedimentation bay H2 showing lowest number of settlers. With increasing total and filamentous algal cover coral mortality rates decreased and with increasing filamentous algal cover I observed a decreasing number of settlers. By contrast, there was positive relationship between settlement rates and coralline algal cover. Growth rates of juvenile corals were higher in the low sedimentation bays compared to the high sedimentation bays, but there was no location effect. The lowest growth of juvenile corals

occurred in the high sedimentation bay H2. No significant relationship could be identified between growth rates calculated with and without degradation rate and any measured reef factors, but total annual degradation rate decreased with increasing distance from the head of the bays towards their headlands.

5.5.1 Mortality rates

Mortality rates were 21.2% in period I (around 239 days long) and 23.1% in period II (around 166 days long). Mortality rates were significantly higher in period II, also termed the summer period, which actually was the shorter period. It is possible that increased water temperature in summer has a direct negative effect on juvenile coral mortality, or an indirect effect by increasing algal growth (Stimson et al. 1996). It is also possible that sedimentation input was greater in period II. However, this is difficult to test because I only have measured sedimentation rates and rainfall for three to four weeks within each period. Generally, it is likely that sedimentation is an important seasonal stress (Tomascik and Sander 1985), but that also accumulated sediment input over the years has an impact on juvenile coral mortality due to the resuspension effect.

I did not find any significant difference in mortality rates (per 100 days) of juvenile corals between reefs with low and high sedimentation input. Annual mortality rates in the study area were 43% on low sedimentation reefs and 35% on reefs with high sediment conditions. This result differs from those of a study conducted by Wittenberg and Hunte (1992) on two high and two low eutrophic reefs in Barbados. From their data I calculated extremely high mortality rates of juvenile corals on high eutrophic/sediment reefs reaching 74% and 96%, whereas mortality rates on the low eutrophic/sediment reefs were 21% and 33%. The differing results of my study may be a consequence of different levels and types of pollution on St. Lucian reefs. Unfortunately, sedimentation rates cannot be compared because I measured depositing sediment rates, whereas Wittenberg and Hunte (1992) calculated suspended sediment particles in the water column. Furthermore, Wittenberg and Hunte (1992) conducted their study in more shallow waters (1-6m) where disturbances in the form of wave activity and resuspension of sediment may have a greater effect on mortality than in deeper water.

Table 13: Mortality rates (%.yr⁻¹) of juvenile corals in the Caribbean reported from other studies or estimated from other authors' data.

Location (Caribbean only)	Mortality rate (%.yr ⁻¹)	References
St. Lucia	40.7%	this study
Key Largo, Florida	21%	Smith (1997)
St. John, U.S. Virgin Island	37%	Edmunds (2000)
Jamaica	59-65%	Rylaarsdam (1983)
Curaçao and Bonaire	67%	Bak and Engel (1979)
Biscayne National Park, USA (three different reefs)	22 (± 9 SE) 30 (± 12 SE) 49 (± 14 SE)	Miller et al. (2000)
Jamaica	9-23% (only foliaceous corals)	Hughes and Jackson (1980)

Combining both periods, the mortality rate estimated for one year in the whole study area was equivalent to 40.7 %. This reflects a daily mortality rate of roughly 0.15%. My estimates are lower than some juvenile coral mortality rates reported from reefs around the Caribbean, but there are also mortality estimates higher than the ones I found (see Table 13). Reasons for the different rates observed may be that the studies have been conducted in different regions, at different depths, using juvenile coral assemblages with different species compositions and were influenced by regional environmental factors that differ between the study sites.

In my study, juvenile coral survivorship was greatest at the midbay location. If the inbay, midbay and offbay locations are compared, it becomes clear that these three locations differ in benthic substrate composition and sediment input (Chapter 2). Macroalgal cover is highest at offbay locations and sedimentation is highest at the inbay locations (see Chapter 2). The same observation was made by Drew (1988) who conducted a study on reefs of the Great Barrier Reef and reported increasing standing crop of *Halimeda* with increasing distance from terrestrial inputs. Umar et al. (1998) observed on inshore reefs of the Great Barrier Reef that sediment deposition inhibited recruitment and growth of the macroalgal species *Sargassum*. This may be due to unstable substrate on reefs with high sedimentation making the attachment process difficult or causing it to fail, smothering, and reduced light conditions. Given this evidence, it is therefore reasonable to hypothesise that at the inbay locations, sedimentation threatens the survivorship of juvenile corals, whereas at the offbay locations macroalgae are the main cause of mortality. At the midbay locations, just enough sedimentation occurs to keep macroalgal cover down, but not enough to kill off juvenile corals.

I found greater mortality rates of juvenile corals at the offbay locations than at the inbay locations, raising two questions: (1) Are macroalgae a greater threat to juvenile corals than sedimentation? (2) Are there different macroalgal/algal species in inbay and offbay locations that have different effects on juvenile coral survivorship? Miller and Hay (1996) studied competition between a coral species and seaweed on temperate reefs in North Carolina, USA.

They found that this coral species was more abundant on reefs with high turbidity compared with more pristine reefs, dominated by seaweed. When transplanting coral colonies into weeded and non-weeded patches on the more pristine reefs, corals survived and grew well in habitat cleared of seaweed, whereas corals surrounded by seaweed showed mortality or decreased growth (Miller and Hay 1996). This suggests that on these reefs turbidity was a less harmful stressor compared to competition with seaweed. Miller and Hay (1996) also showed that settlement rates of this coral species were greater on substrates where all seaweed was removed than on patches dominated by stands of seaweed.

In general, it is difficult to separate different causes and relationships of juvenile coral mortality and benthic substrate variables, herbivorous fish biomass, sedimentation and distance, because they are all directly or indirectly linked with each other. For example, filamentous algal cover was higher on reefs with high sediment input, whereas macroalgae was more common on low than on high sedimentation reefs (see Chapter 2). Sedimentation rate and filamentous algae have a negative relationship with juvenile coral mortality. However, no relationship could be found between macroalgal cover and mortality rates of juvenile corals.

A further explanation why I did not find any difference in juvenile coral mortality rates between high and low sedimentation reefs might be that, because the low sedimentation bays were impacted by Hurricane Lenny in 1999, they differ in benthic substrate composition compared to high sedimentation reefs. In the low sedimentation areas I observed an increase in cover of blue-green algae in the year after the hurricane event (see Chapter 2). Blue-green algae form mats above the substrate and could easily smother organisms underneath and reduce light penetration.

5.5.2 Settlement rates

Settlement rates were higher in period II than in period I. This might be because of increasing water temperatures in period II that enhance larval settlement

(Zaslow and Benayahu 1996, Nzali et al. 1998). Changes between the two periods may be also due to seasonality in reproduction and/or environmental conditions.

This study shows that on reefs of the west coast of St. Lucia, settlement onto natural substrata equalled 18.8% of the original juvenile coral number. In comparison with a study by Rylaarsdam (1983) who estimated settlement rates of 44% and 49%, these were lower results. Rates I estimated equate to a total settlement rate of around 21 settlers.m⁻².yr⁻¹. These rates are higher compared with settlement rates on natural substrata of other studies conducted in the Caribbean, even higher than settlement rates on the reef substrata on the Great Barrier Reef (see Table 14). However, Connell et al. (1997) explained that rates usually differed among study areas and between sites since years of good or poor settlement were not consistent. Hence, comparisons of different larval settlement studies are difficult to do and interpretations of studies conducted only for a short time have to be done carefully. Additionally, it has to be taken into account that reef factors such as currents, water temperature and species composition differ in all regions and that the studies are not standardised, but conducted under different circumstances e.g. different depths.

In this study, I failed to find a significant difference in the number of new settlers between reefs with high and low quantities of sediment. However, settlement rates to natural substrata were significantly higher at the mouths of the bays (0.5 settlers.600cm⁻².100d⁻¹ ± 0.07 SE) than at their heads (0.2 settlers.600cm⁻².100d⁻¹ ± 0.06 SE). This difference may be influenced by sedimentation impact since significantly higher sediment input occurs in the inbay locations as I showed in Chapter 2. Furthermore, I found that increasing sedimentation decreased settlement rates significantly.

In Chapter 4, where I presented a study on larval settlement using artificial substrata conducted on the same reefs which supports results from this study. In that study, settlement rates were also higher at the mouth of bays (0.4 settlers.225cm⁻².100d⁻¹ ± 0.08 SE) than at their heads (0.1 settlers.225cm⁻².100d⁻¹ ± 0.03 SE) (Chapter 4). Settlement rates were higher on artificial than natural substrata substrata and there are several reasons why this might be. It is possible

Table 14: Settlement rates ($\text{no.m}^{-2}.\text{yr}^{-1}$) on natural reef substrata reported from other studies or estimated from other author's data.

Location (Caribbean only)	Settlement rate ($\text{no.m}^{-2}.\text{yr}^{-1}$)	References
St. Lucia	21	this study
Key Largo, Florida	2-6	Smith (1992)
Biscayne National Park, USA (three different reefs)	1, 2 and 15	Miller et al. (2000)
Jamaica	8 (only foliaceous corals)	Hughes and Jackson (1980)
Hérons Island, Great Barrier Reef	14	Connell (1997)

that very small settlers were not reassured on natural reef substrata due to the complexity including growth of algae and other benthic substrate components. Another reason may be that there was less competition with other benthic organisms on the artificial substrata because the tiles (used as artificial substrata) had spent much less time in the water. In contrast to findings from artificial substrata (see Chapter 4), the bays differed significantly in their settlement rates to natural substrata. This may be due to different reef substrata preventing, inhibiting or also attracting coral larvae to settle, whereas there was no difference in the type of substrate when tiles were used as artificial settlement traps.

Results of this study also showed that settlement rates decrease with increasing filamentous algal cover. Is this due to the link between sedimentation rate and filamentous algae (see chapter 2) or are there some chemical substances in filamentous algae that prevent coral larvae from settling? Allelopathy (a chemical process that a plant uses to keep other plants and organisms from growing too close to it) of algae was observed against alcyonacea (De Nys et al. 1991), but has not been shown to occur against scleractinian corals. Therefore, the combination of sedimentation and filamentous algae might have an impact on coral larval settlement. Sediment gets trapped in algal turf and could worsen settlement possibilities for coral larval settlement (e.g. Walker and Ormond 1982, Maida et al. 1994).

My results did not show a relationship between larval settlement rates and adult coral cover suggesting that coral cover as source of or attractant to coral larvae does not play an important role in larval supply for areas close by. Larvae might be transported to other reef areas by currents (Roberts 1997, Lugo-Fernandez et al. 2001). However, I found that increasing cover of coralline algae increases settlement rates. The same observation was made in other studies that show coralline algae is a very important substrate for coral larval settlement due to chemical cues that enhance settlement (Morse and Morse 1991). However, coralline algae appears not to be affected by sedimentation in this area (see Chapter 2) and, hence, other factors must be responsible for differences in settlement rate between the locations. For example, in inbay locations sediment

deposition on the substrate could cover coralline algae preventing coral larvae from successfully settling.

5.5.3 Species – mortality and settlement

Settlement and mortality rates of the different species clearly show the different life strategies of corals. *Agaricia spp.* and *Porites asteroides* show relatively high settlement and high mortality rates compared, whereas species such as *Colpophyllia natans* and *Meandrina meandrites* have low settlement but also low mortality rates. However, *Siderastrea siderea* a species known to have low settlement and mortality rates (Smith 1992, Lewis 1997), did not show any settlement in this study but relatively high mortality rates. Overall, if the rates I observed represented the real mortality and settlement rates of the species, none of them would be able to sustain themselves and balance out high mortality rates with high settlement rates. However, it is unlikely that this is the case because this would mean that over a period of several years, no new settlers would be found. Hence, it is more likely that the year I conducted my study either mortality rates were very high or settlement rates low. Long-term studies are necessary to limit variability over the years.

Annual mortality rates of *Agaricia spp.* calculated by Hughes and Jackson (1985) on reefs in Jamaica were equivalent to 26%, compared to 12% estimated from data collected by Van Morsel (1985). Van Morsel (1985) working in Curaçao, Netherland Antilles in the Caribbean, only investigated mortality rates of two *Agaricia* species. From his data, I estimated an annual mortality rate of 6.1% for both species together at a depth of more than 11m. This mortality rate is low compared to the mortality rate of *Agaricia spp.* that I found when all the locations were pooled together (43%). However, my rate was similar to that found by Smith (1992) who reported that 33% of this species died over one year on the reefs of Key Largo. The mortality rates that I observed for *Agaricia spp.* are on the other hand lower than rates estimated by Edmunds (2000) and Rylaarsdam (1983). Edmunds (2000) observed annual mortality rates of 50% for *Agaricia spp.* on

reefs of St. John, U.S. Virgin Islands, and Rylaarsdam (1983) reported that the annually mortality rate of *Agaricia* spp. on Jamaican reefs were 56%.

When I compared mortality rates of *Agaricia* spp. between high and low sedimentation conditions, I did not find a significant difference (low: 46%, high: 40%). However, mortality rates of both sedimentation levels were much lower compared with annual mortality rates in four bays with different eutrophication and sedimentation levels found by Hunter and Wittenberg (1992). They observed higher mortality rates on the high eutrophic/sediment bays (94%) compared to the low eutrophic/sediment bays (62%). As mentioned before, differences in our study areas and/or the possibility that one year was a better one for juvenile survivorship than the other, might have caused different results.

For *Porites astreoides*, I also estimated very similar annual mortality rates for the low and high sedimentation bays (low: 46%, high 52%). In contrast, Hunte and Wittenberg (1992) found much lower mortality rates of *P. astreoides* on low eutrophic/sediment sites (18%) and much greater ones on high/eutrophic sediment reefs (82%). Pooling all locations together, I found mortality rates for *P. astreoides* of 48%. This is twice as high as mortality rates for *P. astreoides* reported by Smith (1992) which was 23% spread over a depth of 10 to 30m on reefs of Key Largo. Again, caution needs to be taken when comparing different mortality rate observations because although all studies talk about juvenile corals, they include different size classes, studies were conducted at different depths and may describe total mortality rates of a juvenile coral community with different species compositions.

5.5.4 Growth rates

Growth rates were higher in period I, the winter period, than in period II, covering summer. This is mainly due to different growth rates in the high sedimentation bays in the two periods, whereas growth of juvenile corals in the low sedimentation bays did not differ between period I and II. It seems likely that sediment input in the two periods differed due to seasonal events such as rainfall.

In St. Lucia, the rainy season is from June to October, covered by period I. Unfortunately, sedimentation measurements only cover a small time scale in each period, six weeks in period I and 8 weeks in period II, and a quantitative comparison in sedimentation rates between the two periods cannot be conducted. Hence, it can only be speculated that rainfall and subsequent sediment run-off into the high sedimentation bays was higher in period I causing reduced growth rates. However, resuspension by waves could also have an effect increasing sedimentation stress on reefs if one period is rougher than the other. Resuspension is greater on high sedimentation reefs due to deposited sediment particles. That higher sedimentation affects juvenile coral growth rates is supported by the fact that growth rates were greater on reefs with low sedimentation ($0.15\text{cm}\cdot 100\text{d}^{-1} \pm 0.02$ SE) than with high sedimentation ($0.09\text{cm}\cdot 100\text{d}^{-1} \pm 0.01$ SE). The negative impact of sedimentation on the growth rate may be due to increased energy loss caused by sediment rejecting mechanisms, decreased light availability that decreases photosynthetic output of the zooxanthellae, and increased energy use for regeneration of tissue injuries caused by sediment particles (see Rogers 1990).

In contrast to my findings, Edinger et al. (2000) did not observe a significant difference when measuring extension rates of annual density bands of massive corals collected from land-based polluted and unpolluted reefs in South Sulawesi, Indonesia. However, live coral cover and bioerosion intensity were higher on the polluted reefs (Edinger et al. 2000). Tomascik and Sanders (1985) who studied growth rates of adult *Montastrea annularis* species along a eutrophication and sedimentation gradient (using the same method as Edinger et al. (2000)) found that growth rates first increased with increasing eutrophication and sedimentation and then decreased again. They hypothesised that suspended particulate matter may be an energy source for reef corals, increasing growth to a certain maximum concentration, and after this, reduction of growth occurs due to smothering and/or shading (Tomascik and Sanders 1985). Given that the studies investigated growth rates of adult colonies by measuring extension rates of density bands, whereas I measured changes in the greatest diameter of living corals, sedimentation rates that may not have an impact on adult corals might still

be harmful to juvenile corals (Richmond 1993) and/or affect adults and juveniles in different ways (Richmond 1997).

Since there was no difference in degradation rate between low and high sedimentation levels, it can be concluded that the differences in growth rates between the high and low sedimentation bays is due to the actual increase in size or a combination of size increase and degradation, but not to degradation rates alone. However, I found that degradation rates decreased with increasing distance from the head of bays. This may be due to increased harmful impacts acting in the inbay locations such as higher levels of sediment particles that might damage corals by abrasion. This explanation is supported by the fact that the sedimentation bay H2 has a close to negative growth rate during the study period probably.

Overall, I observed a total annual growth rate pooled across locations and species of $0.47 (\pm 0.04 \text{ SE}) \text{ cm.yr}^{-1}$ including measured reduction in size and of $0.78 (\pm 0.04 \text{ SE})$ excluding degradation measurements. Edmunds (2000) studying juvenile corals on the reefs of St. Johns, U.S., noted that growth rates were low and that many juvenile corals shrank. He calculated a total growth rate of $0.21 (\pm 0.04 \text{ SE}) \text{ cm.yr}^{-1}$ which is half of my estimation. Growth of 2.8 and 2.9 cm.yr^{-1} was reported for *A. agaricites* and *A. humilis* in Curaçao (Van Moorsel 1985). Growth rates for *P. astreoides* from the same reefs are $2.3 (\pm 0.04 \text{ SE}) \text{ cm.yr}^{-1}$ (Van Moorsel 1988), which is similar to growth rates for *Agaricia* spp. However, (Van measurements do not correspond with growth rates that I found on reefs of St. Lucia which were much lower for both species (*Agaricia* spp. $0.80 (\pm 0.04 \text{ SE}) \text{ cm.yr}^{-1}$, *P. astreoides*: $0.92 (\pm 0.04 \text{ SE}) \text{ cm.yr}^{-1}$. Growth rates measured for *Agaricia* sp. on Jamaican reefs were 1.1 cm.yr^{-1} which is much closer to growth rates I observed. It may be that *A. agaricites* and *A. humilis* are very fast growing species whereas other *Agaricia* species grow slower. *Porites* spp. growth rates on Jamaican reefs are also higher than growth rates I observed for *P. astreoides*, but this may be because *P. porites* is in general a much faster growing species and, hence, may have increasing effect on total rates for Poritiids. Generally, differences in growth rates between different studies may be due to locational

characteristics such as different depths, season, and even years. High rates of variation would therefore be expected since growth has been reported to differ between species, individuals, regional settings and environments (Birkeland 1977, Babcock 1985, Chou 1988, Rice and Hunter 1992). Since growth rates of smaller juvenile corals have been frequently found to be higher than those of juvenile corals with larger diameter (Van Morsel 1988), I will not compare growth rates calculated from extension rates of adult colonies.

5.3.5 Coral reef recovery and recolonisation

The total mortality rate for all locations for the study period was 40.7%, whilst the number of new settlers was equivalent to 18.8% of the original coral number. Mortality rates appear very high in comparison to settlement rates. However, it is difficult to draw any conclusions on the dynamics of these processes since one year is not enough to really see what is going on. A similar result was found by Porter and Meier (1992) who studied loss and changes in Floridian reef coral communities who found that net losses of coral cover ranged between 7.2% and 43.9% over a period of seven years (1984 and 1991). Throughout their study they did not observe a single larval settlement event in any of their permanent photoquadrats. They therefore concluded that coral losses of this magnitude cannot be sustained.

Smith (1992) summarised different studies and concluded that coral assemblages of the West Atlantic region were more unstable than of the Indo-Pacific. Declines without subsequent recovery occurred in 57% of West Atlantic examples but in only 29% of those in the Indo-Pacific. The principal reason corals recovered in some local sites but not in others seems to relate to the type of disturbance that caused the decline. Coral cover recovered after 69% of acute, short-term disturbances but after only 27% of the chronic, long-term ones. Since sedimentation on these reefs is a chronic threat, we are dealing with a long-term problem. Even if sediment input can be stopped, sedimentation stress will still affect these corals by resuspension.

Coral reefs that are already weakened by a chronic disturbance may be more susceptible to a further impact (Brown 1997, Connell 1997, Scheffer et al. 2001). After a natural disturbance, such as a hurricane event, recovery of the reef by growth and recolonisation may be slow or may even fail if other disturbances such as chronic sedimentation continue to act in the background (Nyström et al. 2000). The positive side of my results is that I found settlement on high sedimentation reefs in St. Lucia and that on these reefs mortality rates were actually lowest. However, overall I suggest from my study findings that sedimentation, combined with low biomass of herbivorous fish forms a severe threat for survival and growth of juvenile corals on St. Lucia's reefs. It remains to be seen whether or not new settlers can replace what has been lost.

5.6 Conclusion

In summary, this study shows that sedimentation has a negative effect on the replenishment of coral reefs by reducing settlement and growth. Settlement rates were higher in locations that are further away from a potential source of sedimentation. However, it is difficult to determine the mechanisms that act on juvenile coral survivorship and growth, since many factors correlate with each other. Sedimentation decreases macroalgae (see chapter 2), but macroalgae might be a more detrimental threat to juvenile corals than sedimentation, causing their mortality by competing for space and shading them. Herbivorous fish reduce algal cover, but may damage juvenile corals due to unselective grazing. Additionally, prior to this study, in 1999 Hurricane Lenny hit coral reefs of the low sedimentation bays more severely than high sedimentation bays. This caused high coral mortality and enhanced algal growth (especially blue-green algae, see Chapter 2) reducing suitable substrata for coral larval settlement and presumably decreasing juvenile coral survivorship. This study also showed that algal cover (probably mainly macroalgae) has a detrimental effect on juvenile coral survivorship.

Bak and Meesters (1999) predict that over the next decades global change will skew coral colonies towards larger colonies as a result of changes in mortality patterns or recruitment failure. My findings suggest that growth rates are lower on high sedimentation reefs, leaving juvenile corals at a critical size for longer on the more stressed reefs. However, I could not find any significant difference in mortality and settlement rates between reefs with different levels of sediment input. Nevertheless, settlement rates increased with increasing distance from the head of the bays to their headlands which might be linked sediment run-off. Overall, it seems that different factors seem to affect the early life history of corals simultaneously making it difficult to distinguish between different factors and their impacts.

One limitation of this study is that it was conducted over a short period and so the mortality, settlement and growth rates observed may not give a true indication of long-term trends in some processes e.g. settlement rates may be sporadic. It is, however, questionable whether even high pulses of settlement would be enough to sustain the coral communities on the reefs studied.

5.7 References

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Summary, Implications and Conclusion

6.1 Introduction

In this thesis I investigated the effects of multiple stresses on the replenishment of coral communities. Stress factors can be human-induced or natural. Hurricanes and storms are natural disturbances causing wave destruction and/or heavy rainfall (Woodley et al. 1981, Sladek Nowlis et al. 1997). Three major human-induced impacts are sedimentation, eutrophication and fishing (Roberts 1993, Ginsburg 1994). Rising sea water temperature causing mass coral bleaching and mortality events world-wide is a further factor adding to coral reef degradation (Glynn 1984, Sheppard 1999). Due to a growing human population and global climate change a significant decline in coral cover and coral health is being experienced world-wide (Hoegh-Guldberg 1999, Wilkinson 2000). The long-term impact of these declines will depend on processes that replenish depleted populations. This makes reproduction, coral larval settlement and post-settlement survival essential processes for coral reef recovery. It is therefore vital that we advance our understanding of the effects of human and natural stresses on these processes.

In Chapter 1, I reviewed existing literature on the impacts of sedimentation, eutrophication, overfishing and rising sea temperature on the early life history processes of corals. I then summarised the findings and looked at the impacts of multiple stresses on these processes. Finally, I presented two simple

models describing the impacts of additive and synergistic effects on the energy budget of a coral colony and on a coral population.

Chapters 2 to 5 present data collected on coral reefs in St. Lucia, West Indies. I concentrated on the effects of sedimentation, fishing and the impacts of hurricanes. In Chapter 2, I investigated the impacts of these stresses on the benthic substrates such as coral cover, different functional groups of algae, sand and rubble. I also tested the role of marine reserves in reversing phase-shifts from coral to algal domination. In Chapter 3, I described juvenile coral assemblages on the reefs and the effects of sedimentation on their abundance, diversity, composition and health status. Coral larval settlement rates on artificial substrata on the same reefs were estimated, and the influence of sedimentation and herbivorous fish biomass on settlement rate is described in Chapter 4. In Chapter 5, I looked at larval settlement on the natural reef itself and studied mortality and growth rates of juvenile corals.

6.2 Summary of the results from Chapter 1 to Chapter 5

The main findings of my research, as analysed and described in Chapter 1 to Chapter 5, are summarised below:

- Most research investigating the effects of disturbance on the replenishment of coral communities has concentrated on the effects of one individual stress on one single process of the early life history of corals (reproduction, settlement or post-settlement). Synthesising across the different studies I showed how different stresses can affect the same process. Stresses can act additively or synergistically, where the addition of stress enhances the effect of another. Stresses can reduce the energy budget of a coral by so much that it may have to cut off energy supply to reproduction and growth. If too many stresses threaten the coral, its basal metabolism could be so far reduced that the colony will die. Allee effects can also compound the impacts of stress on coral populations through fertilisation failure caused by low population densities.

Stresses that reduce gamete output could raise the threshold population density below which Allee effects occur. Subsequent stresses can lead to extinction of a coral population because more coral colonies are needed to ensure a gamete output sufficient for successful fertilisation. Additionally, stresses decrease the maximum capita growth of populations by reducing survival of larvae, settlement rates and by increasing post-settlement mortality.

- In the St. Lucian study area, coral cover decreased from 1995 to 2001 while algal cover increased reciprocally. Most severe coral damage was caused by waves from a hurricane in 1999 leading to dramatic changes in benthic substrate composition. In shallow water, I found that coral cover decreased by 44%, whereas in deeper water I measured a coral cover reduction of 29%. Additionally, sedimentation was identified as a serious chronic threat to coral reefs. Over a 3 years period, it caused a steady decline in coral cover, especially in deeper water (3% decline at 5m, 19% decline at 15m). Lost coral cover was immediately replaced by algae. Functional algal groups reacted differently to sedimentation stress, especially macroalgae which seems to be very susceptible to sedimentation. In the study area, marine reserves have rebuilt herbivorous fish stocks on the reefs, and in the years without physical disturbance, the coral cover in marine reserves showed stability or even a tendency to increase. However, in combination with sedimentation, marine reserves could not prevent coral decline.
- The density of juvenile corals was approximately 5 juvenile corals per 0.48m². With increasing sedimentation rate, the number of juvenile corals decreased. I found fewer juvenile coral species and a different species composition in low sedimentation compared to high sedimentation reefs. This was probably due to differential susceptibility of species to sedimentation stress. The health of juvenile corals was significantly reduced by sedimentation. On reefs with the highest sedimentation stress, around 80% of juvenile corals showed signs of overgrowth, damage and poor health. On low sedimentation reefs, up to 40% of the colonies were healthy. Size was negatively affected by sedimentation.

Juvenile coral abundance showed a negative relationship with algal cover and a positive relationship with adult coral cover, indicating that adult corals serve as direct source of coral larvae which settle close to the parental colony or attract larvae from elsewhere. This is supported by the fact that most coral settlers were brooders.

- Generally, coral larval settlement was higher on artificial substrata ($0.3 (\pm 0.04 \text{ SE}) \text{ settlers.}225\text{m}^{-2}.\text{100d}^{-1}$) than on natural ($0.1 (\pm 0.02 \text{ SE}) \text{ settlers.}225\text{cm}^{-2}$ in up to 7 months) probably because it is easier to find small corals on artificial substrata. On both artificial and natural substrata, there was no significant difference in settlement rates between low and high sedimentation reefs. However, on both substrata settlement rates differed along the coast. I found the lowest settlement rates where water activity was lowest and sedimentation highest. This indicates that a combination of sedimentation and calm water negatively affect larval settlement, perhaps because in calm water the sediment particles deposit on the reef, whereas higher water turbulences effectively remove the particles from the substrate.
- Mortality rates of juvenile corals did not differ significantly between reefs with low and high sediment input, but significantly lower mortality rates were found where wave exposure was intermediate. I suggest that this is due to a combination of different effects. In the low sedimentation reefs, sedimentation stress inhibits juvenile survival, whereas at the most exposed reefs spatial competition, especially with macroalgae, increases mortality rates. Hence, between these two extremes, sedimentation level is not too stressful to juvenile corals but still enough to inhibit macroalgal growth. On reefs of the whole study area, I estimated total mortality rates of juvenile corals to be 40.7% (compared to coral larval settlement rates to natural substrata of 18.8% of the original coral number).
- I investigated the effects of marine reserves on replenishment of coral communities by looking at the influence of herbivorous fish biomass on coral

larval settlement and mortality rates of juvenile corals. I found no relationship between any of the variables. However, the highest number of settled corals on artificial substrata occurred where herbivorous fish biomass was intermediate or high.

- Growth rates of juvenile corals were significantly lower on high rather than low sedimentation reefs. This is probably the result of reduced energy supply of corals on high sedimentation reefs caused by reduced light penetration and increased sediment rejecting activities (see Rogers 1990).

6.3 Implications for the future of coral reefs and their management

My studies show that multiple stresses have severe impacts on coral communities in St. Lucia. It has not always been easy to separate the different effects of the stressors influencing the reefs. Nevertheless, I found that sedimentation, fishing and hurricanes acting together can cause phase-shifts from coral to algal dominance. This shift has been reported from several reefs in the Caribbean (e.g. Hughes 1994, Shulman and Robertson 1996, McClanahan and Muthiga 1998). Several causes have been cited for inducing these shifts including the *D. antillarum* sea urchin die-off in 1983/4, overfishing of herbivorous fish populations, coral disease outbreaks and increasing eutrophication (e.g. Gladfelter 1982, Hay 1984, Lessios 1988, Lapointe 1997).

My thesis presents the first study to test the effects of marine reserves in reversing phase-shifts. Marine reserves have been shown to increase the biomass of herbivorous fish stocks (Roberts et al. 2001, Hawkins in prep.). An increase in herbivorous fish stocks may significantly decrease algal cover due to increased grazing (Done 1992). However, in St. Lucia it seems that fish stocks have not yet sufficiently recovered to have a significant impact on algal cover (Chapter 2). Macroalgae are probably the most detrimental type of algae for corals (Tanner 1995, Tanner 1997) and in marine reserves with low sedimentation stress, I found

macroalgal cover to be highest (Chapter 2). This supports other studies reporting that herbivorous fish avoid eating macroalgae (Hatcher 1984).

Recovery of degraded reefs occurs by new settlement of coral larvae (Pearson 1981). On some reefs in St. Lucia, coral mortality exceeded 50% (loss of coral) after Tropical Storm Debbie in 1994 (Sladek Nowlis et al. 1997) and from 1995 to 2001 I observed a further 23% loss across the study area (Chapter 2). The settlement rates that I observed on the same reefs, may not be able to compensate for the coral loss the reefs suffered, but longer term research is needed to confirm this. My research suggests that a negative feedback is taking place: larval settlement shows a positive relationship with adult coral cover (Chapter 4 and 5) and if these adult coral colonies succumb to outbreaks of diseases (Nugues 2002), destruction by hurricanes (Chapter 2, Sladek Nowlis et al. 1997) or sedimentation (Chapter 2, Nugues 2002), settlement rates may also decline due to lower densities of reproductively active corals.

Hard and stable substrate is needed to ensure coral larvae can settle. Sediment particles on substrate suitable for settlement have been shown to inhibit the larval settlement process (Hodgson 1990, Te 1992, Wittenberg and Hunte 1992). In my study area, I found the lowest settlement rates where sedimentation was high and water movement low (Chapter 4 and 5). In these locations, adult coral cover is also low and corals on these reefs are most threatened by sedimentation (Chapter 2). Hence, the replenishment of these coral communities will be impaired by chronic pollution stress. This scenario is reflected in the models that I presented in Chapter 1. Corals in a stressed environment show a decreased energy budget resulting in lower gamete production. Low densities of coral can lead to fewer successful fertilisations, due to greater dilution of the gametes at the sea surface. Furthermore, successfully developed larvae might be prevented from settling on the reefs if the substrate is altered by sediment particles. An additive stress, for example sedimentation, which can decrease post-settlement survivorship, can push species towards local extinction more quickly. Therefore, the high sedimentation reefs I studied in St. Lucia are under threat of further degradation. A point may be reached when recovery is no longer possible.

In contrast to the long-term data set I presented for components of the benthic substrate and reef fish assemblages, my studies on coral larval settlement, mortality rates of juvenile corals and their growth rates were only conducted over a period of one year. Settlement, mortality and growth are processes that are very variable in space and time (Babcock 1985, Hughes et al. 1999). To understand the dynamics of these processes long-term data are necessary. Hence, it would have been better to study these processes for longer. Generally, long-term studies on the early life history of corals are very rare and we should consider focusing more on these processes because large-scale destruction of coral reefs is currently taking place (Bryant 1998). To determine the fate and future prospects of coral reefs, we need to know more about the reefs' ability to recover .

For practical reasons marine park managers need to be made aware of the importance of early life history processes to the survival of the reefs they protect. While it is important to follow changes in the cover of benthic reef components, it is equally, if not more important to follow their recovery after disturbances that lead to coral loss. The methods I used to estimate coral settlement and mortality rates of juvenile corals (in Chapters 3 to 5) were straight forward and could be taught to non-specialists. Hence, I advise coral reef managers to add the monitoring of these processes to their scientific program.

A further message for reef managers from my study is that marine reserves cannot protect reefs from chronic pollution and natural disturbances. Coral reefs face multiple stresses and these are increasing in severity and frequency. Hence, it is necessary to reduce chronic stress as much as possible. Sedimentation is a chronic stress that can easily be reduced by limiting construction works in the rainy season, preventing building on the beach zone, leaving hedges along rivers to prevent soil erosion and by improved soil management in agriculture. Coral reefs need to be spared from chronic stress if they are to recover between natural disturbances. This is now especially important, since further coral mass mortalities caused by bleaching events and diseases are expected to materialise (Harvell et al. 1999, Hoegh-Guldberg 1999, Knowlton 2001, Porter 2001, Patterson et al. 2002).

6.4 Conclusion

Marine reserves are effective tools for rebuilding depleted fish stocks, but their role in reversing phase-shifts is still not clear. For example, macroalgae may be a serious threat to coral reefs if they cannot be controlled by herbivorous fish. Sedimentation can counteract the positive effects of marine reserves on corals, as can uncontrollable natural events such as storm and bleaching events. Recovery of damaged reefs by new coral larvae is a slow process and is detrimentally affected by sedimentation and algal cover. In St. Lucia, the density and survival of new settlers may be too low to replace corals killed off by multiple stresses. Improved management to reduce sediment inputs will be necessary to halt reef degradation.

Users and managers have to be clear about the ecological and economic value of reefs. The conservation of these ecosystems requires a much higher level of attention or it may be too late to reverse the degradation trend. More research should focus on the effects of multiple stresses on the early life processes of corals. Just as we need to assure the survival of new generations of trees, we need to guarantee that there are enough offspring of coral communities to sustain reefs in the future.

6.5 References

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Appendix 1: Sample sizes for reef (number of quadrats) and fish (number of counts) monitoring. For site location and description see Figure 1 and Table 1 of Chapter 2.

Site	Depth	Reef monitoring						Fish monitoring					
		1995	1996	1997	1998	2000	2001	1995	1996	1997	1998	2000	2001
1	5m	10	11	14	16	16	18	6	6	6	6	6	6
	15m	10	10	13	16	15	17	6	6	6	6	6	6
2	15m	10	10	13	13	15	17	6	6	6	6	6	6
3	5m	10	11	11	16	17	17	6	6	6	6	6	6
	15m	9	11	12	16	15	17	6	6	6	6	6	6
4	5m	10	10	12	14	17	17	6	6	6	6	6	6
	15m	10	10	13	14	24	14	6	6	6	6	6	6
5	5m	10	13	11	18	17	17	6	6	6	6	6	6
	15m	10	11	12	17	13	14	6	6	6	6	6	6
6	5m	10	10	12	18	12	17	6	6	6	6	6	6
	15m	10	12	11	15	12	14	6	6	6	6	6	6
7	5m	10	10	12	12	17	17	6	6	6	6	6	6
	15m	9	9	12	12	14	17	6	6	6	6	6	6
8	5m	nd	nd	12	18	16	16	nd	nd	6	6	6	6
	15m	nd	nd	12	18	14	17	nd	nd	6	6	6	6
9	5m	11	11	13	16	17	17	6	6	6	6	6	6
	15m	11	10	11	13	16	13	6	6	6	6	6	6
10	5m	10	10	13	16	17	17	6	6	6	6	6	6
	15m	7	11	10	13	15	14	6	6	6	6	6	6
11	5m	10	10	12	16	12	17	6	6	6	6	6	6
	15m	10	10	10	12	14	14	6	6	6	6	6	6
12	5m	nd	10	13	16	17	17	6	6	6	6	6	6
	15m	nd	19	10	14	11	15	6	6	6	6	6	6
13	5m	nd	11	10	12	12	17	6	6	6	6	6	6
	15m	nd	10	7	12	13	15	6	6	6	6	6	6
14	5m	10	11	13	16	17	17	6	6	6	6	6	6
	15m	7	10	11	13	10	14	6	6	6	6	6	6
15	5m	11	10	12	17	17	17	6	6	6	6	6	6
	15m	8	10	11	12	12	13	6	6	6	6	6	6
16	5m	10	10	10	15	17	17	6	6	6	6	6	6
	15m	10	10	13	14	13	15	6	6	6	6	6	6
17	5m	10	11	11	16	17	17	6	6	6	6	6	6
	15m	9	10	11	13	13	14	6	6	6	6	6	6
18	5m	nd	10	12	14	17	17	6	6	6	6	6	6
	15m	nd	11	12	12	14	13	6	6	6	6	6	6
19	5m	10	12	13	16	17	17	6	6	6	6	6	6
	15m	10	12	14	16	16	17	6	6	6	6	6	6
20	5m	9	13	13	16	17	17	6	6	6	6	6	6
	15m	10	12	12	14	16	17	6	6	6	6	6	6
21	5m	10	12	12	17	18	18	6	6	6	6	6	6
	15m	nd	10	12	16	14	17	6	6	6	6	6	6
22	5m	nd	13	13	18	17	17	6	6	6	6	6	6