



**Factors influencing Structure
and Dynamics of Subtidal
Assemblages on Walls at a South
Eastern Australian Rocky Reef**

**Dissertation zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen
Fakultät der Christian-Albrechts-Universität
zu Kiel**

**vorgelegt von
Simone Dürr**

Kiel, im Mai 2003

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Summary

Assemblages on vertical surfaces at the Rocky Reef at Flinders Islet, South Eastern Australia, appear to differ in structure. Tall wall assemblages seem highly diverse in regard to encrusting invertebrates, while low wall assemblages seem to be characterised by low diversity and dominated by crustose coralline red algae. In this study, I investigated the question why the structure of subtidal benthic assemblages on tall (more than 4 m height) and low walls (1 to 2 m height) on the Rocky Reef at Flinders Islet in the Western Tasman Sea is different from each other. The walls are all in a depth of 9 to 15 m.

Assemblages were photographically monitored by Scuba from July 1999 to February 2002. Assemblages had higher percentage cover, more species and higher diversity on tall than on low walls. Possible causes for the observed pattern were differences in recruitment, successional dynamics, hydrodynamics and grazing pressure between tall and low walls. Sea urchins (*Centrostephanus rodgersii*, Agassiz, 1863) were more than four times more abundant on low than on tall walls. To investigate sea urchin effects separately from wall height effects, sea urchin densities were manipulated on walls. Every tall and every low wall was split in half and sea urchins were added or removed to achieve high and low sea urchin density for every wall. All experiments were designed as split-plot experiments and accordingly statistically analysed.

To test for differences in recruitment, unglazed ceramic tiles (98 x 98 mm) were attached to the walls and left there for at least six weeks. The experiment was done twelve times from April 2000 to May 2002. Recruitment was more diverse, richer in species and had higher total cover percentage on tall than on low walls. The composition of recruitment was different on tall and low walls. When sea urchin density was high, total cover percentage, numbers of species and diversity was lower than when sea urchin density was low. Effects of tall and low walls and sea urchin density were in the majority of experiments absent. Water motion was only very slightly (not statistically significant) higher on tall than on low walls.

The development of assemblages on tall and low walls with high and low sea urchin density was followed on unglazed ceramic tiles that were photographically sampled after 21 and 24 months. While effects were not statistically significant, tall and low walls and sea urchin density had the same effects as found in the recruitment experiment. Composition of the assemblages was significantly different between tall and low walls.

After 21 months of development, assemblages were transferred (changed-over) between habitats (Tall wall – high sea urchin density, tall wall – low sea urchin density, low wall – high sea urchin density, low wall – low sea urchin density). A direct carry-over effect

(formative effect of a previous habitat on the assemblage) of habitat before change-over on habitat effect after change was not found. The move affected total cover, numbers of species and diversity, but was a transfer effect in most cases. Change in percentage total cover of assemblages originating on tall walls with low sea urchin density and changed-over to other habitats was different from the original assemblage. Enhanced sea urchin grazing decreased percentage total cover in these other habitats, while percentage total cover on tall walls with low sea urchin density increased. Assemblages originating on low walls with high sea urchin density diverged from the low wall – high sea urchin density assemblage when changed-over to a different habitat. Assemblages did not converge after change-over from different habitats to the same habitat.

I conclude all three processes - recruitment, succession and sea urchin grazing - differ among wall types and contribute to the observed different assemblages. However, similar low sea urchin densities on tall and low walls do not have similar impacts: tall walls offer far less shelter for the sea urchin to evade predation by fish. High cover of soft-bodied invertebrates impede grazing and attachment to the wall. Low walls offer more shelter for the sea urchin against predation and the high cover of crustose coralline red algae allows for unhindered grazing. Grazing impact is greater on low than on tall walls.

Assemblages on tall and low walls determine their own specific larval pool and therefore recruitment. Recruitment on tall walls is more diverse than recruitment on low walls and different in composition. These differences in diversity and especially composition between tall and low walls are further transferred in succession, on tall walls, growth from the surrounding area into the newly developing assemblage gets more and more important for the differences. Sea urchin grazing impact enhances the distinction of tall and low walls by decreasing diversity on low walls. Two assemblages differing in diversity and composition develop. Tall wall assemblages are more diverse than low wall assemblages. Assemblages on tall walls are dominated by sponges, ascidians and cnidarians, while assemblages on low walls are dominated by crustose coralline red algae. Tall and low walls represent two different habitats that may effectuate two alternative community states, the low wall assemblage being less stable than the tall wall assemblage diverging soon when habitat changes during succession.

Zusammenfassung

Am Felsriff von Flinders Islet im Südosten von Australien haben die Gemeinschaften an den vertikalen Oberflächen den Anschein sich in ihrer Struktur zu unterscheiden. Gemeinschaften an hohen Felswänden erscheinen sehr divers an sessilen Invertebraten. Dahingegen fällt auf, dass Gemeinschaften an niederen Wänden wenig divers sind und von Krustenrotalgen dominiert werden. In dieser Studie habe ich die Frage untersucht, warum sich die Struktur von subtidalen benthischen Gemeinschaften an hohen (mehr als 4 m Höhe) und niederen Wänden (1 bis 2 m Höhe) am Felsriff von Flinders Islet unterscheiden.

Die Gemeinschaften wurden taucherisch untersucht und fotografiert von July 1999 bis Februar 2002. Die Gemeinschaften an hohen Wänden zeichnen sich im Vergleich zu niederen Wänden durch höhere Bedeckung, Artenzahl und Diversität aus. Mögliche Gründe hierfür sind Unterschiede im Rekrutment, der Sukzession, der Hydrodynamik und dem Druck durch Abweiden zwischen hohen und niederen Wänden. Seeigel der Art *Centrostephanus rodgersii* waren viermal häufiger an hohen als an niederen Wänden vertreten. Seeigeldichten wurden manipuliert, um Seeigel-Effekte getrennt von Einflüssen, die auf unterschiedliche Wandhöhe zurückzuführen sind, untersuchen zu können. Jede Wand wurde deshalb in der Mitte geteilt und Seeigel wurden hinzugefügt oder entfernt, um sowohl hohe als auch niedere Dichte an jeder Wand zu erzielen. Jedes der Experimente wurde als sogenanntes Split-Plot-Experiment entworfen und dementsprechend statistisch analysiert.

Unglasierte Keramikfliesen (98 x 98 mm) wurden an den Wänden angebracht und dort für mindestens sechs Wochen belassen, um auf Unterschiede im Rekrutment hin zu untersuchen. Das Experiment wurde zwölf mal durchgeführt in der Zeit vom April 2000 bis Mai 2002. An hohen Wänden war das Rekrutment diverser, artenreicher und bedeckte mehr Fläche als an niederen Wänden. War die Seeigeldichte hoch, dann war die Bedeckung, die Artenzahl und die Diversität niedriger, denn wenn die Seeigeldichte niedrig war. Jedoch waren in der Mehrzahl der Experimente Effekte, die auf hohe oder niedere Wände oder Seeigeldichte zurückzuführen waren, abwesend.

Die Entwicklung von Gemeinschaften auf unglasierten Keramikfliesen an hohen und niederen Wänden mit hoher und niederer Seeigeldichte wurde untersucht. Die Gemeinschaften wurden nach 21 und 24 Monaten fotografiert. Effekte waren nicht statistisch signifikant, aber für die gemessenen Parameter kann man für die Wandtypen und Seeigeldichten dieselben Trends erkennen wie im Rekrutment-Experiment. Auch war die Zusammensetzung der Gemeinschaften unterschiedlich an hohen und niederen Wänden.

Nachdem sich die Gemeinschaften bis zum Alter von 21 Monaten entwickelt hatten, wurden sie zwischen Habitaten verpflanzt ('change-over'). Die Habitate waren hohe Wand mit hoher Seeigeldichte, hohe Wand mit niederer Dichte, niedere Wand mit hoher Dichte und niedere Wand mit niederer Dichte. Ein direkter Übertragungseffekt ('carry-over effect') eines Habitats vor der Verpflanzung auf den Effekt eines Habitats nach der Verpflanzung wurde nicht nachgewiesen. Die Verpflanzung beeinflusste die Bedeckung, die Artenzahl und die Diversität und war in den meisten Fällen ein direkter Effekt der Verpflanzung selbst. Allerdings war die Änderung in der Bedeckung von Gemeinschaften, die aus dem Habitat hohe Wand mit niederer Seeigeldichte stammten, unterschiedlich zur im Habitat verbliebenen Gemeinschaft, wenn sie in ein anderes Habitat verpflanzt wurden. Verstärktes Abweiden durch Seeigel senkte dann die Bedeckung, wohingegen die Bedeckung der im Habitat verbliebenen Gemeinschaft anstieg. Außerdem divergierten Gemeinschaften, die von niederen Wänden mit hoher Seeigeldichte stammten, von der Ausgangsgemeinschaft, wenn sie in ein anderes Habitat verpflanzt wurden.

Zusammenfassend lässt sich feststellen, dass alle drei Prozesse - Rekrutment, Sukzession und Abweidung durch Seeigel - an den Wandtypen verschieden ablaufen und so zu den beobachteten Gemeinschaftsunterschieden beitragen. Jedoch haben ähnliche niedere Seeigeldichten an hohen und niederen Wänden nicht ähnliche Einflüsse. Hohe Wände haben viel weniger Schutzmöglichkeiten für die Seeigel, um Räubern zu entgehen. Außerdem beeinträchtigt die hohe Bedeckung an weichen Invertebraten das Abweiden und das Festhalten an den hohen Wänden. Niedere Wände dahingegen bieten mehr Verstecke für die Seeigel, und die Dominanz der Krustenrotalgen lässt die Seeigel uneingeschränkt die Felswände abweiden. Der Einfluss des Abweidens ist damit größer an niederen als an hohen Wänden.

Die Gemeinschaften an hohen und niederen Wänden haben jeweils bestimmte Larven, die besiedeln können, und dies führt zu unterschiedlichem Rekrutment. Das Rekrutment an hohen Wänden ist diverser als an niederen Wänden. Die Unterschiede der Gemeinschaften in Diversität, und vor allem in der Zusammensetzung des Rekrutments, werden weitertransferiert in der Sukzession. Zusätzlich ist in der Sukzession das Hineinwachsen von kolonialen Organismen der Umgebung in die sich gerade entwickelnde Gemeinschaft an hohen Wänden wichtig. Der Einfluss des Abweidens durch Seeigel verstärkt die Unterschiede zwischen den Wandtypen weiter, denn das Abweiden senkt die Diversität an niederen Wänden. Zwei Gemeinschaften entwickeln sich, die sich in Diversität und Zusammensetzung unterscheiden. Gemeinschaften an hohen Wänden sind diverser als Gemeinschaften an

niederen Wänden. Gemeinschaften an hohen Wänden sind dominiert von Schwämmen, Ascidien und Cnidariern, wohingegen Gemeinschaften an niederen Wänden von Krustenrotalgen dominiert werden. Hohe und niedere Wände bestehen als zwei unterschiedliche Habitate, die womöglich zwei alternative Zustände der Gemeinschaft herbeiführen. Dabei sind die Gemeinschaften an den niederen Wänden weniger beständig als die Gemeinschaften an den hohen Wänden und divergieren schnell, wenn sich das Habitat während der Sukzession ändert.

1. Introduction

An ecosystem known for its high diversity are Rocky Reefs. Rocky Reefs often form the only available hard substratum for invertebrate larvae and algal spores to settle on. Through their high abundance and diversity of sessile invertebrates and algae and their high spatial heterogeneity, they form a very complex environment that not only attracts various predatory species, but is also used by many pelagic species, like fish, as nursery ground for their young. Rocky Reefs are cosmopolitan and a major part of ecological work in the marine environment was done in their intertidal zone (e.g. Connell, 1961a, b; Paine, 1966; Dayton, 1971; Menge, 1976; Wootton, 1993; Petraitis and Dudgeon, 1999). Subtidal work at Rocky Reefs has got more common since the early 1980s mainly due to Scuba diving becoming more widespread (e.g. Vance, 1979; Ayling, 1981; Scheibling, 1984; Breitburg, 1985; Witman, 1985; Sebens, 1985; Barkai and Branch, 1988; Smith, 1999). Prominent features of the subtidal of Rocky Reefs worldwide are kelp forests and crustose coralline red algae flats. The crustose coralline red algae flats are often called 'barren' habitat (e.g. Breen and Mann, 1976; Ayling 1981). The barren habitat is not only characterized by high abundance of crustose coralline red algae, but also by high density of sea urchins (e.g. Ayling 1981; Wharton and Mann, 1981; for review see Lawrence 1975). Sea urchins can be key-herbivores on Rocky Reefs in many parts of the world (e.g. North Eastern Atlantic: Leinaas and Christie, 1993; Mediterranean: Bulleri et al., 1999; North Eastern Pacific: Ebert, 1977; North Western Atlantic: Himmelman et al., 1983; Chapman and Johnson, 1990; South Western Pacific: Ayling, 1981; Fletcher, 1987; Andrew and Underwood, 1993). Generally, grazing by sea urchins leads to a switch from a community dominated by macroalgae to a community dominated by crustose coralline red algae, the barren habitat. Sea urchins are usually omnivores and feed on algae and sessile invertebrates (Ayling, 1978; Karlson, 1978; Vance, 1979; Ayling, 1981; Himmelman et al., 1983; Biscoe and Sebens, 1985; Witman, 1985), dislodge or damage them, while grazing. Effects of sea urchin grazing on the community can be various. Sea urchin foraging may decrease species richness and diversity and may change also the rank order of dominance in the community.

Often there are changes in community structure, where there is vertical extension of hard substratum forming walls, and mechanisms found to be important for horizontal surfaces may lose significance there. Very tall rock walls, as along fjords, can have extremely high diversity patches of sessile invertebrates due to hydrodynamics and weakly dispersing larvae (Smith and Witman, 1999). Some consumers may have limited access to taller walls. In the

Mediterranean, the sea urchin *Arbacia lixula* is abundant on vertical walls, whereas another sea urchin living in the same habitat, *Paracentrotus lividus*, can mainly be found at the bottom of walls, which is probably due to the species being less able to resist wave-shock (Bulleri et al., 1999).

Australian Rocky Reefs are very different from other Rocky Reefs, especially North American ones (Keough et al., 1990). Large mussel beds are absent and monocultures of other species are rare. There is no keystone predator in the intertidal at Australian Rocky Reefs. Therefore, generalisations made for other Rocky Reefs, especially for the intertidal zone, do not fit the Australian Reefs. Comparing organisms in the intertidal and subtidal zone in Australia, we find that invertebrates in the subtidal often have different life histories from their counterparts in the intertidal (Keough et al., 1990). They are often clonal rather than solitary and they produce very weakly dispersing larvae rather than long-lived ones. The major grazer of subtidal Rocky Reefs in temperate Eastern Australia is the sea urchin *Centrostephanus rodgersii* Agassiz, 1863. On horizontal surfaces, the sea urchin regulates abundances of algae, often shifting the community to a state dominated by crustose coralline red algae, the barrens (Fletcher, 1987), estimated to amount to 50 % of the area of subtidal Rocky Reefs in New South Wales. The sea urchin is a nocturnal forager (grazing radius about three meters) and can be mainly found during the day in crevices, fissures and gaps between rocks (Fletcher, 1987; Andrew, 1993) or attached between rock and invertebrates with massive, solid growth forms like the sponge *Ircinia* sp. or the solitary ascidians *Herdmania momus* and *Cnemidocarpa radicata* (own observation). Here, the sea urchin is somewhat protected from their major predator, the Eastern Blue Groper *Achoerodus viridis* (Andrew, 1993; Gillanders, 1995; own observation), and others, like the shark *Heterodontus portjacksoni* (McLaughlin and O’Gower, 1971), stingrays and octopi. The density of sea urchins on horizontal surfaces depends on the number of refuges. A high number of refuges leads to high recruitment and immigration of the sea urchin and grazing is increased. Therefore, a high number of refuges in an area results in the creation of the barren habitat (Andrew, 1993). The complete removal of the sea urchin *Centrostephanus rodgersii* from the barren habitat can lead to the development of an assemblage of foliose algae (e.g. *Ecklonia radiata*; Fletcher, 1987), while crustose coralline red algae decline to less than 10 % cover (usually 85 % cover; Andrew and Underwood, 1993). Partial reductions in sea urchin densities results only in a slight increase in filamentous algae (Andrew and Underwood, 1993). These coherences certainly show the importance of this sea urchin species in New South Wales as a key-grazer in the barren habitat. Limpets are often associated with the sea

urchin (Fletcher, 1987; Andrew, 1991, 1993). The sea urchin removes foliose algae and makes it possible for limpets to graze unhindered in the barren habitat denuding the habitat further.

On vertical surfaces of Rocky Reefs in southern New South Wales, the importance of the sea urchin for the structure of sessile communities may be varying. Depending on the height of these walls, the structure of the sessile community and the biomass of the sea urchin *Centrostephanus rodgersii* differ (Davis et al., submitted). Number of species and invertebrate colony size is higher on tall (more than four meters height) than on low walls (less than two meters height). Low walls are dominated by crustose coralline red algae characteristic of the barren habitat. Biomass of foliose algae on the walls is neglectable. The authors attribute differences between community structure on tall and low walls to sea urchin grazing, since sea urchin biomass was high on low walls and low on tall walls. These findings contrast strongly with the authors' results for the North Western Mediterranean, where community structure between tall and low walls did not differ and there even were only small sea urchin biomass differences. However, biomass of foliose algae was high on both wall types in the Mediterranean. Davis et al. (submitted) investigated these differences in community structure on tall and low walls at two sites in southern New South Wales (differences are common in New South Wales; A. Davis, D. Ward, personal communication, own observation). One of their study sites was Flinders Islet near Wollongong. I observed similar differences in community structure on walls at this site as they did. Assemblages on tall walls appear to be more diverse in species than on low walls. Low walls appear to be dominated by crustose coralline red algae, while on tall walls various sponges, ascidians and cnidarians coexist. The sea urchin *Centrostephanus rodgersii* appears to be more abundant on low than on tall walls. The **aim** of this study is to answer the question **why assemblages are different on vertical surfaces with different height at the Rocky Reef at Flinders Islet in the Western Tasman Sea**. If sea urchin grazing regulates the assemblages, or if other processes, like recruitment or environmental factors, are crucial, is not known. Firstly, I describe assemblages on tall and low walls of the Rocky Reef at Flinders Islet and examine: **Do assemblages differ in structure between tall and low walls and abundances of the sea urchin *Centrostephanus rodgersii*? Does community structure change with time and does the rate of structural change differ between tall and low walls?**

The structure of a community is determined by species composition of the colonizer pool, sequence of settlement, and early mortality of settlers and recruits (e.g. reviews by Gosselin and Qian, 1997; Hunt and Scheibling, 1997). From the time of settlement onwards,

individuals and species are exposed to processes like competition, mutualism, parasitism and consumption (e.g. Connell, 1961a, b; Dayton, 1971; Paine, 1971; Menge, 1976; Underwood et al., 1983) and the surrounding abiotic environment (e.g. Molis, 2002; Lenz, 2003). These processes can have direct, but also indirect effects that change the structure and dynamics of the community (e.g. Menge, 1995).

The structure of recruitment is determined by the larva or spore that is, after being released from the adult, under the influence of presettlement processes and factors, like predation (e.g. pelagic, benthic), oceanography (e.g. currents, upwelling), local hydrography (e.g. tides, wakes), larval quality, larval behaviour (e.g. phototaxis), benthic predation (e.g. adult suspension-feeders), substratum electivity (review by Todd, 1998). Graham and Sebens (1996) demonstrated that weakly dispersing larvae or larvae that are ready to settle accumulate near (1 to 5 cm) vertical rock surfaces, especially if the surface is already covered with invertebrates, compared to crustose coralline red algae covered surfaces. This pattern was not observed for long-distance dispersers that are not ready to settle. Larvae of subtidal Rocky Reef invertebrates at South Eastern Australia are mainly lecithotrophic with low abundance, short residence in the plankton and are only weakly dispersed (Keough et al., 1990; Ayre et al., 1997). After the larva is ready to settle, settlement and recruitment processes and factors like successful encounter/attachment to a substratum, responses to substratum cues, environmental factors, detection of conspecifics/funders, detection/avoidance of superior competitors and predators, responses to allelochemical agents, energy reserves and the successful completion of metamorphosis are crucial for the larva to become a settler after having survived all the dangers in the plankton (reviews by Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Todd, 1998). Post-settlement processes like intraspecific competition, interspecific competition, biotic interactions, parasitism/disease, physical disturbance, reproductive performance/success, abiotic stresses and the density related immigration/emigration of juveniles and adults decide then, if the recruit develops into a reproducing adult. Juvenile mortality is high and often exceeds 90 % (Gosselin and Qian, 1997).

Recruitment in different habitats may be different due to specific pre-settlement and settlement processes. Farnsworth and Ellison (1996) demonstrated for fouling assemblages on mangrove roots at cays in Central America that larval supply (pre-settlement factors) may shape the composition on short time scales and small and very large spatial scales (cays), while variation in physical factors like flow (settlement and post-settlement factors) may influence the community long term and at intermediate scales. Larval supply can depend on

local hydrodynamics. In a bay in Ireland, more species recruit in intermediate flow than in highly disturbed or benign areas (Maughan and Barnes, 2000a). Total cover is higher in high flow areas, where early successional species dominate. Flow micro-habitats on rock walls are used by different invertebrates depending on their ability as filter-feeders indicating differing recruitment in these habitats (Leichter and Witman, 1997).

Recruitment on different substrata can vary in the impact predators or grazers have on new settlers. Especially grazing or bulldozing by sea urchins can cause high juvenile non-species-specific mortality (Ayling, 1980; Sammarco, 1980; Breitburg, 1986). In California, grazing by the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* decreases numbers of recruiting species and abundances (Breitburg, 1986). In the Caribbean, the sea urchin *Diadema antillarum* reduces numbers and diversity of recruiting corals and abundances of recruiting algae (Sammarco 1980). In the Mediterranean, the sea urchin *Paracentrotus lividus* causes high mortality in sponge recruits (Maldonado and Uriz, 1998). On the other hand, Smith and Witman (1999) found no effects of sea urchin grazing on the diversity of recruitment. New settlers are generally more influenced by grazers than older individuals since the probability of dislodgement or mechanical damage by a through coming grazer is very high in a stadium when attachment is not so strong yet, the calcareous skeleton is not complete and the settler is generally very delicate, even when the settler gets not eaten. In the experimental part of my study, I investigate the impact of recruitment and water motion addressing: **Does structure of recruitment differ between tall and low walls and high and low sea urchin density? Is water motion different on tall and low walls?**

Recruitment into the established community is a continuous process; therefore factors influencing recruitment affect the community, also during the establishment of a community after a disturbance. Succession is depending on propagule availability, settlement preferences and replacement of species due to competition, consumers or environmental factors. Early colonists can facilitate, inhibit or tolerate later colonists (Connell and Slatyer, 1977; Connell et al., 1987). However, an early colonist may not have the same effect on different later colonists (Farrell, 1991). Different species of early colonists may not have the same effects on the same later colonist. Between the transitions of successional stages different mechanisms can be involved and indirect effects should not be neglected from consideration. This suggests that when the composition of the recruiting assemblage is different in different habitats, these different early colonists have different effects on species later in succession, and also later colonists may be different in the different habitats. During succession, diversity and numbers of species may either steadily increase or peak in mid-successional phase (Odum, 1969).

Disturbances can accelerate or decelerate succession or even deflect the trajectory. Hixon and Brostoff (1996) demonstrated that damselfish could decelerate tropical algal succession inside their territory by selective grazing. The grazer keeps the assemblage at a mid-successional stage with high diversity. Outside the territories grazing can be very intense by schooling herbivores that remove all erect algae. The direction of succession is then deflected, a low diversity assemblage establishes with algal crusts and cyanobacteria mats. Osman (1977) and Sousa (1979) showed that assemblages on rocks being kept at a mid-successional stage by an intermediate frequency of overturning the boulder as disturbance had the highest diversity, whereas when the frequency of disturbance was very high, diversity was low, assemblage stayed at early-successional stage. When frequency is very low, diversity is low, because assemblages can get dominated by one or a few species. Farrell (1991) found that consumers usually slow down succession. Only when the prey species inhibits later colonists, is succession accelerated. The intensity of consumption will influence the magnitude of consumer influence on the rate of succession. In the second experiment, I investigate, how far the differences in the established assemblage can be explained by the developing assemblage, thereby testing for differences due to wall height and sea urchin density, asking; **How does structure and successional dynamics of a newly developing assemblage vary with wall height and/or sea urchin density?**

The described processes like recruitment or succession shape the developing community. The established community always is a product of its history. Since communities generally are frequently disturbed, succession usually never stops. Different patches of the community are in different states of succession depending on the extent and frequency of disturbance. On a large spatial scale, the species composition stays constant, forming an average of all the patches (Connell, 1987). When succession is not interrupted, the whole community will reach theoretically a stage characterized by change only due to dying and replacement of an individual (Connell and Slatyer, 1977). When the individual is replaced by an individual of its own species, the community is called in classical terms stable. The judgement of a community as stable depends on the time and spatial scale of investigation (Connell and Sousa, 1983). Therefore, stability of a community may better be defined as the persistence of a community within stochastically defined bounds (e.g. Connell and Sousa, 1983; Kay and Butler, 1983; Keough and Butler, 1983; Crowley, 1992; Bingham and Young, 1995). Depending on the origin or history of a community, or on the level of disturbance, there can be different stable points for the community, or different alternate states (Lewontin, 1969; Sutherland, 1974). Petraitis and Latham (1999) pointed out the dependence on scale of the switch to another

alternate state. When the original disturbance is large enough to exclude effects of the surrounding area from the open substratum, a switch is possible.

During succession of a community, structural changes are under the influence of internal, like interactions, and external factors, like colonizers (e.g. White and Pickett, 1985). The relative importance of these factors determines how easily a community switches to a different community state. Present factors determine the structure of the present community, but exactly the composition and interactions within the present community may be important determinants for the identity and abundance of future recruits. However, the surrounding assemblage and the environment may also influence the assemblage. Therefore, when the formative effect of the habitat of origin (= carry-over effect) is neglectable, assemblages may converge after transfer from different habitats or diverge after transfer to different habitats. There are some examples demonstrating the importance of these factors. Baird and Hughes (2000) transplanted nine week-old assemblages grown on panels at Lizard Island/Great Barrier Reef underneath staghorn corals of the species *Acropora hyacinthus*. After eight weeks, cover of filamentous algae had reduced in cover due to shading by the coral. Farrell (1988) changed the presence of limpets and therefore the grazing pressure on assemblages developing in clearings in the rocky intertidal in Oregon, USA. He introduced limpets into 16 and 28 months-old developing assemblages. After 17 months, the assemblage had converged in abundances and composition with assemblages, where limpets were present the whole time.

In my last experiment, I examine: **Is there a formative effect of the habitat of origin on the structure of the assemblage after external factors change? Does the structure of assemblages change when assemblages of the same origin are transferred to different habitats or assemblages of different origins are transferred to the same habitat? Do assemblages converge or diverge when assemblages of the same origin are transferred to different habitats or assemblages of different origins are transferred to the same habitat?**

2. Material and Methods

2.1. Study Site

All experiments were conducted at the North to Northeastern end of Flinders Islet ($34^{\circ} 27' 35''$ S $150^{\circ} 55' 75''$ E) near Wollongong, New South Wales, Australia (Fig. 2.1) in a depth of 9 to 15 m. The average yearly sea surface temperature at Wollongong in 1998 was 20.6°C , with a minimum of 17.7°C in August and a maximum of 23.5°C in February and March (Australian Oceanographic Data Centre, NODC – World Ocean Atlas 98). Temperature at the study site and at the depth of the experiment ranged from 17°C in winter to 24°C in late summer during the study (own observation). The average yearly salinity at Wollongong in 1998 was 35.61, with a minimum of 35.6 and a maximum of 35.7 (Australian Oceanographic Data Centre, NODC – World Ocean Atlas 98). Tidal range is about 1.5 m and semi-diurnal. Yearly average winds at Port Kembla Signal Station near the study site ranged from 17.4 to 24.4 km per hour with maximum wind gusts of 135.4 km per hour (Bureau of Meteorology). Strongest winds are from the South in winter associated with low-pressure systems (Rendell and Pritchard, 1997; own observation) and can lead to downwelling. During winter, winds are mainly offshore (westerly). From spring to early autumn, the diurnal sea breeze/land breeze system dominates, favouring upwelling. Sea breeze winds in the afternoons during summer reach usually 20 to 30 knots from the Northeast, increasing seas to 2.5 to 3 m (own observation). Swell is dominantly southerly or southeasterly, 1.5 m in average height and 10 s in period. Swell can reach up to 6 m height during storms (Bureau of Meteorology; own

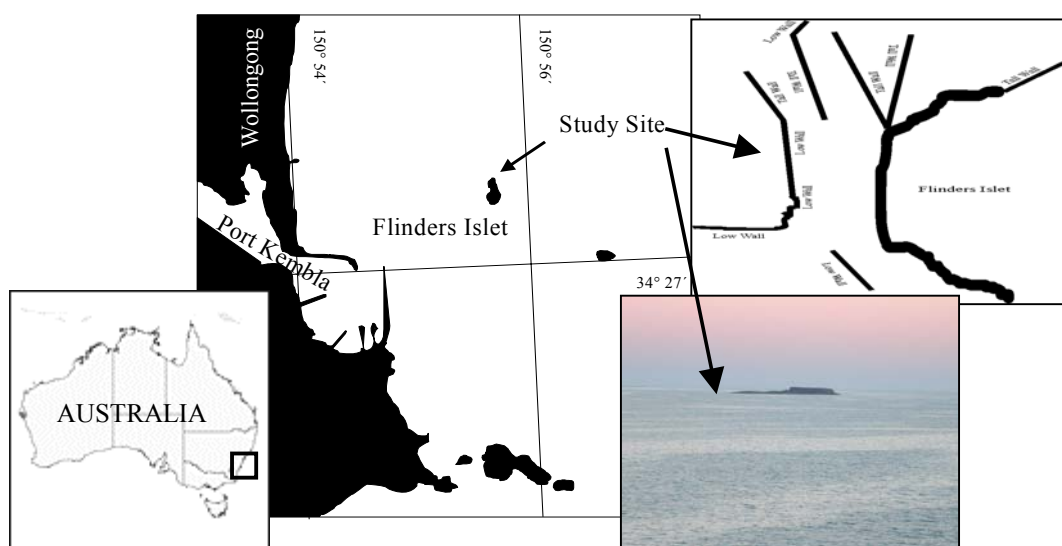


Fig. 2.1: Geographical position of the study site and position of the rock walls at Flinders Islet near Wollongong, New South Wales, Australia. Tall and low walls are marked.

observation). From late winter to early spring, conditions are calm with very low wave heights. Temperature stratification usually breaks up in winter, which allows mixing of the water column and thereby allowing nutrient rich water to reach the surface. Usually, nitrate concentration at the surface is less than 1 μg atom per litre and phosphate concentration is less than 0.25 μg atom per litre and therefore rather low. At greater depths, concentrations can reach more than 10 μg atom per litre for nitrate. In late winter and early spring, patchy algal blooms can appear at the study site reducing visibility to less than 3 m, associated with the island wake and therefore highly likely due to local upwelling (own observation).

The oceanic region surrounding the island is called Tasman Sea and is strongly influenced by the East Australian Current (EAC; Tomczak and Godfrey, 1994). The current system flows southward along the east coast of Australia and has its origin in the Coral Sea. The current therefore transports water from the Coral Sea with high temperature and low salinity (20 – 26°C, 35.4 – 35.6 salinity; Australian Oceanographic Data Centre) into the Tasman Sea with low temperature and high salinity (> 35.7 salinity). The EAC separates from the coast at about 34 ° S flowing to New Zealand and the Tasman front develops. The EAC is then very unstable and this leads to the formation of large warm core anti-cyclonic eddies containing Coral Sea water that detach from the current and wander further south. Cold core cyclonic eddies that enclose cold water from the southern Tasman Sea and wander north are also formed, but rather rarely. The warm core eddies can be 150 to 250 km in diameter and reach the coast. They are quite stable and last for months. The EAC can cause upwelling of nutrient rich continental shelf water towards the coast. The EAC and his eddies are the dominant oceanic processes overwhelming existing patterns (Rendell and Pritchard, 1997), even at the study site (Anderson et al., 1992). These patterns are created by northward propagating coastal-trapped waves, internal waves and tides, local winds and swell waves. Up-welling and thermal stratification vary seasonally and fluctuate irregularly, thereby influencing dispersion and advection of material.

The Australian East Coast is very much influenced by the Southern Oscillation (Tomczak and Godfrey, 1994). During the time of the study, the region experienced two La Niña events. The first event occurred in 1998 and 1999. This episode weakened to neutral conditions and reformed then in 1999 and 2000 to weaken again to become neutral. During a La Niña event, the probability of rainfall and storms increases dramatically in Eastern Australia (Bureau of Meteorology). This may have an effect on the studied community by increasing the frequency of abiotic disturbance (own observation).

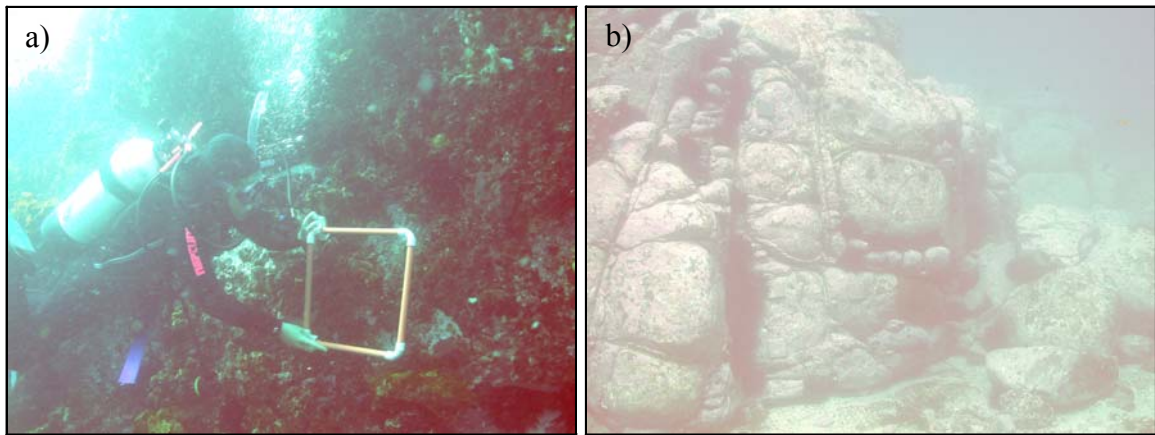


Fig. 2.2: The Rocky Reef at Flinders Islet in 9 to 15 m depth. a) high diversity area on a wall with more than 4 m height, b) low diversity area on a wall less than 2 m high, shown are crustose coralline algae (pink) and sea urchins (*Centrostephanus rodgersii*).

Since the study site is part of an island, another oceanographic feature is important. At one end of the island, currents can cause the development of an island wake (Wolanski, 1988; Wolanski et al. 1996). The wake as a cyclonic eddy develops at the downstream end of the island in shallow water. Spirals rotate anticlockwise away from the centre. Downwelling exists in the core of the eddy and the perimeter and upwelling is near the centre. On the bottom, there is a radial flow towards the centre. A thin shear free layer like a vertical curtain separates waters inside and outside the eddy. Here buoyant material gets trapped influencing dispersion. The island wake at Flinders Islet is usually situated at the north-western end of the island due to the main swell coming from the southeast (Anderson et al., 1992; own observation). However, I observed the island wake also directly at the study site.

Flinders Islet is part of the Rocky Reef System that runs along the coast of New South Wales alternating with sandy areas. The reef at the study site consists of red brown and grey volcanic sandstones of Budgong Sandstones in the Shoalhaven Group from the Late Permian (S. Fyfe, personal communication), forming platforms, boulders and walls. The reefs generally are important nurseries for juvenile fish and are characterized by a high level of diversity. The most dominant macroalga surrounding the reef and on rocks is the kelp *Ecklonia radiata* growing on sandy patches. Dominant algae on the rocks are crustose coralline red algae. At the study site and depth, other algae are rather rare. Some areas are dominated by diverse invertebrate growth, consisting of sponges, ascidians, cnidarians and barnacles. These areas are mainly vertical rock walls with great height (more than 4 m; fig. 2.2 a). Other areas look pauperised in species diversity. Crustose coralline red algae dominate with only a few sponges and barnacles present. These areas are primarily horizontal surfaces

without kelp cover, boulders and low vertical rock walls (less than 2 m; fig. 2.2 b). Dominant grazer is the diadematid sea urchin *Centrostephanus rodgersii*; other consumers of invertebrates and algae may be molluscs, like limpets and nudibranchs, but also fish of the families Pomacentridae (damselfish; e.g. *Parma unifasciata*), Labridae (wrasses; e.g. *Achoerodus viridis*, *Coris picta*), Scorpididae (sweeps; e.g. *Atypichthys strigatus*) and different Monacanthidae (leatherjackets) were observed by me. The study site is relative to other Rocky Reefs undisturbed due to the inaccessibility of the island to the public as a bird sanctuary. However, the waters around it are not under protection and are visited by boat by recreational divers, spear fishermen and other recreational fishermen.

2.2. Experimental design, set-up and sampling

2.2.1. General

The study was conducted at vertical surfaces of rock walls. Walls were randomly chosen (Fig. 2.1), and monitoring and experiments were done at the same walls. Walls were categorised in tall walls with more than four meters height and low walls with one to two meters height. All walls are in a depth of nine to fifteen meters. All work underwater was done by Scuba.

Three experiments were conducted. As figure 2.3 indicates the general experimental design consists of two orthogonal factors (wall height and sea urchin density) arranged in a split-plot design. On every wall type (tall and low) both sea urchin densities (high and low) are present. Wall halves are nested within walls. There are four treatments: tall wall – high sea urchin density, tall wall – low sea urchin density, low wall – high sea urchin density, low wall – low sea urchin density. Every treatment was replicated five times for the recruitment experiment, three times for the succession experiment and three times for the experiment about divergence, convergence and formative habitat effects. One block consists of one set of one tall and one low wall. Within blocks, treatments were replicated twice and were nested within wall halves. Experimental units within the wall halves were randomly selected and units were at least three times their length distanced from each other (Hurlburt, 1984). Every wall was split in half. The density of the sea urchin *Centrostephanus rodgersii* was manipulated on one half of every wall. Transects were run along the walls to monitor abundances of sea urchins (see below and results section). Average abundance of sea urchins was determined as $11.09 (\pm 0.86)$ sea urchins per m^2 on low walls and $2.68 (\pm 0.42)$ sea urchins per m^2 on tall walls. One wall half of every wall was left non-manipulated. On the other wall half sea urchin density was adjusted to levels typical for the other wall type. This meant for tall walls that sea urchins

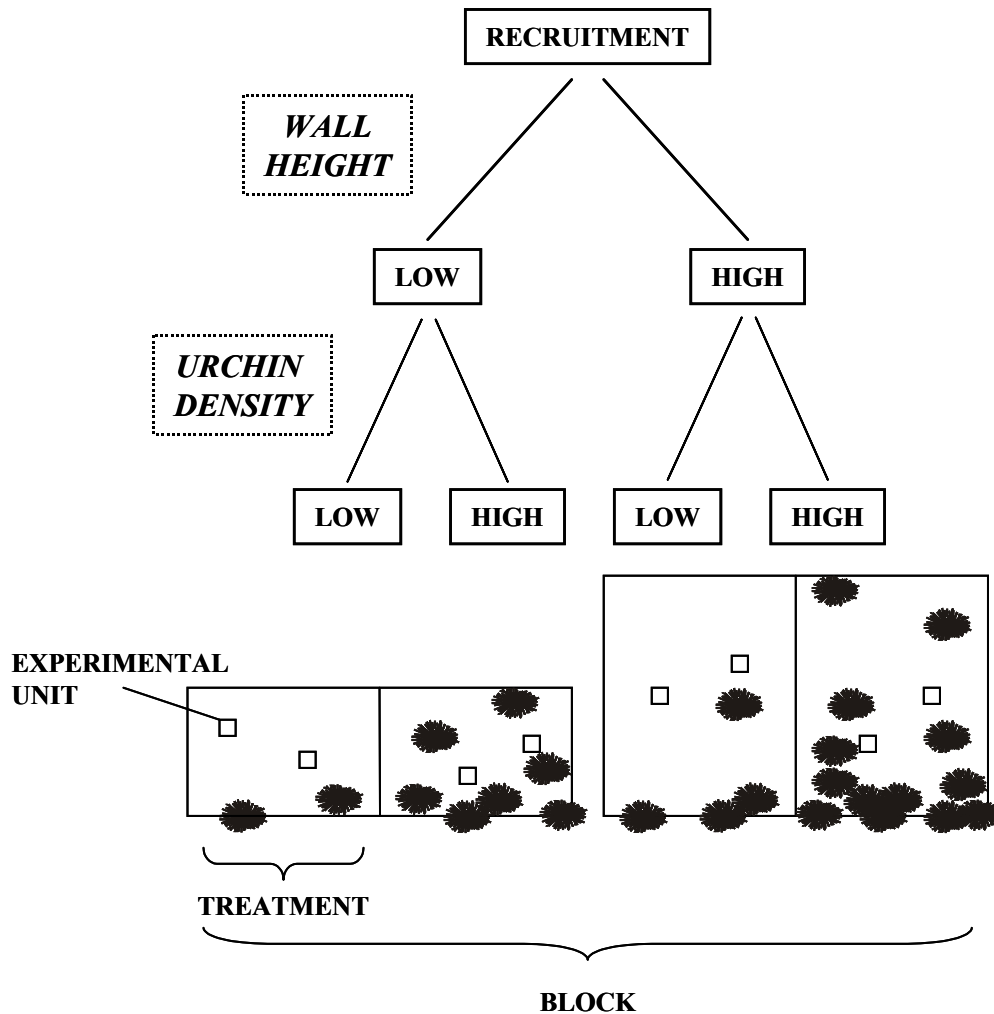


Fig. 2.3: General experimental design and set-up. High and low sea urchin density is present on every tall and low wall. Experimental units are nested within wall halves. Shown is the recruitment experiment. Further explanations in the text.

had to be added to the manipulated half, whereas from one half wall of every low wall sea urchins had to be removed. Which half of the wall was manipulated was randomly selected. I did not manipulate abundances of sea urchins, but densities since exact manipulations were neither biologically nor logistically possible. Densities of the manipulated wall halves were checked from time to time via transect and sea urchins were added or removed where necessary. A map, where walls were number coded and treatments were noted, was prepared. Every panel was coded for wall, wall half and replicate within wall half, and position of every panel and plot on every wall half was noted.

Grey unglazed ceramic tiles (98 x 98 mm) were always used as settlement substratum. Experimental areas within the wall halves were cleaned from invertebrates and algae prior to gluing. Only crustose coralline red algae could not be removed, but the surface was roughened by wire brushing and scraping.

Photographical equipment used was a Nikonos V on a framer with strobe (Ikelite) and a Nikon Coolpix 990 in a waterproof housing (Ikelite) with video light (Ikelite), respectively.

Photos were digitalized. Photos and panels were overlaid with a mask with 100 random dots. From the masks for the photographed panels and recruitment panels an one-cm-edge was spared out to avoid edge effects reducing the investigated area to 78 x 78 cm². I estimated coverage of every species (including sea urchins) from determinations of percentage occurrence under the dots (1 % per dot). Species that were not found under any dot, but were present on the photo were counted as 0.5 % to include rare species in the estimation. This and the addition of epibionts on other species to total cover sometimes increased total cover to over 100 %.

2.2.2. Do Structure and Dynamics vary with Wall Height?

The description of assemblages on tall and low walls was done on three tall and three low walls. Two permanent plots were chosen randomly on every wall and marked with plastic numbers (sheep mini-tags; Allflex, Morningside, Queensland, Australia) that were glued on the rock with epoxy (Z-Spar A-788, Kop-Coat Marine Group, USA). All plots were 30 x 30 cm. Photos of permanent plots were taken three times, in April 2000, June 2000 and February 2002. Only one permanent plot per wall could be used in the temporal analysis due to equipment failure and loss of markers (overgrowth, divers, storms, grazing). Additionally, photos (Fig. 2.4) of two random plots per wall were taken four times, in July 1999, April 2000, June 2000 and February 2002. Photos were always taken on three tall and three low walls, except in July 1999, when only two tall and two low walls were photographed. Monitored walls were the same for permanent and random plots. At the beginning of the

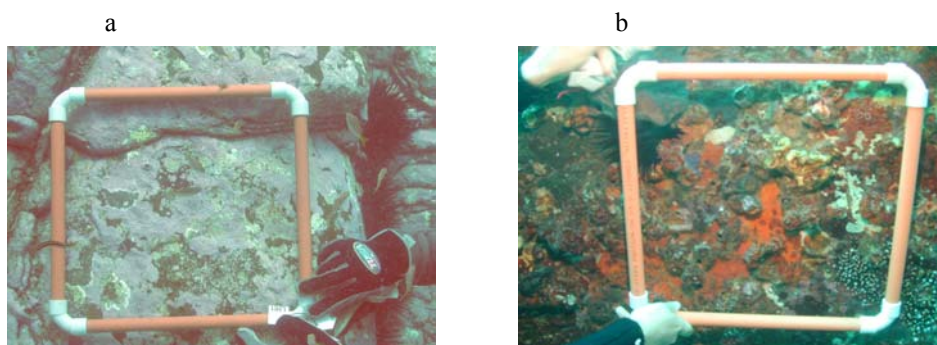


Fig. 2.4: Assemblages on two random plots on a) low wall and b) tall wall. Area of investigation was 30 x 30 cm.

experiment, three 5 x 1 m transects were run along each of the three tall and three low walls and sea urchins (*Centrostephanus rodgersii*) were counted. Data were transformed to individuals per m².

2.2.3. Does Structure of Recruitment vary with wall height and/or sea urchin density? Does water motion vary with wall height?

The recruitment experiment was done on five tall and five low walls. For the experimental design see figure 2.3. Panels were attached via Velcro (Velcro Australia Pty. Ltd., Australia) directly onto the rock walls. The ‘hooks’ part of the Velcro was glued with Araldite (Araldite K340, Ciba-Geigy Adhesives, Australia) onto PVC panels (5 x 11 cm); the ‘loops’ part was glued onto the backside of the ceramic tile (Velcro strip: 5 x 9.5 cm) with Araldite. PVC panels with ‘hooks’ were then glued onto the rock with epoxy (Z-Spar A-788, Kop-Coat Marine Group, USA). Some of the PVC panels had to be re-glued after some time in the field due to lost ceramic tiles (storms, fishes, divers) that enabled sea urchins to eat off Velcro making reattachment of panels impossible.

To measure recruitment, all forty ceramic tiles were attached to the rock walls during one dive day. Panels were left there untouched for on average two months. Due to unpredictable weather conditions (swell, wind, storms), logistics and volunteer availability (general problems during this study), single recruitment experiments had not the exact same duration, but ranged from 40 to 108 days. At the end of the experiment, panels were recovered in seawater filled labelled boxes and brought immediately to the lab for census. After census and prior to re-use, panels were brushed and then soaked in seawater with HCl to remove all

Table 2.1: Recruitment-Experiments, period of investigation and duration.

Experiment	Date	Duration [days]
1	28.04. - 08.06.2000	41
2	08.06. - 24.07.2000	46
3	24.07. - 13.09.2000	51
4	13.09. - 23.10.2000	40
5	23.10. - 27.12.2000	65
6	27.12. - 19.03.2001	45
7	19.03. - 03.06.2001	76
8	05.06. - 18.09.2001	105
9	18.09. - 30.10.2001	42
10	30.10. - 14.12.2001	45
11	16.12. - 03.04.2002	108
12	06.04. - 16.05.2002	40

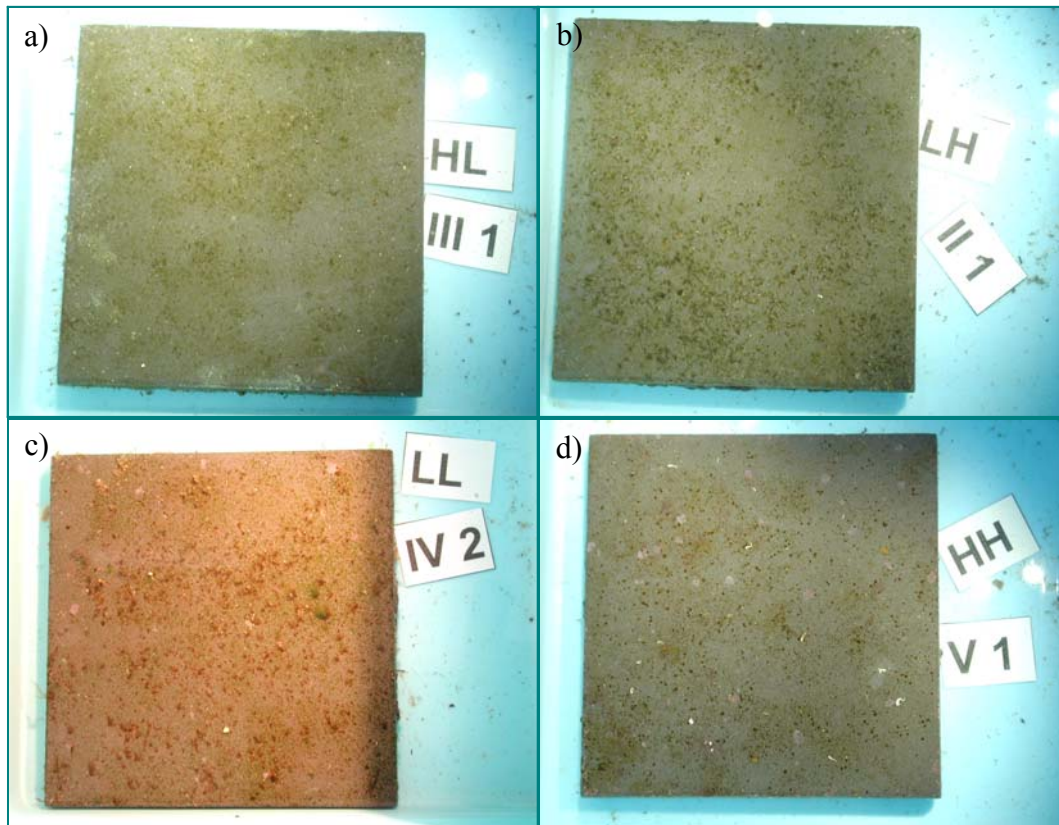


Fig. 2.5: Recruitment-panels of the experiment starting on the 18th of September and ending on the 30th of October 2001 (42 days). Shown are diatom (green and brown), crustose coralline algae (pink), hydroids, the serpulid *Pomatostegus* spp.. Photo a) low wall, high sea urchin density, b) tall wall, low sea urchin density, c) low wall, low sea urchin density, d) tall wall, high sea urchin density

calcareous remains. Panels were then soaked in freshwater for at least a week.

Twelve experiments were run in total over two years (Table 2.1). Because only panels from high sea urchin density treatments could be retrieved, the experiment ending at the 3rd of April 2002 was not statistically analysed, but data were included in the graphs.

Panels (Fig. 2.5) in seawater filled boxes were stored in the fridge until examination. Panels were examined under the dissecting microscope in the lab starting immediately after recovery. A specimen collection was set-up and specimens were photographed.

The influence of wall height on water motion was measured using the dissolution rates of dental pinkstone half-spheres (Muus, 1968; Jokiel and Morrissey, 1993; Fabricius and De'ath, 1997). The experimental design is 2-factorial (factor one: wall height; level 1: tall, level 2: low). The blocking consists of experimental units (four half spheres per wall) being nested within walls. Walls (factor 2) are then nested within the factor wall height. Replication is five (five tall and five low walls).

Dental pinkstone (Dental Supplies, Australia) was mixed with water (50 grams powder + 20 ml water per half sphere), filled into cookie-trays and left to dry. Half spheres were then put into the drying oven at 60°C for three days. Dried half spheres were immediately weighed

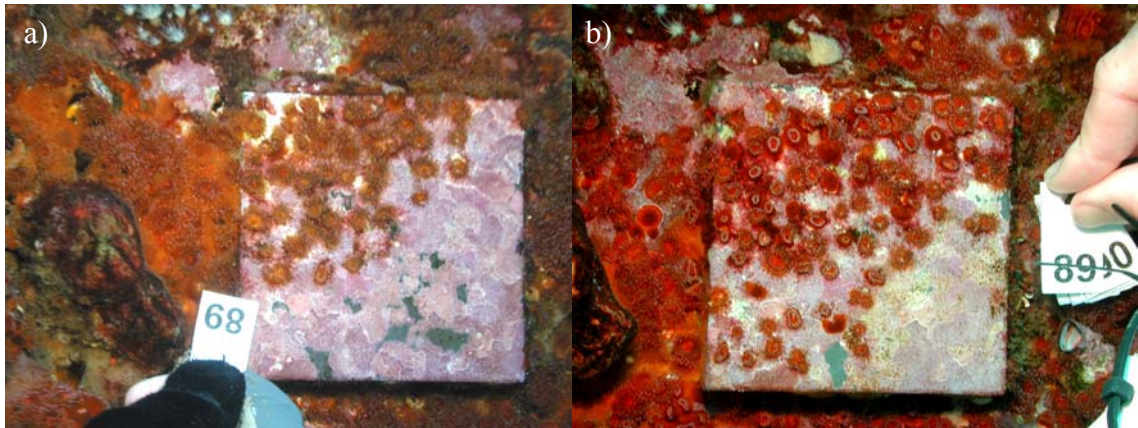


Fig. 2.6: Assemblage on the same panel in a) February and b) May 2002. The assemblage developed on a tall wall with low sea urchin density. Recognisable are crustose coralline red algae (pink) and the corallimorphan *Corynactis australis* (red).

and numbered on the front and back. On the backside (= flat side), velcro was glued on with marine silicone (Silastic Marine; Dow Corning Australia Pty Ltd, Australia). Half spheres were attached via velcro to the in the recruitment experiment used PVC panels in between recruitment experiments. Position on the walls and walls were noted. After the experiment, half spheres were recovered and brought to the lab. Velcro and marine silicone was removed. Half-spheres were put into the drying oven at 60°C for three days and weighed again. Weightloss for every half-sphere was calculated.

Three experiments were run, from the 3rd to the 5th of June 2001 (48 hours), from the 14th to the 16th of December 2001 (48 hours; springtide) and from the 3rd to the 6th of April 2002 (72 hours).

2.2.4. Do Structure and Successional Dynamics of Newly Developing Assemblages vary with Wall Height and/or Sea Urchin Density?

For the development experiment three tall and three low walls were used. For the experimental design see figure 2.3. 24 panels were glued onto the walls from May to June 2000. Some panels got lost during the experiment reducing replication within some half walls and eliminating one half wall from the statistical analysis. First census of the developing assemblages on panels was only done in February 2002 since panels were observed to be very slow in development and to look very similar to recruitment panels for a long time. After the first census, panels were removed carefully from the walls and re-glued in the same position since they were used as controls in the experiment below. None of the algae and sessile

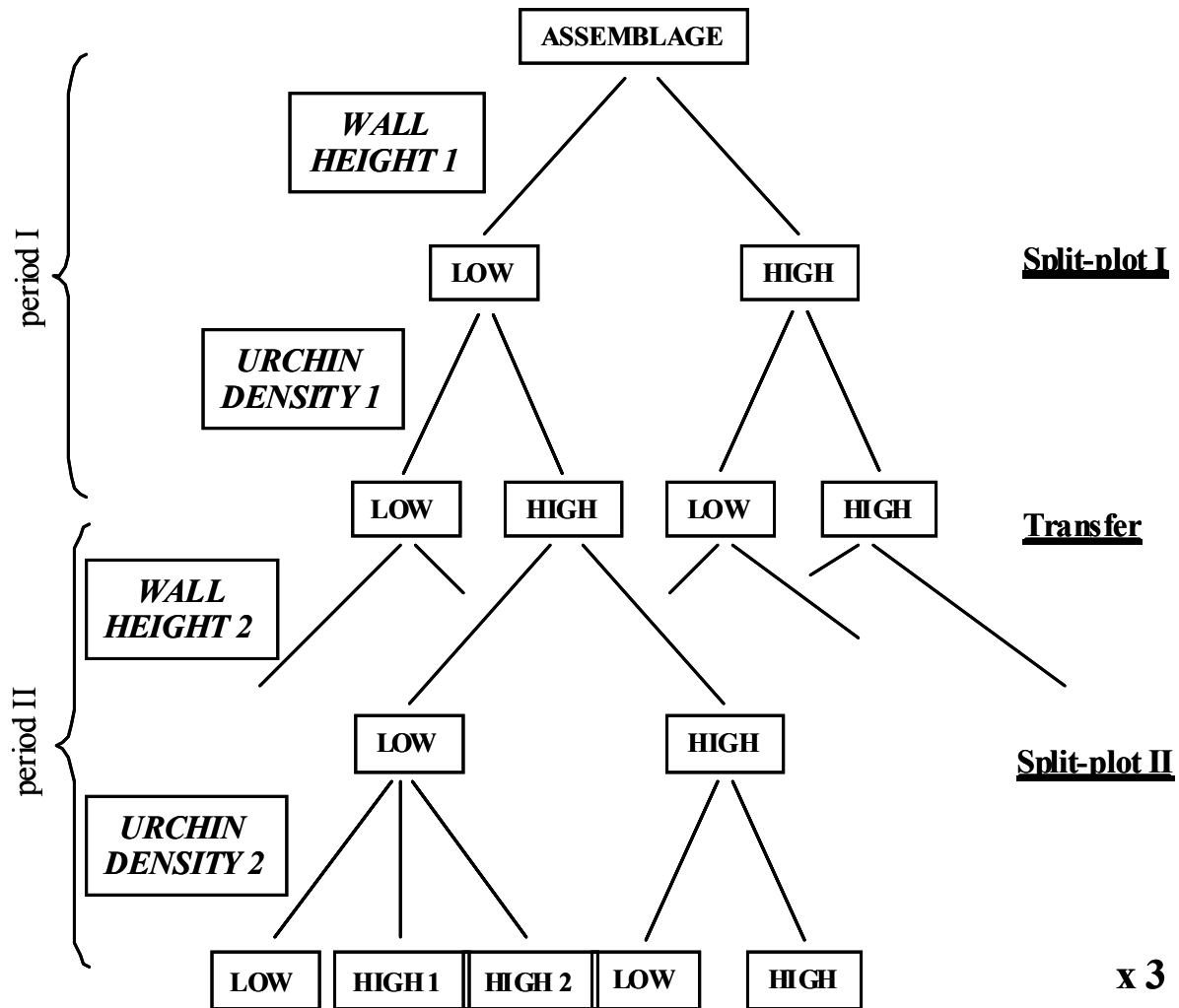


Fig. 2.7: Experimental design. High 1 = control, that stayed at the wall, high 2 = control, that changed wall. Transfer indicates change-over. Period I = time elapsed till first census, period II = time elapsed till second census. Further explanation in the text.

invertebrates on the panels were observed to have been damaged or killed by this procedure. The second survey of developing assemblages was done in May 2002 (Fig. 2.6).

2.2.5. Divergence and Convergence of Transplanted Assemblages: the Relative Importance of Formative Habitat Effects in Early Succession

The experiment was done on three tall and three low walls. Some definitions are important for this experiment: change-over means that the experimental unit is transferred from the original habitat to a different habitat that is then the habitat of residence. Carry-over effect means the effect of the habitat before change-over, still persisting in the assemblage after change-over of habitat as formative effect. The experimental design (Fig. 2.7) consists of four factors (wall height 1 and 2, sea urchin density 1 and 2) in a change-over or carry-over (cross-over) design arranged in two split-plot designs. In the change-over design, experimental units

are ‘switched’ after a certain time. This means here, experimental units arranged in the split-plot design (split-plot I) change treatments after a certain time, and are rearranged in a split-plot design (split-plot II) again. For example, an experimental unit was on a low wall with high sea urchin density (split-plot I) and is after a certain time period transferred to a tall wall with high sea urchin density. Experimental units can change only wall height, only sea urchin density or they can change wall height and sea urchin density. Two types of controls were used, where treatments were not changed. The first control experimental unit was only removed from the area on the wall and then reattached at the same place (panels also used in the succession experiment), whereas the second control experimental unit was transferred to a different wall of the same habitat type. In total, there were twenty different treatments (Table 2.2) and 120 experimental units in total.

Table 2.2: Treatment combinations before and after change-over. Wall height: tall, low; sea urchin density: high, low. 1 = control, that remained at wall, 2 = control, that was transferred to another wall in the same habitat.

Treatment before Change-Over		Treatment after Change-over	
Wall Height	Sea Urchin Density	Wall Height	Sea Urchin Density
Low1	Low1	Low1	Low1
Low2	Low2	Low2	Low2
Low	Low	Low	High
Low	Low	Tall	Low
Low	Low	Tall	High
Low1	High1	Low1	High1
Low2	High2	Low2	High2
Low	High	Low	Low
Low	High	Tall	Low
Low	High	Tall	High
Tall1	Low1	Tall1	Low1
Tall2	Low2	Tall2	Low2
Tall	Low	Tall	High
Tall	Low	Low	Low
Tall	Low	Low	High
Tall1	High1	Tall1	High1
Tall2	High2	Tall2	High2
Tall	High	Tall	Low
Tall	High	Low	Low
Tall	High	Low	High

120 panels were glued onto the walls from May to June 2000. The first census of panels was done prior to the change-over of treatments, in February 2002. In March and April 2002, panels were removed pair-wise (replicates within blocks) from the walls, carefully transported in plastic containers to the designated experimental area (for example, from a tall wall with high sea urchin density to a low wall with high sea urchin density), and then re-glued there. Some panels got lost between start of the experiment and the second census due to storms, but primarily during the 24 hours the glue took to dry to resist swell pressure.

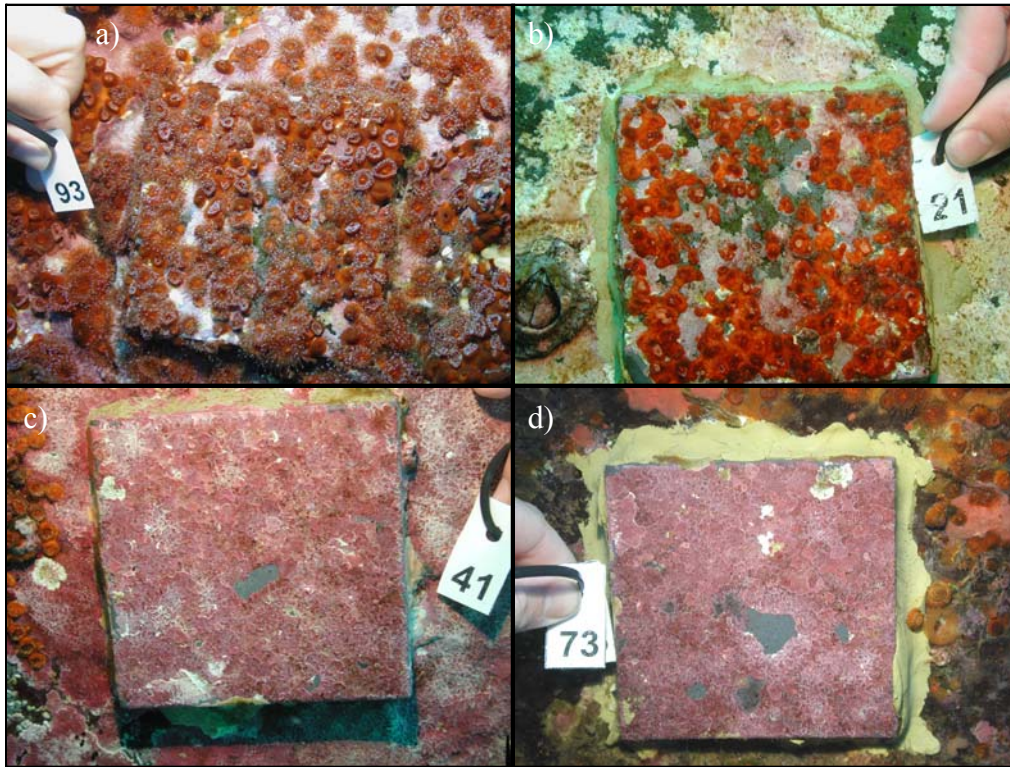


Fig. 2.8: Panels that were changed-over. a) panel on a tall wall with high sea urchin density before change-over, shown are crustose coralline red algae (pink) and the corallimorphan *Corynactis australis* (red); b) the same panel as in a), but after change-over to a low wall with low sea urchin density, shown is to the left of the panel the barnacle *Austrobalanus imperator*; c) panel on a low wall with high sea urchin density before change-over, shown is to the left of the panel the scleractinian *Culicia* sp.; d) the same panel as in c), but after change-over to a tall wall with high sea urchin density. Please note the grazing marks of the sea urchins!

Photos were made in February 2002 prior to transfer or change-over of panels and in May 2002 after transfer (Fig. 2.8).

2.3. Statistical Analysis

2.3.1. General

Per cent total cover, number of species and diversity H' (Shannon-Index) were calculated for every plot and panel. Statistical software used was JMP 4.0 (SAS Institute Inc.), STATISTICA 5.1 (StatSoft Inc.), PRIMER 5.2.2 (PRIMER-E Ltd.) and NP-MANOVA by M. J. Anderson). Univariate data were checked for normality (Shapiro-Wilk Test), variance homogeneity (residual against predicted values plot; Levene's test) and were transformed to either fourth root or arcsine, where necessary. Sphericity of the variance-covariance matrix was tested with the Mauchly Criterion, if there were more than two sampling dates, but the number of degrees of freedom did not have to be adjusted. However, usually sphericity was not checked, since as in classical split-plot designs, the within-plots factor, sea urchin density, was randomly allocated, the sphericity assumption being met (Quinn and Keough, 2002). As

method of variance component estimation was the restricted maximum likelihood estimation (REML)-method used since the model included a random factor. This method is preferable to the traditionally expected mean square (EMS)-method used usually in ANOVA since unwanted negative variance component estimates do not appear in unbalanced multifactor designs (Underwood, 1997; Quinn and Keough, 2002). Note should be taken that the denominator of the F-ratio is different from the one that would be used in the EMS-method for a split-plot analysis. Tukey's HSD test was used as an a-posteriori test, if the ANOVA had a significant result and there were more than two levels to compare (Sokal and Rolf, 1995). Assemblage (multivariate) data for all plots were fourth root transformed and Bray-Curtis dissimilarity matrices (Bray and Curtis, 1957) were calculated and analysed with non-parametric MANOVA (Anderson, 2000; Anderson, 2001; McArdle and Anderson, 2001) followed by pair-wise comparison testing. If tests were significant, species primarily contributing to the dissimilarity between groups were determined using a similarity percentage analysis (SIMPER; Clarke, 1993). Significance level was 5 % in all analyses, but p-Values were adjusted using the Bonferroni Method to keep the 5 % level, if multiple comparisons were done and observations were not independent (Sokal and Rolf, 1995; Quinn and Keough, 2002). Usually, only significant results are indicated in the results section.

2.3.2. Do Structure and Dynamics of Established Assemblages vary with wall height?

Univariate data for random plots were analysed over time (4 sampling dates, $n = 2$, replicates within wall $n = 2$) for effects of wall height, time and wall as block factor with a 3-way partly nested ANOVA (split-plot) with the factor wall nested in wall height. Data for each sampling date as well as sea urchin data (individuals per m^2) were also analysed with a 2-way nested ANOVA with the factor wall nested in wall height.

Multivariate data for random plots were analysed over time (4 sampling dates, $n = 2$, replicates in wall $n = 2$) for effects of wall height, time and walls as block factor with a 2-way factorial (factors time and wall height) and a 2-way nested (walls nested in wall height) non-parametric MANOVA.

Bray-Curtis dissimilarities (Bray and Curtis, 1957) were calculated for individual permanent plots between April 2000 and June 2000, June 2000 and February 2002 and April 2000 and February 2002 as a rate of structural change of the assemblage. I assumed, if the dissimilarity in per cent determined for the same plot between two sampling dates is higher than zero the assemblage has changed over this time period. Change (dissimilarity) per month was calculated to get a uniform rate of change for every sampling period. Data were

analysed with a partly nested 3-way ANOVA (factor 1: time period, 3 levels; factor 2: wall height, 2 levels; factor 3 nested in factor 2: wall, 3 levels).

For the comparison of random and permanent plots and wall height, total cover, number of species and diversity data were analysed over time (3 sampling dates, $n = 3$, no replication in wall) with a 4-way ANOVA (split-plot). For each sampling date, data were also analysed with a 3-way nested ANOVA. Assemblage data were analysed with 2-way non-parametric MANOVAs (Analysis 1: randomisation x wall height, analysis 2: randomisation x time).

2.3.3. Does Structure of Recruitment vary with Wall Height and/or Sea Urchin Density?

Univariate data for every experiment (3.4.02 excluded) were analysed with a 3-way split-plot ANOVA. Factor one (wall height, fixed, 2 levels) and factor two (sea urchin density, fixed, 2 levels) were orthogonal. The factor three (wall, random, 5 levels) was blocked and nested in factor one (wall height). The nesting of factor one and three was also crossed with factor two to check for block effects in factor two.

Multivariate data (3.4.02 excluded) were analysed with a 2-way non-parametric MANOVA (factor one: wall height, fixed, 2 levels; factor two: sea urchin density, fixed, 2 levels). Assemblage data for the 18th of September 2001 had to be left out from analysis since the requirement of the design being balanced did not leave any replicates.

Weightloss data for every experiment were analysed with a 2-way ANOVA with walls (random) nested in wall height (fixed). Replication within walls was four.

2.3.4. Do Structure and Successional Dynamics of Newly Developing Assemblages vary with Wall Height and/or Sea Urchin Density?

Bray-Curtis dissimilarities (Bray and Curtis, 1957) were calculated for every panel between February and May 2002 (dissimilarity between census one and two) as rate of structural change in per cent per day of the assemblages.

Univariate data for single times were analysed with a 3-way partly nested ANOVA. Factor one (wall height, fixed, 2 levels) and factor two (sea urchin density, fixed, 2 levels) were orthogonal. Factor three (wall, random, 3 levels) was nested in factor one (wall height) and blocked. Data were compared over time with a 4-way partly nested ANOVA. Factor four (time, fixed, 2 levels) was orthogonal to factor one (wall height) and factor two (sea urchin density). For both ANOVAs, factors were pooled, if there were no statistically significant differences. Data for every time were analysed by a 2-way crossed non-parametric MANOVA

(factor one: wall height, fixed, 2 levels; factor two: sea urchin density, fixed, 2 levels) and a 2-way nested non-parametric MANOVA (factor one: wall height, fixed, 2 levels; factor two: wall, random, 3 levels or less). Assemblages were compared over time by 2-way crossed non-parametric MANOVAs with factor one (time, fixed, 2 levels) either being analysed with the factor wall height (fixed, 2 levels) or factor sea urchin density (fixed, 2 levels). If the factor time was not significant, data were pooled and factors wall height and sea urchin density were analysed over time with a 2-way crossed non-parametric MANOVA.

2.3.5. Divergence and Convergence of Transplanted Assemblages: the Relative Importance of Formative Habitat Effects in Early Succession

Statistical analysis of total cover in per cent, species numbers and diversity to check for carry-over effects and effects of the habitat of residence was done with a modified change-over analysis by Assoc. Prof. Ken Russell, University of Wollongong. In the design used in the experiment, treatments were only changed-over once. This is not the usual procedure in a normal change-over experiment, where the number of change-overs equals the number of treatments and every experimental unit is subjected to every treatment once (Quinn and Keough, 2002). However, such a design was not appropriate here. The modified change-over analysis consists of multiple linear regression analysis with all variables being indicator (dummy) variables (e.g. Quinn and Keough, 2002) incorporated into the model. The following model is assumed for the data set prior to change:

Observation = mean (μ) + effect of half wall (w_i) + effect of first period (p_1) + effect of current treatment ($t_{\text{wall height/sea urchin density}}$) + random error .

The model for the data set after the change-over:

Observation = mean (μ) + effect of half wall (w_i) + effect of second period (p_2) + effect of current treatment ($t_{\text{wall height/sea urchin density}}$) + carry-over effect of previous treatment ($r_{\text{wall height/sea urchin density}}$) + random error.

The analysis was done not with the raw data, but with the differences (e.g. total cover in per cent after change-over minus total cover in per cent prior to change-over). For example, for a transfer control panel that originated on a low wall with high sea urchin density and was transferred to another low wall with high sea urchin density, this gives an expected value of

$$\begin{aligned}
& (\mu + w_2 + p_2 + t_{\text{low wall/high sea urchin density}} + r_{\text{low wall/high sea urchin density}}) - (\mu + w_1 + p_1 + t_{\text{low wall/high sea urchin density}}) \\
& = (w_2 - w_1) + (p_2 - p_1) + r_{\text{low wall/high sea urchin density}}
\end{aligned}$$

Since the treatment prior to and after change-over is the same, the carry-over effect can be excluded. To estimate these terms in a regression analysis, ‘dummy’ categorical variables with the possible values of 1, 0 and – 1 were used as factor variables multiplication by these values giving the correct expected value.

There are 16 possible terms other than the mean: $p_1, p_2, w_1, w_2, w_3, w_4, w_5, w_6, t_{\text{low wall/high sea urchin density}}, t_{\text{low wall/low sea urchin density}}, t_{\text{tall wall/high sea urchin density}}, t_{\text{tall wall/low sea urchin density}}, r_{\text{low wall/high sea urchin density}}, r_{\text{low wall/low sea urchin density}}, r_{\text{tall wall/high sea urchin density}}, r_{\text{tall wall/low sea urchin density}}$. The treatment effects were always associated with an effect of a wall half, therefore these terms are inextricably linked. This reduces the number of terms that can be estimated in the regression to twelve. Since every observation is associated with a treatment, then if an observation did not result from one of the first three treatments, it must have resulted from the fourth and the number of ‘dummy’ variables is eleven. The following terms can be estimated: $p_2 - p_1, (w_1 + t_{\text{low wall/high sea urchin density}}) - (w_4 - t_{\text{tall wall/high sea urchin density}}), w_2 - w_1, w_3 - w_1, t_{\text{low wall/low sea urchin density}} - t_{\text{low wall/high sea urchin density}}, w_5 - w_4, w_6 - w_4, t_{\text{tall wall/low sea urchin density}} - t_{\text{tall wall/high sea urchin density}}, r_{\text{low wall/low sea urchin density}}, r_{\text{low wall/high sea urchin density}}, r_{\text{tall wall/low sea urchin density}}, r_{\text{tall wall/high sea urchin density}}$. Therefore, it was not possible to estimate all terms of interest (e.g. $t_{\text{tall wall/high sea urchin density}} - t_{\text{low wall/low sea urchin density}}$).

To test whether an assemblage looks like the control assemblage it came from, only the data of total cover in per cent, number of species and diversity after change-over were used for analysis. If this test was significant, assemblages did not look like the assemblage they originated from due to transfer and/or the treatment after change-over. Data were categorized by the wall halves from which they came. For every wall half, the value of the control assemblage that had not changed its wall half (y_5) was subtracted from the values of the treatments that had changed wall half (y_1, y_2, y_3, y_4). This resulted in four differences per wall half. A sum of squares of differences was calculated for every half wall: $S = 4[(y_1 - y_5)^2 + (y_2 - y_5)^2 + (y_3 - y_5)^2 + (y_4 - y_5)^2] - 2[(y_1 - y_5)(y_2 - y_5) + (y_1 - y_5)(y_3 - y_5) + (y_1 - y_5)(y_4 - y_5) + (y_2 - y_5)(y_3 - y_5) + (y_2 - y_5)(y_4 - y_5) + (y_3 - y_5)(y_4 - y_5)]$. These 12 sums were added up to a grand sum. The grand sum was multiplied by 2 and then divided by the Residual SS from the Regression Analysis, resulting in a so-called F-ratio. This F-ratio should be a random observation from a distribution, that had been simulated under the assumption that the null hypothesis (H_0 = the assemblage that has been transferred is not different from the assemblage

that did not get transferred) is true. Based on 50 000 simulations, there can be a statistically significant move-effect assumed, if the F-ratio exceeds 1.444 (level of significance: 5 %).

If the previous test was found to be significant for total cover in per cent, number of species or diversity, meaning there is a significant move-effect due to transfer and/or the treatment after transfer, the calculated differences (4 per half wall) were tested for effects of the treatment after change.

Bray-Curtis dissimilarities (Bray and Curtis, 1957) were calculated for every panel between the assemblage prior to and after the change-over as rate of structural change in per cent per day of the assemblage (rate of succession).

Assemblages were tested for differences in change in total cover, numbers of species, diversity and rate of structural change with a Mann-Whitney U-test. Data were analysed for 'divergence' within groups (same origin) and 'convergence' within groups (same present residence) by creating one group for the control assemblages that did not change habitat and one group for the assemblages that changed habitat and comparing these groups, resulting in four comparisons per response variable. Within groups of the same origin or of the same present residence, assemblages, that had changed-over to the same habitat were compared with the control assemblage that stayed in the original habitat (e.g. group 1: low wall low sea urchin density - high wall low sea urchin density, group 2: low wall low sea urchin density - low wall low sea urchin density for 'divergence'; group 1: low wall low sea urchin density - high wall low sea urchin density, group 2: high wall low sea urchin density - high wall low sea urchin density for 'convergence').

To test for convergence and divergence of assemblages, Bray-Curtis dissimilarities were calculated. For the convergence analysis, dissimilarities between assemblages that changed-over, were transplanted, to a different habitat and assemblages that already were in residence in this habitat and only changed wall and therefore not habitat (= control) were calculated before change-over and after change-over (e.g. dissimilarity 1 between low wall - high sea urchin density changing over to low wall - low sea urchin density and low wall - low sea urchin density changing over to different wall within the habitat). For the divergence analysis dissimilarities between assemblages that changed-over to a different habitat and assemblages that remained in the original habitat and only changed wall (= control) were calculated before and after change-over. Dissimilarities were compared group-wise for each habitat between before and after change-over with a Mann-Whitney U-test. If tests were significant, dissimilarity means were examined. If dissimilarity was higher after change-over the alternative hypothesis was accepted and assumed that assemblages diverged. If tests for

convergence were significant, assemblages were assumed to converge, if the dissimilarity mean after change-over was smaller.

3. Results

3.1. Do Structure and Dynamics of Established Assemblages vary with Wall Height?

Altogether, I observed 37 different species on the walls (see Appendix); three algal groups (crustose and erect coralline algae, filamentous algae), fourteen sponges (*Callyspongia* sp., *Chondrilla australiensis* Carter 1873, *Clathria* sp., *Cliona* sp., *Darwinella cf. australiensis*, *Euryspongia* sp., *Hymedesmia* sp., *Ircinia* sp., *Niphates* sp., *Pronax* sp., four unidentified species), four cnidarians (*Anthothoe albocincta* Hutton 1878, *Corynactis australis* Haddon & Duerden 1896, *Culicia* sp., hydroids), one polychaete (unidentified serpulid), two barnacles (*Austrobalanus imperator* Darwin 1854, *Balanus trigonus* Darwin 1854), two molluscs (*Serpulorbis siphon* Lamarck 1818, unidentified bivalves), three bryozoans (*Celleporaria* sp., *Rynchozoon* sp., *Tubulipora* species 1), seven ascidians (*Botrylloides magnicoecum* Hartmeyer 1912, *Botrylloides leachi* Savigny 1816, *Cnemidocarpa radicata* Herdman 1882, *Didemnum* sp., *Herdmania momus* Savigny 1816, *Lissoclinum* sp., *Sycozoa cerebriformis* Quoy & Gaimard 1834) and two mobile grazer groups (the diadematid echinoid *Centrostephanus rogersii* Agassiz 1863, limpets).

Limpets were only present on low walls whereas the corallimorph *Corynactis australis*, bivalves, the sponges *Hymedesmia* sp., *Niphates* sp. and two unidentified sponge species, the bryozoan *Celleporaria* sp. and the colonial ascidians *Botrylloides magnicoecum*, *Sycozoa cerebriformis* and *Didemnum* sp. were only present on tall walls.

For statistical results see table 3.1. Total cover was significantly different on tall and low walls in June 2000, almost 1.1 times higher on tall than on low walls (Fig. 3.1). Over time,

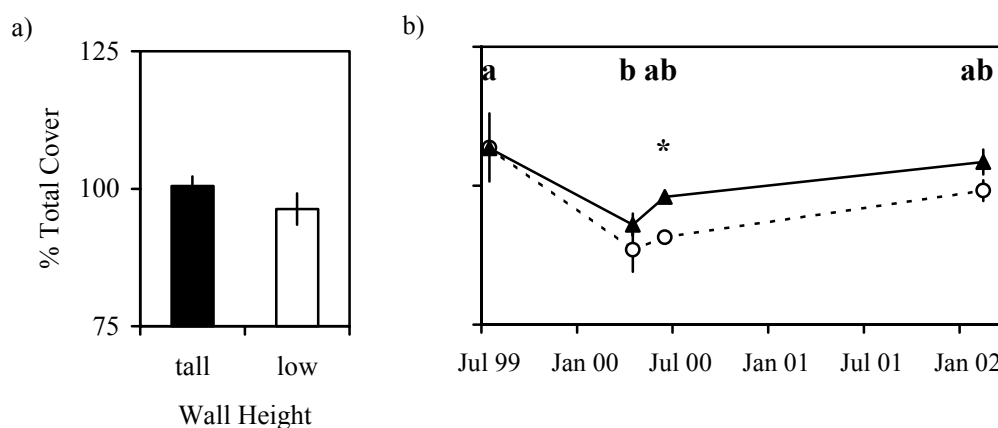


Fig. 3.1: Influence of wall height and time on total cover in per cent (mean \pm SE). a) total cover of tall and low walls averaged over time. b) total cover of tall and low walls for every sampling date. Tall walls = black triangles, low walls = white circles. Different letters or a star indicate significant differences; a star between tall and low walls, letters between different sampling dates. Please note the start of the y-axis at 75 % total cover.

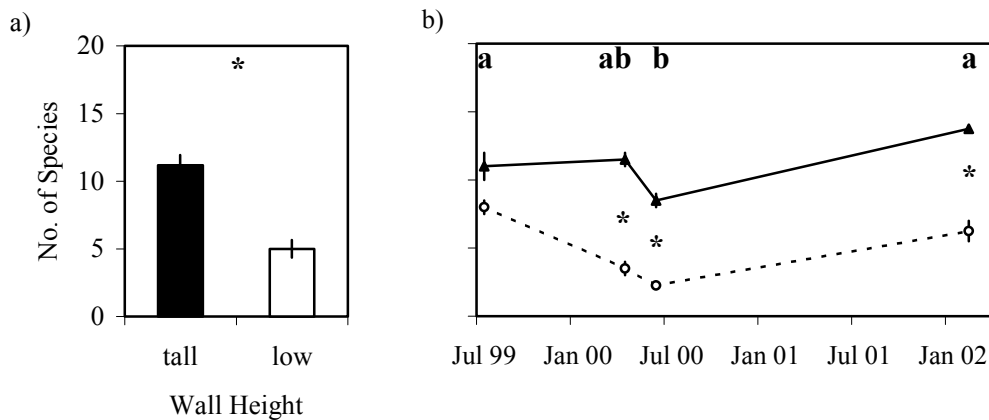


Fig. 3.2: Influence of wall height and time on number of species (mean \pm SE). a) number of species of tall and low walls averaged over time. b) number of species of tall and low walls for every sampling date. Further explanation see fig. 3.1.

there was a significant change in total cover. Total cover decreased significantly by 0.8 times from July 1999 to April 2000, after that it tended to increase.

Overall, species numbers were significantly different between tall and low walls (Fig. 3.2), being twofold greater on tall than on low walls. In April and June 2000, there were 3.8 times more species on tall walls than on low walls. In February 2002, there were 2.2 times more species on tall than on low walls. Species numbers changed significantly over time. Over the first eleven months, there was a significant decrease by 0.6 times, then species numbers increased by 1.9 times till February 2002.

Overall, diversity was significantly 3.7 times higher on tall than on low walls (Fig. 3.3). In July 1999, diversity was 1.8 times higher on tall than on low walls. In April 2000, diversity

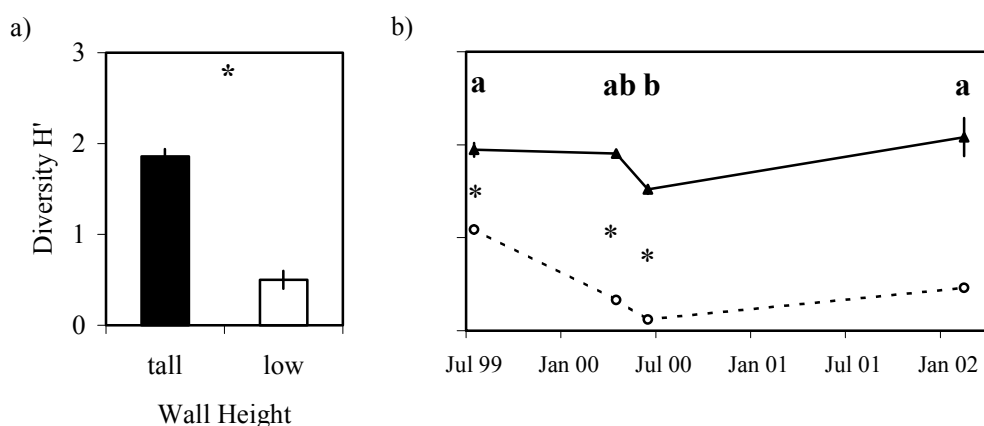


Fig. 3.3: Influence of wall height and time on diversity H' (mean \pm SE). a) diversity of tall and low walls averaged over time. b) diversity of tall and low walls for every sampling date. Further explanation see fig. 3.1.

Table 3.1: Statistical test results for % total cover, number of species, diversity H', composition of the assemblage, structural change rate, abundance of sea urchins of wall height and time averaged over all sampling dates, in July 1999, April and June 2000 and February 2002, between sampling dates or random versus permanent plots. Shown are only the most important test results.

	Parameter	Effect Wall Height	Effect Time	Rand/Perm
Overall Jul-99 April-00 Jun-00 Feb-02	% Total Cover	F _{1,2} = 1.58, p = 0.218 F _{1,2} = 0.0004, p = 0.986 F _{1,2} = 1.24, p = 0.360 F _{1,2} = 841.00, p = 0.005 F _{1,2} = 3.06, p = 0.222	F _{3,6} = 9.44, p = 0.045	F _{1,20} = 4.87, p = 0.120
Overall Jul-99 April-00 Jun-00 Feb-02	Number of Species	F _{1,2} = 337.97, p = 0.012 F _{1,2} = 7.20, p = 0.115 F _{1,2} = 231.20, p = 0.001 F _{1,2} = 125.00, p = 0.032 F _{1,2} = 90.00, p = 0.044	F _{3,6} = 23.91, p = 0.004	F _{1,20} = 3.02, p = 0.100
Overall Jul-99 April-00 Jun-00 Feb-02	Diversity H'	F _{1,2} = 542.49, p = 0.002 F _{1,2} = 98.21, p = 0.010 F _{1,2} = 442.58, p = 0.001 F _{1,2} = 798.99, p = 0.001 F _{1,2} = 62.75, p = 0.062	F _{3,6} = 26.73, p = 0.003	F _{1,20} = 0.01, p = 0.913
Overall	Assemblage Composition	F _{1,3} = 17.89, p = 0.004	F _{3,8} = 2.67, p = 0.129	F _{1,2} = 2.31, p = 0.133
2 months 20 months 22 months	Rate of Structural Change	F _{1,4} = 2.51, p = 0.188 F _{1,4} = 7.71, p = 0.150 F _{1,4} = 0.14, p = 0.731	F _{2,15} = 97.10, p < 0.001	
	Sea Urchin Abundance	F _{1,8} = 77.11, p < 0.0001		

was 6.4 times higher on tall walls than on low walls. In June 2000, diversity was 12.7 times higher on tall than on low walls. Even in February 2002, diversity was 4.5 times higher on tall than on low walls, but results were not significant. Irrespective of wall height, diversity decreased significantly by 0.5 times in the first eleven months and increased then significantly by 1.5 times till February 2002. There was a significant interaction between time and wall height ($F_{3,6} = 9.68$, $p = 0.041$). Diversity in June 2000 was almost ten times lower than in July 1999. Also, there was no difference of diversity between low walls in July 1999 and tall walls in June 2000. Tall and low walls were always different, but low walls in July 1999 were not different from tall walls in June 2000.

Overall, assemblages on tall walls were significantly different from assemblages on low walls (Fig. 3.4). Their average dissimilarity was 70.69 %. The four groups with the highest contribution (27.67 %) to the dissimilarity were the jewel anemone *Corynactis australis*, the

Table 3.2: Average per cent cover (\pm SE) on tall and low walls of the four species contributing the most to the dissimilarity of the assemblages.

SPECIES	% COVER (mean \pm SE)		% DISSIMILARITY (mean \pm SE)
	TALL WALLS	LOW WALLS	
<i>Corynactis australis</i>	18.25 (\pm 4.77)	0.00 (\pm 0.00)	6.58 (\pm 1.29)
<i>Culicia</i> sp.	8.00 (\pm 2.88)	0.03 (\pm 0.03)	4.78 (\pm 0.79)
<i>Botrylloides leachi</i>	6.94 (\pm 2.43)	0.00 (\pm 0.00)	4.15 (\pm 0.57)
crustose coralline algae	12.22 (\pm 2.57)	82.50 (\pm 1.97)	4.05 (\pm 1.43)

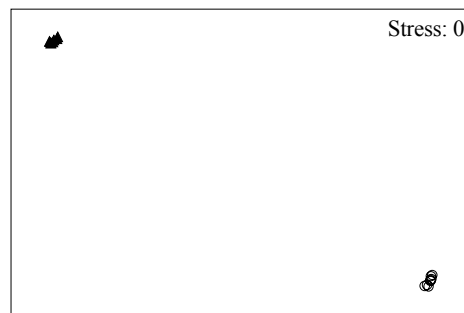


Fig. 3.4: Non-metric multidimensional scaling ordination of the composition of assemblages on tall walls (black triangle) and on low walls (white circles) pooled over time.

scleractine *Culicia* sp., the colonial ascidian *Botrylloides leachi* and crustose coralline red algae. The former three species were more abundant on tall than on low walls, whereas crustose coralline algae were more abundant on low than on tall walls (Table 3.2).

There was no statistical significant difference in the rate of structural change on tall and low walls (Fig. 3.5). The rate of structural change of the assemblages was significantly different with length of period between sampling dates. The change rate of the assemblage of the two months period was ten times significantly higher (16.59 ± 2.64 % dissimilarity per month) than the change rate of the twenty months assemblage (1.66 ± 0.24 % dissimilarity per month) and the twenty-two months assemblage (1.60 ± 0.14 % dissimilarity per month).

Abundance of *Centrostephanus rodgersii* was on low walls four times higher than on tall walls (Fig. 3.6).

Total cover, number of species, diversity and composition of the assemblage were not significantly different on permanent and random plots (Fig. 3.7, 3.8, 3.9).

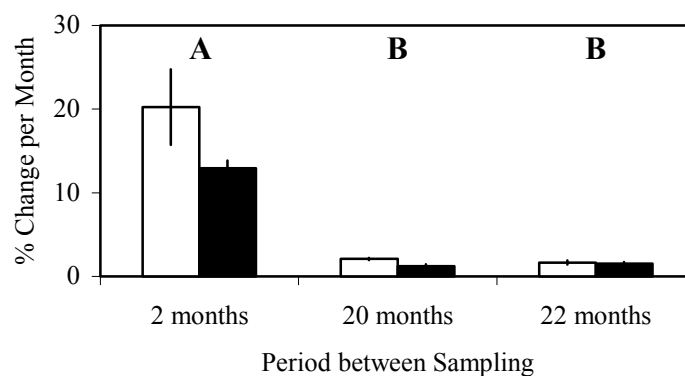


Fig. 3.5: Change rate of the assemblage as dissimilarity (Bray-Curtis) per month in per cent (mean \pm SE) on low (white bars) and tall (black bars) for two, twenty and twenty-two months between sampling dates. Different letters indicate statistically significant differences for the period between sampling dates.

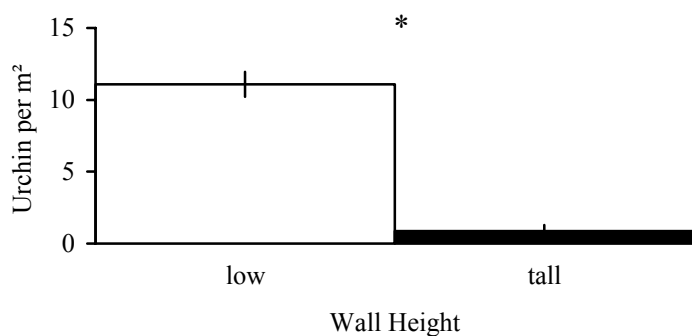


Fig. 3.6: Abundance of the sea urchin *Centrostephanus rodgersii* in urchins per m² (mean ± SE) on low and tall walls. The star indicates significant differences in abundances.

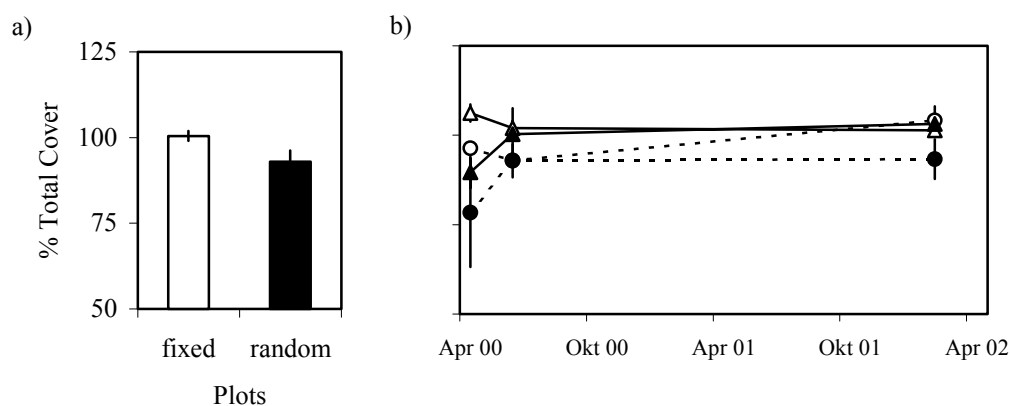


Fig. 3.7: Influence of randomisation vs. permanence of plots and wall height on total cover in per cent (mean ± SE). a) total cover of permanent and random plots averaged over time and wall height. b) total cover of permanent (white) and random plots (black) on tall (triangle) and low walls (circle) for every sampling date. Different letters or a star indicate significant differences; a star between tall and low walls, letters between sampling dates. Please note the start of the y-axis at 50 % total cover.

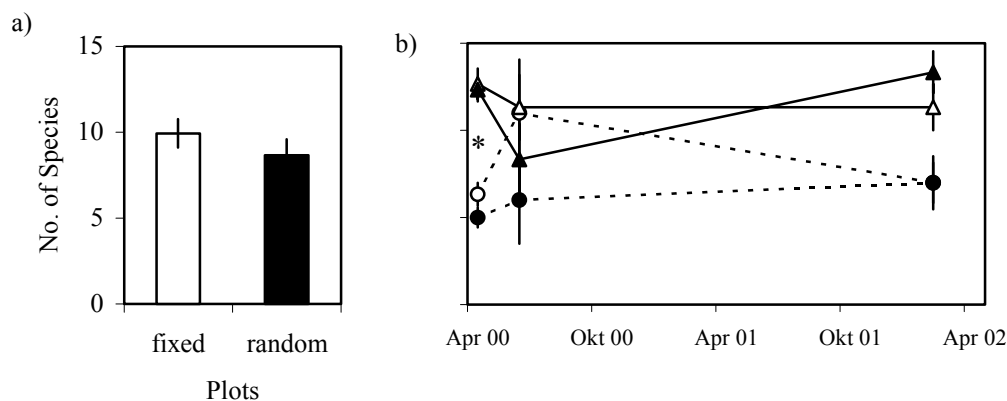


Fig. 3.8: Influence of randomisation vs. permanence of plots and wall height on species numbers (mean ± SE) over time. a) species numbers of permanent and random plots averaged over time and wall height. b) species numbers of permanent and random plots on tall and low walls for every sampling date. Further explanation see fig. 3.7.

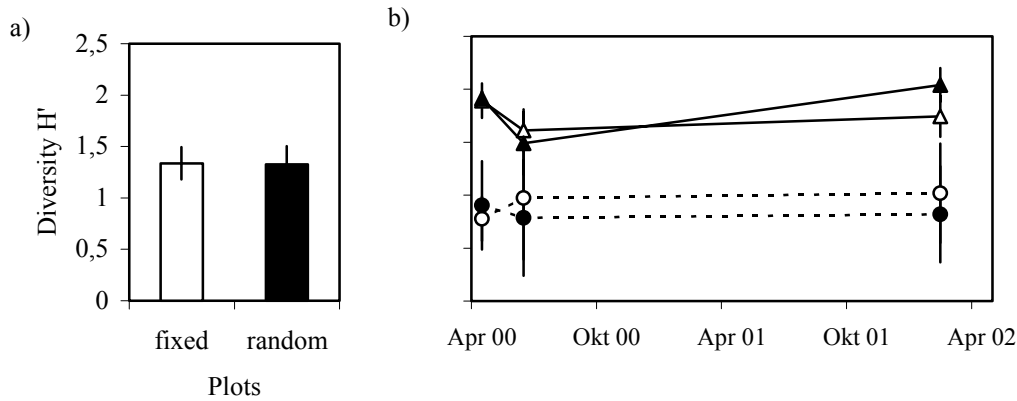


Fig. 3.9: Influence of randomisation vs. permanence of plots and wall height on diversity (mean \pm SE) over time. a) diversity of permanent and random plots averaged over time and wall height. b) diversity of permanent and random plots on tall and low walls for every sampling date. Further explanation see fig. 3.7.

3.2. Does Structure of Recruitment vary with wall height and/or sea urchin density?

In total, 53 taxa recruited (see Appendix). Dominant species having more than 10 % coverage were diatom species 1, 2, 4, hydrozoan species 2, ciliates, and crustose coralline red algae (in summer and autumn over 50 %). Algae contributed eighteen groups, invertebrates 33 groups. Opportunistic species that were present on all treatments were ciliates, foraminifers, most of the diatoms and algae, the hydrozoan species 2, the polychaetes *Pomatostegus* sp., *Pileolaria lateralis*, *Hydroides elegans*, the barnacles *Balanus trigonus*, *Austrobalanus imperator*, the bryozoans *Tubulipora* species 1, *Lichenopera* sp. and bryozoa species 6 and ascidian species 2. Species only present on tall walls with low sea urchin density and low walls with high sea urchin density (non-manipulated habitats) were two diatom species, two algal species, three bryozoan species, two hydroid species, the polychaetes *Spirobranchus* sp., *Filograna implexa*. Species that were only present on tall walls were one diatom species, two red algae, the corallimorph *Corynactis australis*, the hydroids *Stereotheca elongata*, *Aequorea aequorea*, hydroids species 3 and 4, the serpulids *Spirobranchus* sp., *Filograna implexa* and the bryozoans *Tubulipora* species 2, *Conopeum tenuissimum*, bryozoan species 7, 8, 10 and 11. Species only present on low walls were two algal species. Species present only with high sea urchin density were the anemone *Anthothoe albocincta*, the bryozoans *Baenia* sp., bryozoan species 9 and 12. There were no species that were only present at low sea urchin density.

Table 3.3: Statistical test results for % total cover, number of species, diversity H', composition of the assemblage and weight loss (gram) for the 12 recruitment experiments. Shown are only the most important test results. Dates see fig. 2.1.

<i>Experiment</i>	Parameter	Effect Wall Height	Effect Sea Urchin Density	Interaction
1	% Total Cover	$F_{1,20} = 1.18, p = 0.309$	$F_{1,20} = 0.81, p = 0.395$	$F_{1,20} = 23.86, p = 0.001$
2		$F_{1,10} = 0.62, p = 0.458$	$F_{1,10} = 0.001, p = 0.976$	$F_{1,10} = 0.29, p = 0.607$
3		$F_{1,12} = 8.60, p = 0.019$	$F_{1,12} = 0.84, p = 0.386$	$F_{1,2} = 0.17, p = 0.683$
4		$F_{1,4} = 0.78, p = 0.397$	$F_{1,4} = 0.44, p = 0.525$	$F_{1,4} = 0.22, p = 0.651$
5		$F_{1,9} = 0.13, p = 0.727$	$F_{1,9} = 4.64, p = 0.064$	$F_{1,9} = 4.22, p = 0.074$
6		$F_{1,2} = 1.30, p = 0.306$	$F_{1,2} = 48.53, p < 0.001$	$F_{1,2} = 24.93, p = 0.004$
7		$F_{1,1} = 0.02, p = 0.901$	$F_{1,1} = 2.34, p = 0.177$	$F_{1,1} = 0.01, p = 0.911$
8		$F_{1,1} = 0.13, p = 0.733$	$F_{1,1} = 0.02, p = 0.884$	$F_{1,1} = 0.50, p = 0.519$
9		$F_{1,1} = 0.22, p = 0.662$	$F_{1,1} = 0.01, p = 0.938$	$F_{1,1} = 0.003, p = 0.959$
10		$F_{1,1} = 0.83, p = 0.394$	$F_{1,1} = 0.98, p = 0.356$	$F_{1,1} = 0.35, p = 0.572$
11		No Analysis	No Analysis	No Analysis
12		$F_{1,5} = 0.20, p = 0.667$	$F_{1,5} = 0.39, p = 0.557$	$F_{1,5} = 0.31, p = 0.600$
1	Number of Species	$F_{1,20} = 0.02, p = 0.897$	$F_{1,20} = 2.27, p = 0.170$	$F_{1,20} = 0.82, p = 0.392$
2		$F_{1,10} = 0.05, p = 0.836$	$F_{1,10} = 0.13, p = 0.726$	$F_{1,10} = 2.73, p = 0.143$
3		$F_{1,12} = 0.22, p = 0.653$	$F_{1,12} = 3.97, p = 0.082$	$F_{1,12} = 1.23, p = 0.299$
4		$F_{1,4} = 0.45, p = 0.520$	$F_{1,4} = 0.49, p = 0.504$	$F_{1,4} = 0.14, p = 0.717$
5		$F_{1,9} = 10.40, p = 0.012$	$F_{1,9} = 0.08, p = 0.788$	$F_{1,9} = 0.11, p = 0.751$
6		$F_{1,2} = 5.37, p = 0.068$	$F_{1,2} = 19.54, p = 0.007$	$F_{1,2} = 3.89, p = 0.106$
7		$F_{1,1} = 2.43, p = 0.170$	$F_{1,1} = 2.11, p = 0.196$	$F_{1,1} = 0.01, p = 0.943$
8		$F_{1,1} = 0.06, p = 0.826$	$F_{1,1} = 0.07, p = 0.801$	$F_{1,1} = 0.07, p = 0.801$
9		$F_{1,1} = 5.59, p = 0.064$	$F_{1,1} = 0.02, p = 0.893$	$F_{1,1} = 8.56, p = 0.033$
10		$F_{1,1} = 0.06, p = 0.820$	$F_{1,1} = 0.51, p = 0.607$	$F_{1,1} = 0.02, p = 0.910$
11		No Analysis	No Analysis	No Analysis
12		$F_{1,5} = 6.89, p = 0.039$	$F_{1,5} = 0.06, p = 0.821$	$F_{1,5} = 1.23, p = 0.310$
1	Diversity H'	$F_{1,20} = 4.88, p = 0.058$	$F_{1,20} = 6.11, p = 0.039$	$F_{1,20} = 1.68, p = 0.231$
2		$F_{1,10} = 0.27, p = 0.619$	$F_{1,10} = 0.83, p = 0.392$	$F_{1,10} = 1.37, p = 0.280$
3		$F_{1,12} = 0.35, p = 0.572$	$F_{1,12} = 0.001, p = 0.972$	$F_{1,12} = 0.81, p = 0.394$
4		$F_{1,4} = 0.34, p = 0.579$	$F_{1,4} = 0.50, p = 0.500$	$F_{1,4} = 0.29, p = 0.604$
5		$F_{1,9} = 7.06, p = 0.029$	$F_{1,9} = 0.15, p = 0.707$	$F_{1,9} = 0.06, p = 0.817$
6		$F_{1,2} = 12.90, p = 0.016$	$F_{1,2} = 17.29, p = 0.009$	$F_{1,2} = 0.32, p = 0.596$
7		$F_{1,1} = 3.44, p = 0.110$	$F_{1,1} = 1.13, p = 0.329$	$F_{1,1} = 0.90, p = 0.380$
8		$F_{1,1} = 0.34, p = 0.590$	$F_{1,1} = 0.63, p = 0.470$	$F_{1,1} = 0.21, p = 0.674$
9		$F_{1,1} = 15.50, p = 0.011$	$F_{1,1} = 0.36, p = 0.577$	$F_{1,1} = 5.60, p = 0.064$
10		$F_{1,1} = 0.09, p = 0.778$	$F_{1,1} = 0.09, p = 0.782$	$F_{1,1} = 0.09, p = 0.772$
11		No Analysis	No Analysis	No Analysis
12		$F_{1,5} = 7.69, p = 0.032$	$F_{1,5} = 0.80, p = 0.788$	$F_{1,5} = 0.03, p = 0.859$
1	Assemblage Composition	$F_{1,16} = 2.34, p = 0.091$	$F_{1,16} = 0.99, p = 0.370$	$F_{1,16} = 0.28, p = 0.866$
2		$F_{1,8} = 4.06, p = 0.028$	$F_{1,3} = 2.05, p = 0.125$	$F_{1,3} = 1.60, p = 0.197$
3		$F_{1,12} = 5.90, p = 0.006$	$F_{1,12} = 1.02, p = 0.353$	$F_{1,12} = 0.40, p = 0.755$
4		$F_{1,8} = 5.22, p = 0.015$	$F_{1,8} = 2.48, p = 0.084$	$F_{1,8} = 1.19, p = 0.281$
5		$F_{1,12} = 4.25, p = 0.017$	$F_{1,12} = 1.06, p = 0.363$	$F_{1,12} = 0.59, p = 0.640$
6		$F_{1,4} = 2.86, p = 0.081$	$F_{1,4} = 0.65, p = 0.652$	$F_{1,4} = 0.99, p = 0.404$
7		$F_{1,4} = 0.35, p = 0.882$	$F_{1,4} = 1.06, p = 0.434$	$F_{1,4} = 0.32, p = 0.884$
8		No Analysis	No Analysis	No Analysis
9		$F_{1,4} = 1.95, p = 0.124$	$F_{1,4} = 1.34, p = 0.233$	$F_{1,4} = 1.47, p = 0.279$
10		$F_{1,4} = 0.82, p = 0.563$	$F_{1,4} = 0.09, p = 0.994$	$F_{1,4} = 0.60, p = 0.646$
11		No Analysis	No Analysis	No Analysis
12		$F_{1,8} = 0.54, p = 0.729$	$F_{1,8} = 0.58, p = 0.688$	$F_{1,8} = 0.75, p = 0.545$
1	Weight Loss	$F_{1,22} = 1.16, p = 0.314$		
2		$F_{1,14} = 1.78, p = 0.219$		
3		$F_{1,16} = 0.09, p = 0.773$		

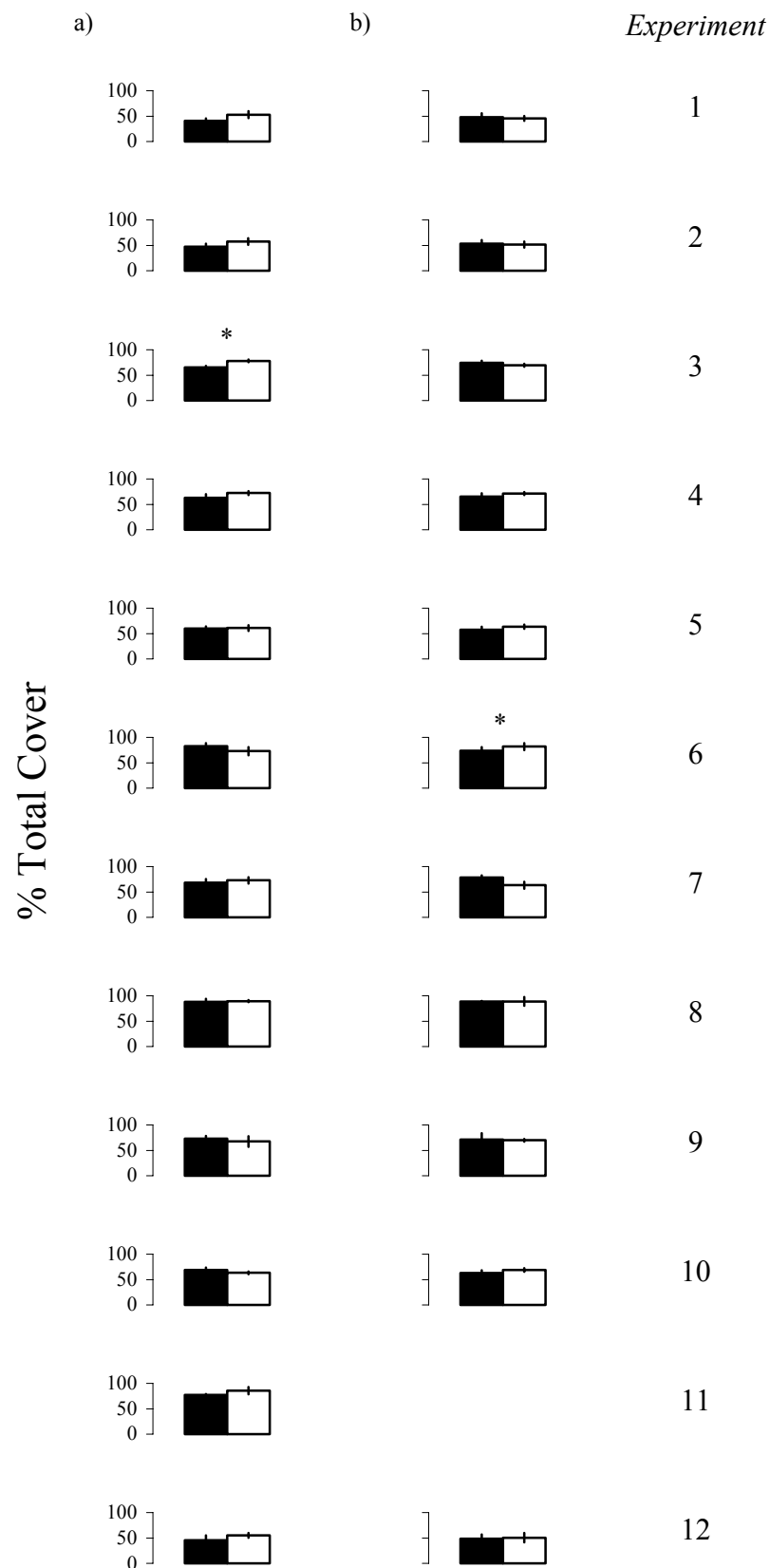


Fig. 3.10: Total cover of recruitment in per cent (mean \pm SE) in experiments 1 to 12 a) on tall (black) and low (white) walls, b) with high (black) and low (white) sea urchin density. A star (*) indicates significant differences. In experiment 11, there were no data for both sea urchin densities and the experiment was not statistically analysed.

Statistical test results are shown in table 3.3.

Total cover of recruitment was not significantly different on tall and low walls in experiment 1, 2, 4, 5, 6, 7, 8, 9, 10, 11 and 12 (Fig. 3.10 a). In experiment 1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12 total cover of recruits was not significantly different, when sea urchin density was high or low (Fig. 3.10 b). However, there was a significant interaction between tall and low wall and sea urchin density effects in experiment 1 and 6. In experiment 1, total cover of recruits on low walls was 1.4 times higher when sea urchin density was high than when it was low. In experiment 6, total cover of recruits was about 1.3 times higher on tall walls with high and low sea urchin density and on low walls with low sea urchin density than on low walls with high sea urchin density. Also in experiment 6, total cover of recruits was significantly affected by sea urchin density, but the difference was rather small and total cover of recruits was only 1.1 times higher, when there was low sea urchin density than when there was high sea urchin density. In experiment 3, total cover of recruits was significantly different on tall and low walls and 1.2 times higher on low than on tall walls. In experiment 1, 6 and 12, effects of tall and low walls on total cover of recruitment were significant different for different walls (experiment 1: $F_{1,20} = 11.93$, $p = 0.001$; experiment 6: $F_{5,2} = 44.25$, $p < 0.001$, experiment 12: $F_{6,5} = 7.38$, $p = 0.014$). In experiment 4 and 9, effects of sea urchin density on total cover of recruitment were significant different for different walls (experiment 4: $F_{1,4} = 6.68$, $p = 0.042$, experiment 9: $F_{5,1} = 428.16$, $p = 0.043$).

Numbers of recruited species were not significantly different on tall and low walls in experiment 1, 2, 3, 4, 6, 7, 8, 9, 10 and 11 (Fig. 3.11 a). In experiment 1, 2, 3, 4, 5, 7, 8, 9, 10, 11 and 12 numbers of recruited species were not significantly different for high and low sea urchin density (Fig. 3.11 b). However, there was a significant interaction of wall height and sea urchin density in experiment 9. Species numbers of recruits on tall walls with high sea urchin density were 1.5 times higher than numbers of species on tall and low walls with low sea urchin density, and 2.6 times higher than recruited species numbers on low walls with high sea urchin density. In experiment 5 and 12, numbers of recruited species on tall and low walls were significantly different. In experiment 5, there were on average 1.55 times more recruited species, and in experiment 12, 1.4 times more on tall than on low walls. In experiment 6, sea urchin density affected numbers of recruited species significantly. When sea urchin density was low, 1.6 times more species recruited than when it was high. In experiment 6, effect of tall and low walls was different for different walls ($F_{5,2} = 48.37$, $p = 0.0003$). In experiment 2, 8 and 9, effects of sea urchin density on numbers of recruited

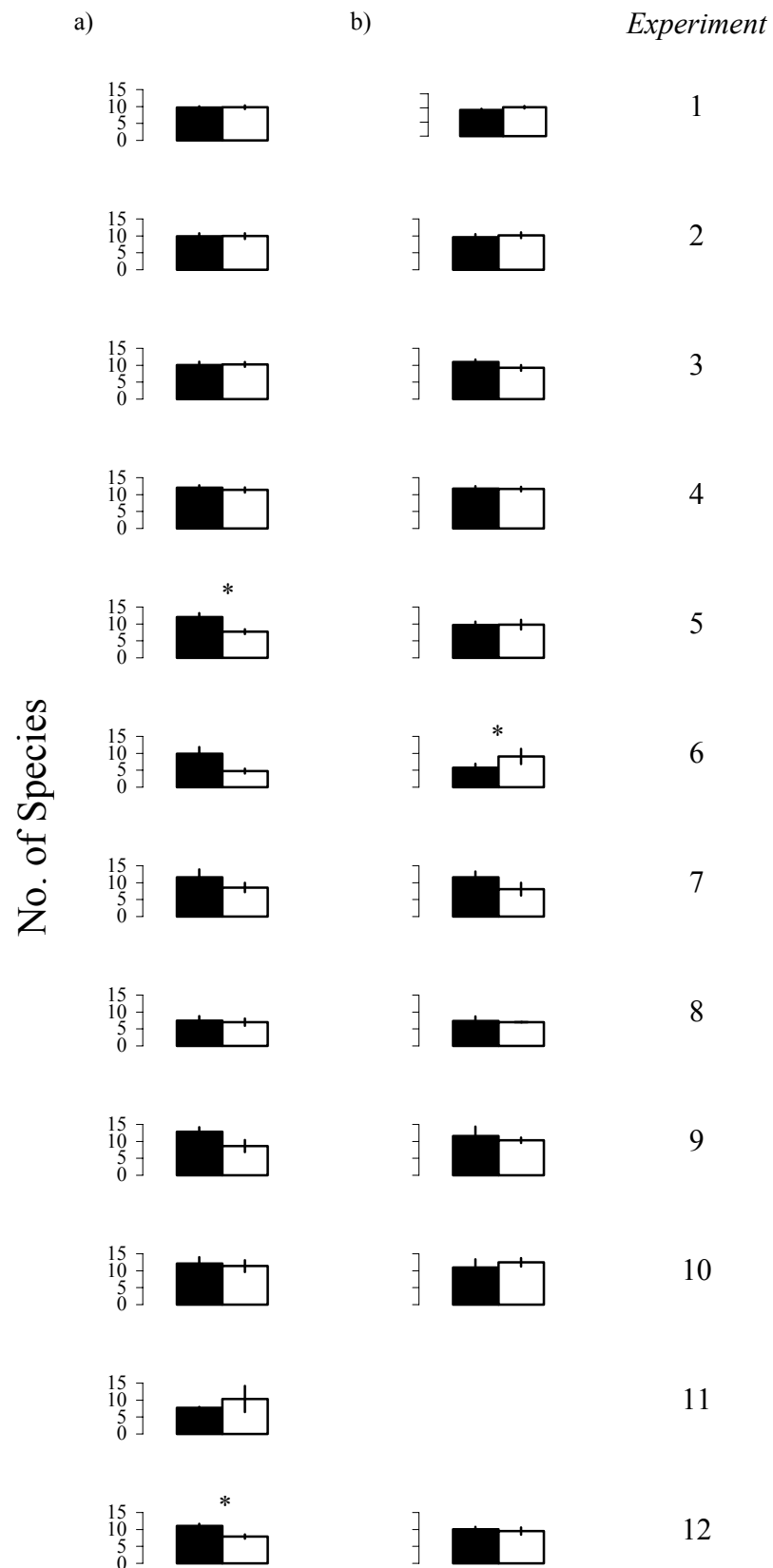


Fig. 3.11: Number of recruited species (mean \pm SE) in experiments 1 to 12. a) on tall (black) and low (white) walls, b) with high (black) and low (white) sea urchin density. Further explanations see fig. 3.10.

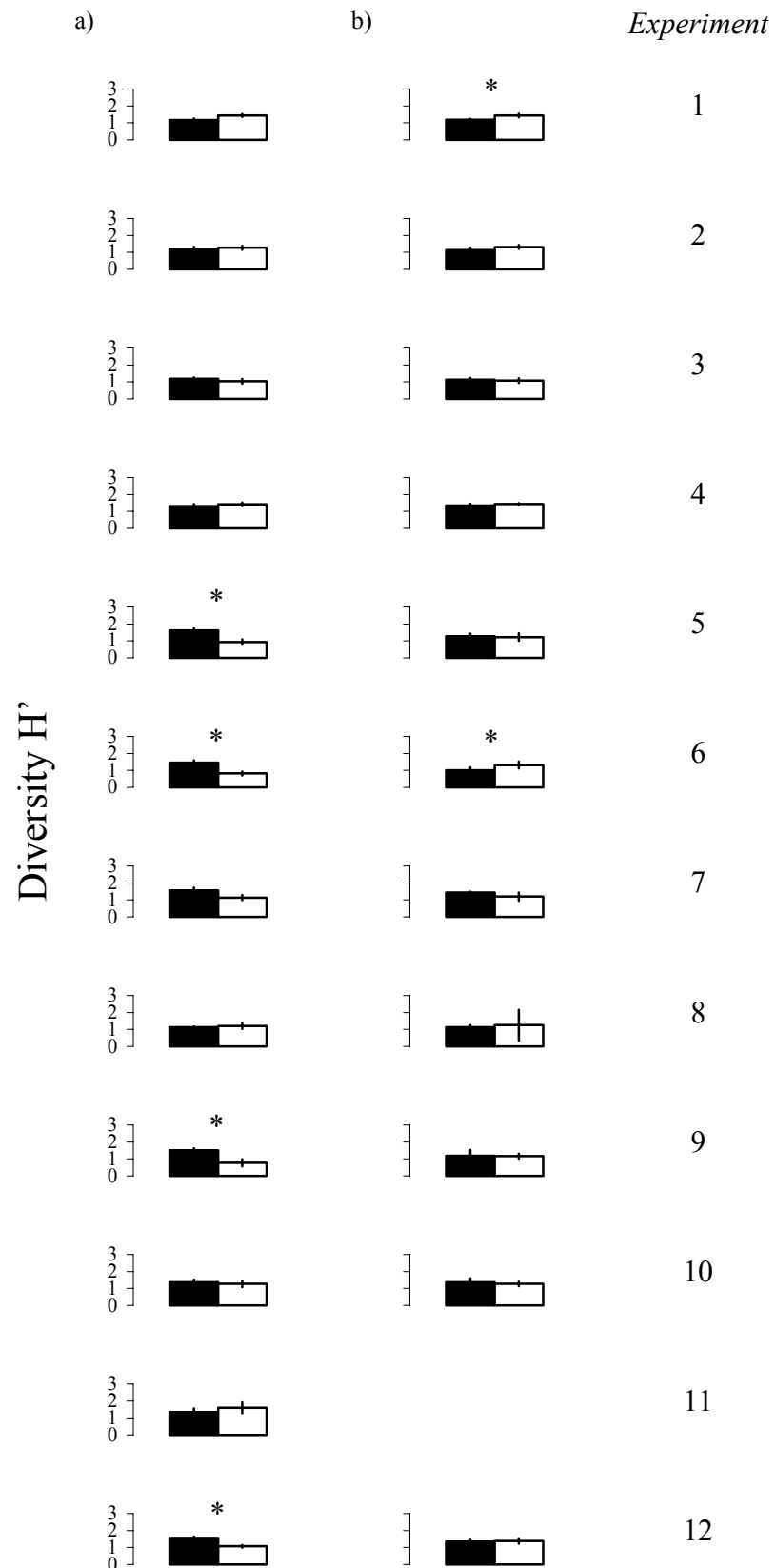


Fig. 3.12: Diversity H' of recruitment (mean \pm SE) in experiments 1 to 12 a) on tall (black) and low (white) walls, b) with high (black) and low (white) sea urchin density. Further explanation see fig. 3.10.

species were different for different walls (experiment 2: $F_{1,10} = 5.84$, $p = 0.007$, experiment 8: $F_{4,1} = 12857143.75$, $p < 0.001$, experiment 9: $F_{5,1} = 12666666.67$, $p < 0.001$).

Diversity of recruitment was not significantly different on tall and low walls in experiment 1, 2, 3, 4, 7, 8, 10 and 11 (Fig. 3.12 a). In experiment 2, 3, 4, 5, 7, 8, 9, 10, 11 and 12, diversity of recruitment was not significantly different for high and low sea urchin density (Fig. 3.12 b). In experiment 5, 6, 9 and 12, diversity of recruitment was significantly different on tall and low walls and always higher on tall than on low walls. Diversity of recruitment was 1.7 times higher on tall than on low walls in experiment 5, 1.8 times higher in experiment 6, twice higher in experiment 9 and 1.5 times higher in experiment 12. Sea urchin density had a significant influence on diversity of recruitment in experiment 1 and 6, but was only slightly higher when sea urchin density was low than when it was high. Diversity of recruitment was only 1.2 times higher when sea urchin density was low than when sea urchin density was high, in experiment 1, and only 1.3 times higher in experiment 6. In experiment 3 and 6, tall wall and low wall had different effects for different walls (experiment 3: $F_{8,12} = 4.43$, $p = 0.025$, experiment 6: $F_{5,2} = 5.78$, $p = 0.038$).

Assemblage composition of recruitment was not significantly different on tall and low walls in experiment 1, 6, 7, 8, 9, 10, 11 and 12. Sea urchin density had no significant effect in any experiment. Composition of the recruited assemblage was significantly different on tall and low walls in experiment 2, 3, 4 and 5 (Fig. 3.13). Average dissimilarity between tall and low walls was 44.54 % in experiment 2, 43.55 % in experiment 3, 45.97 % in experiment 4,

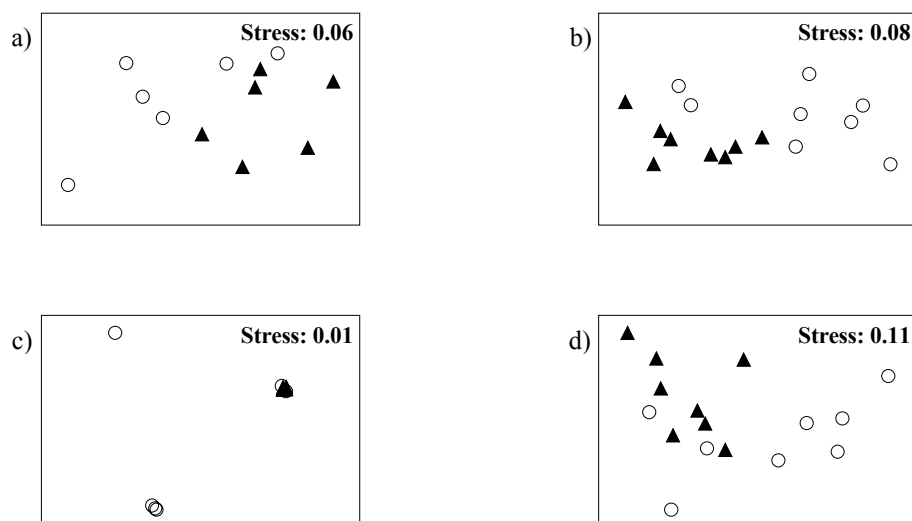


Fig. 3.13: Non-metrical multi-dimensional scaling ordination of the recruited assemblages on tall (○) and low (▲) walls pooled for sea urchin density on the a) 24th of July, b) 13th of September c) 23rd of October d) 27th of December 2000.

39.76 % in experiment 5. Always contributing to the dissimilarity between tall and low walls were diatom species 1, 2, 4 and hydrozoan species 2 (Table 3.4). In experiment 2, the five species having the highest dissimilarities in their abundances between tall and low walls and contributing together 48.94 % to the total dissimilarity of the assemblages were diatom species 2, hydrozoan species 2, ciliates, diatom species 1 and diatom species 4. Diatom species 1 and 2 were more abundant on low walls, whereas hydrozoan species 2, ciliates and diatom species 4 were more abundant on tall walls. In experiment 3, the five species having the highest dissimilarities in their abundances between tall and low walls and contributing 43.66 % to the dissimilarity of the assemblages were diatom species 2, hydrozoan species 2, diatom species 4, diatom species 1 and bryozoa species 6. Diatom species 2 and 4 were more abundant on low walls, whereas hydrozoan species 2, diatom species 1 and bryozoa species 6 were more abundant on tall walls. In experiment 4, the five species having the highest dissimilarities in their abundances between tall and low walls and contributing together 42.14 % to the dissimilarity of the assemblages were diatom species 4, diatom species 2, ciliates, hydrozoan species 2 and diatom species 1. Diatom species 1, 2 and 4 were more abundant on low walls, whereas hydrozoan species 2 and ciliates were more abundant on tall walls. In experiment 5, the seven species having the highest dissimilarities in their abundances between tall and low walls and contributing 40.99 % to the dissimilarity of the assemblages were hydrozoan species 2, diatom species 2, ciliates, diatom species 1, the serpulid *Pomatostegus* sp., diatom species 4 and the red algae *Ceramium* spp.. Diatom species 2 was more abundant on low walls, whereas hydrozoan species 2, ciliates, diatom species 1, the serpulid *Pomatostegus* sp., diatom species 4 and the red algae *Ceramium* spp. were more abundant on tall walls.

Table 3.4: Average dissimilarity (Bray-Curtis) of recruited species contribution the most (SIMPER) to the significant difference between tall and low walls in the np-MANOVA analyses. A hyphen (-) indicates that the species was lower ranking in contribution to the dissimilarity in this experiment and dissimilarity is not shown.

Species	% Dissimilarity (mean \pm SE) between tall and low walls in experiment			
	2	3	4	5
ciliates	3.63 \pm 0.70	-	3.65 \pm 0.87	2.09 \pm 0.74
diatom species 1	3.55 \pm 0.57	3.45 \pm 1.21	2.58 \pm 0.65	2.06 \pm 0.63
diatom species 2	6.78 \pm 0.87	5.89 \pm 0.81	4.11 \pm 0.91	2.71 \pm 0.80
diatom species 4	3.18 \pm 0.74	3.57 \pm 0.82	5.99 \pm 1.05	1.95 \pm 0.58
<i>Ceramium</i> spp.	-	-	-	1.91 \pm 0.58
hydrozoan species 2	4.66 \pm 0.74	3.89 \pm 0.69	3.04 \pm 1.02	3.55 \pm 0.61
<i>Pomatostegus</i> sp.	-	-	-	2.03 \pm 0.67
bryozoa species 6	-	2.21 \pm 0.73	-	-

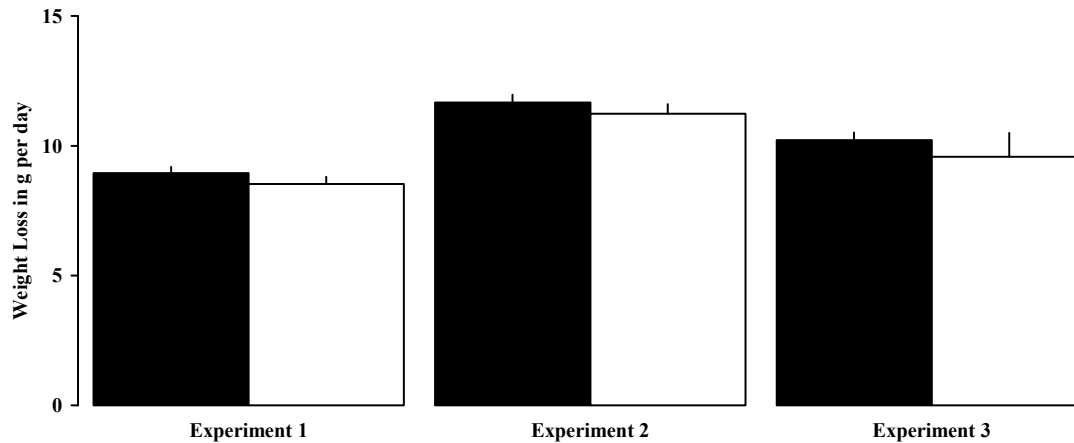


Fig. 3.14: Weight loss of half spheres in gram per day (mean \pm SE) on tall (black bars) and low walls (white bars) during the three experiments.

Weight loss of half-spheres indicating strength of water movement at the walls was not significantly different at tall and low walls neither after 48 hours, 48 hours during springtide or 72 hours. However, there was a slight tendency in all three experiments of more weight loss at tall walls than on low walls indicating more water movement at tall walls (Fig. 3.14).

3.3. Do Structure and Successional Dynamics of Newly Developing Assemblages vary with Wall Height and/or Sea Urchin Density?

Sixteen taxa recruited on the panels (see Appendix). Algae contributed five groups, invertebrates eleven of which one group was mobile (limpets). The diatom species 1 and 2, crustose coralline red algae, the red algae *Ceramium* spp., the bryozoans *Tubulipora* species 1 and *Rhynchozoon* sp. were opportunistic colonizers and present on tall and low walls with high and low sea urchin density. The sponges *Darwiniella* cf. *australiensis*, *Pronax* sp. and porifera species 3, hydroids and the corallimorph *Corynactis australis* were only present on tall walls, while the unidentified green alga and the barnacle *Balanus trigonus* were only present on low walls. The sponges *Darwiniella* cf. *australiensis*, *Pronax* sp. and porifera species 3 and the scleractinian *Culicia* sp. had only recruited, when sea urchin density was high, while the corallimorph *Corynactis australis* and the spirorbid *Pileolaria lateralis* only recruited, when sea urchin density was low. The most dominant species with average abundances above 50 % at all times and in all treatments were crustose coralline red algae. Less dominant species whose average abundances reached 10 % or more were the diatom species 2, the red algae *Ceramium* spp., the sponges *Pronax* sp. and porifera species 3 and the corallimorph *Corynactis australis*.

Table 3.5: Most important statistical test results for the parameters total cover in per cent, number of species, diversity H' , composition of the assemblage and structural change (between February and May 2002) of the developing assemblage (mean \pm SE) overall, in February and in May 2002.

	Parameter	Effect Wall Height	Effect Sea Urchin Density	Interaction
Overall	% Total Cover	$F_{1,12} = 0.07, p = 0.799$	$F_{1,12} = 0.28, p = 0.623$	$F_{1,12} = 0.35, p = 0.586$
Feb-02		$F_{1,7} = 0.61, p = 0.480$	$F_{1,7} = 0.42, p = 0.553$	$F_{1,12} = 0.58, p = 0.490$
May-02		$F_{1,6} = 0.67, p = 0.460$	$F_{1,6} = 0.43, p = 0.546$	$F_{1,12} = 0.20, p = 0.675$
Overall	Number of Species	$F_{1,12} = 4.57, p = 0.099$	$F_{1,12} = 0.03, p = 0.862$	$F_{1,12} = 0.01, p = 0.947$
Feb-02		$F_{1,7} = 1.34, p = 0.312$	$F_{1,7} = 0.03, p = 0.878$	$F_{1,12} = 0.02, p = 0.893$
May-02		$F_{1,6} = 6.80, p = 0.060$	$F_{1,6} = 0.01, p = 1.000$	$F_{1,12} = 0.12, p = 0.747$
Overall	Diversity H'	$F_{1,12} = 2.52, p = 0.188$	$F_{1,12} = 0.80, p = 0.422$	$F_{1,12} = 0.14, p = 0.724$
Feb-02		$F_{1,7} = 1.79, p = 0.252$	$F_{1,7} = 0.12, p = 0.742$	$F_{1,7} = 0.43, p = 0.548$
May-02		$F_{1,6} = 2.54, p = 0.187$	$F_{1,6} = 3.65, p = 0.129$	$F_{1,6} = 1.01, p = 0.373$
Overall	Assemblage Composition	$F_{1,12} = 3.48, p = 0.028$	$F_{1,12} = 1.53, p = 0.189$	$F_{1,8} = 0.36, p = 0.908$ $F_{1,4} = 0.51, p = 0.803$
Feb-02		$F_{1,8} = 1.64, p = 0.133$	$F_{1,8} = 0.33, p = 0.907$	
May-02		$F_{1,4} = 1.28, p = 0.281$	$F_{1,4} = 0.93, p = 0.605$	
3 mon	Rate of Structural Change	$F_{1,6} = 0.02, p = 0.906$	$F_{1,6} = 0.08, p = 0.795$	$F_{1,6} = 0.58, p = 0.490$

Statistical test results are shown in table 3.5 and parameter averages in the Appendix.

Overall as well as in February and in May, total cover of the developing assemblage was not significantly different on tall and low walls neither when sea urchin density was high or low (Fig. 3.15).

Numbers of species of the developing assemblage were not significantly different on tall and low walls or when sea urchin density was high or low, overall as well as in February and May (Fig. 3.16). However, numbers of recruited species was 1.3 times higher overall and 1.5 times higher in May on tall than on low walls.

Diversity of the developing assemblage was not significantly different on tall and low walls and neither when sea urchin density was high or low, overall, as well as in February and

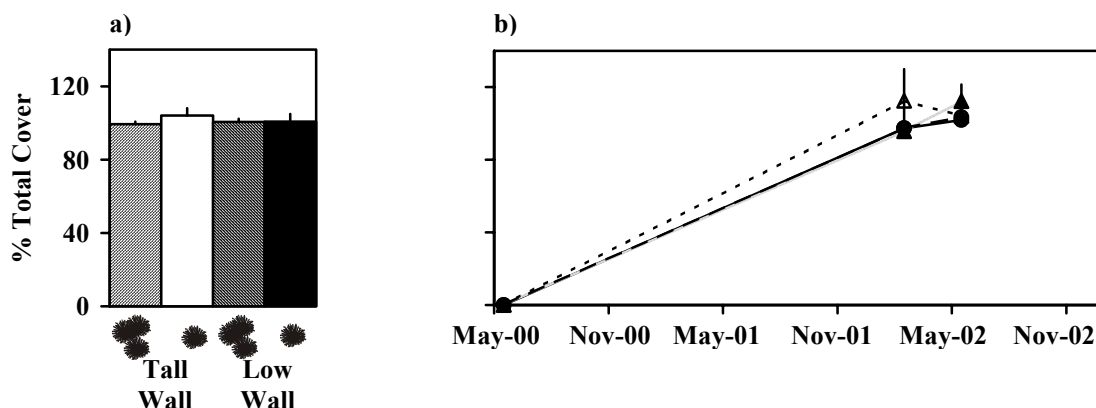


Fig. 3.15: Total cover in per cent (mean \pm SE) of the developing assemblage a) averaged over time for tall and low walls and high (3 sea urchins) and low sea urchin density (1 sea urchin), b) in February and May 2002 for tall walls with high sea urchin density (black circle), tall walls with low density (black triangle), low walls with high density (white circle), low walls with low density (white triangle).

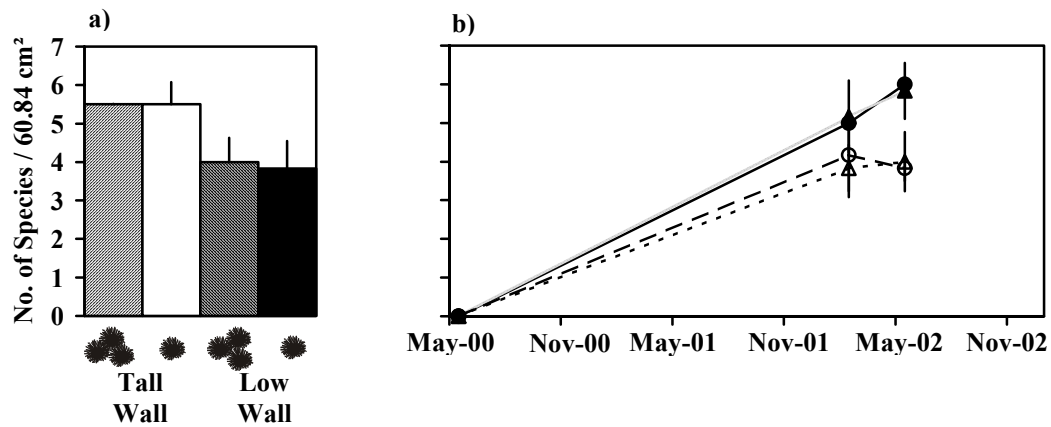


Fig. 3.16: Number of species (mean \pm SE) of the developing assemblage a) averaged over time for tall and low walls and high and low sea urchin density, b) in February and May 2002 for tall and low walls with high and low sea urchin density. For further explanation see fig. 3.15.

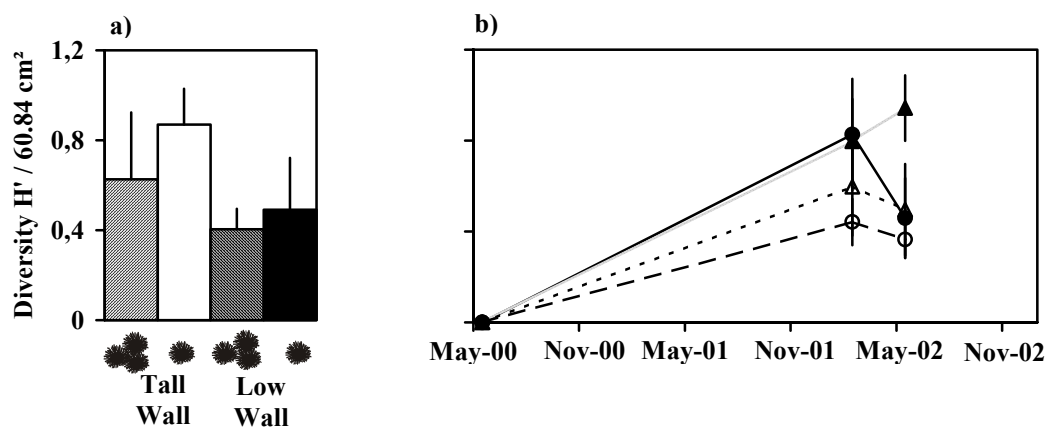


Fig. 3.17: Diversity H' (mean \pm SE) of the developing assemblage a) averaged over time for tall and low walls and high and low sea urchin density, b) in February and May 2002 for tall and low walls with high and low sea urchin density. For further explanation see fig. 3.15.

May (Fig. 3.17). However, diversity was overall 1.7 times higher on tall than on low walls.

Overall, the composition of the developing assemblage was significantly different on tall and low walls (Fig. 3.18), but not in February and May. The average dissimilarity was 42.93

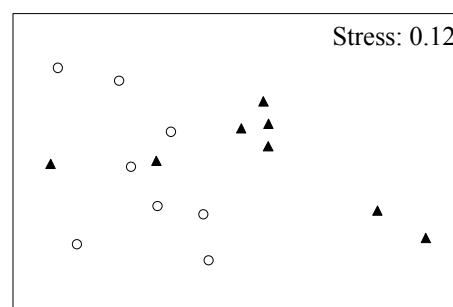


Fig. 3.18: Non-metric multidimensional scaling ordination of the composition of assemblages averaged over time on tall (black triangle) and low walls (white circle).

% over time. The four species, which most (47.32 %) contributed to the dissimilarity, were the corallimorphan *Corynactis australis*, the red algae *Ceramium* spp., the bryozoans *Tubulipora* species 1 and *Rhynchozoon* sp. (Table 3.6). Crustose coralline red algae were lower ranking in their contribution. *Corynactis australis*, *Ceramium* spp. and *Rhynchozoon* sp. were more abundant on tall walls, while *Tubulipora* species 1 and crustose coralline red algae were more abundant on low walls. Sea urchin density had no significant effect on the composition of the developing assemblage over time and neither in February or in May.

The rate of change between February and May of the developing assemblage was neither significantly different between tall and low walls or when sea urchin density was high or low (Fig. 3.19).

Table 3.6: Average per cent cover (\pm SE) on tall and low walls and dissimilarity in per cent between tall and low walls of the four species contributing the most to the dissimilarity of the assemblages and the most dominant species crustose coralline red algae.

SPECIES	% COVER (mean \pm SE)		% DISSIMILARITY (mean \pm SE)
	TALL WALLS	LOW WALLS	
<i>Corynactis australis</i>	13.63 \pm 5.83	0.00 \pm 0.00	6.08 \pm 0.49
<i>Ceramium</i> spp.	6.81 \pm 3.60	2.25 \pm 0.92	5.15 \pm 0.63
<i>Tubulipora</i> sp. 1	0.19 \pm 0.13	2.63 \pm 0.92	4.63 \pm 0.78
<i>Rhynchozoon</i> sp.	3.66 \pm 1.93	0.78 \pm 0.43	4.46 \pm 0.63
crustose coralline red algae	56.63 \pm 1.51	78.31 \pm 7.84	2.70 \pm 0.48

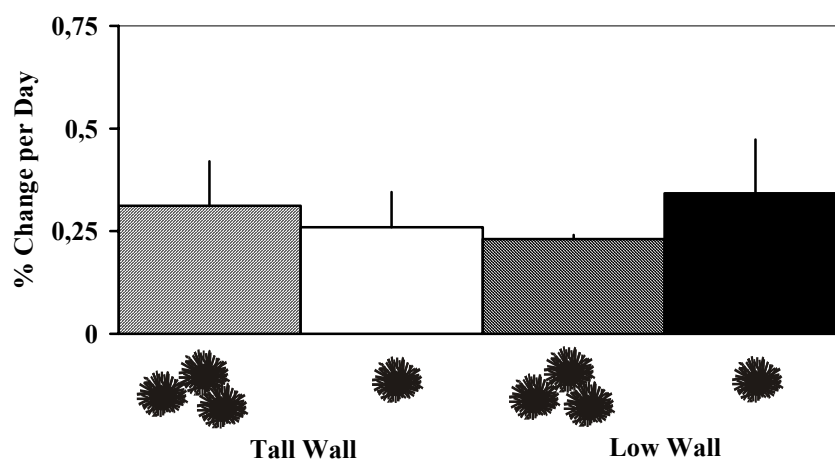


Fig. 3.19: Rate of change per day in per cent (mean \pm SE) as dissimilarity (Bray-Curtis) per day in per cent of developing assemblages on tall and low walls with high (three sea urchins) and low sea urchin density (one sea urchin).

3.4. Divergence and Convergence of Transplanted Assemblages: the Relative Importance of Formative Habitat Effects in Early Succession

In total, I found 23 taxa (see Appendix). Algae contributed five, invertebrates eighteen groups of which one group was mobile (limpets). Opportunistic species, that were present in every treatment combination were the diatom species 2, crustose coralline red algae and the bryozoan *Tubulipora* sp.. The sponges *Callyspongia* sp., *Chondrilla australiensis*, *Darwiniella cf. australiensis* and *Hymedesmia* sp. were only then present, when assemblages were constantly on tall walls; *Callyspongia* sp. was only present, when sea urchin density stayed low, *Chondrilla australiensis*, *Darwiniella cf. australiensis* and *Hymedesmia* sp., when sea urchin density stayed high. There were no species only present, when constantly on low walls. The corallimorph *Corynactis australis* and the barnacle *Austrobalanus imperator* were only present, when the assemblage originated on tall walls. The anemone *Anthothoe albocincta* and the barnacle *Balanus trigonus* were only present, when the assemblage originated on a low wall with low sea urchin density.

The most dominant species were crustose coralline red algae with a cover of over 75 % averaged over all treatment combinations and an average cover of over 50 % in most treatment combinations. Less dominant species that reached at least in one treatment combination an average cover of 10 % or more were the diatom species 2, *Ceramium* spp., the sponges *Callyspongia* sp., *Pronax* sp., porifera species 3, porifera species 4, hydroids, the corallimorph *Corynactis australis* and the barnacle *Balanus trigonus*.

The model equations for change in percentage total cover, number of species and diversity are shown in table 3.7, the estimated terms explained 17 % of the variation in change ('change' of a parameter means in this experiment the difference between after and before

Table 3.7: Equation model and r^2 calculated in the modified change-over analysis for the parameters change of total cover in per cent, number of species and diversity H' . Further explanations to the analysis see chapter two.

Parameter [change]	Model (Regression-Analysis)	R^2
% Total Cover	$= 7.14 + 10.40 ((w_1 + t_{LH}) - (w_4 + t_{TH})) - 3.38 (w_2 - w_1) + 1.45 (w_3 - w_1) - 4.59 (t_{LL} - t_{LH}) + 7.58 (w_5 - w_4) - 0.40 (w_6 - w_4) + 16.32 (t_{TL} - t_{TH}) + 4.03 (r_{LH}) - 7.53 (r_{LL}) - 10.25 (r_{TH}) + 8.45 (r_{TL})$	0.169
No. of Species	$= 0.27 - 1.14 ((w_1 + t_{LH}) - (w_4 + t_{TH})) - 0.29 (w_2 - w_1) + 0.03 (w_3 - w_1) + 0.83 (t_{LL} - t_{LH}) - 0.06 (w_5 - w_4) - 0.67 (w_6 - w_4) + 0.12 (t_{TL} - t_{TH}) - 0.76 (r_{LH}) - 0.33 (r_{LL}) + 0.83 (r_{TH}) + 0.26 (r_{TL})$	0.145
Diversity H'	$= - 0.09 - 0.26 ((w_1 + t_{LH}) - (w_4 + t_{TH})) - 0.02 (w_2 - w_1) - 0.03 (w_3 - w_1) + 0.09 (t_{LL} - t_{LH}) - 0.02 (w_5 - w_4) - 0.13 (w_6 - w_4) - 0.04 (t_{TL} - t_{TH}) - 0.17 (r_{LH}) - 0.08 (r_{LL}) + 0.28 (r_{TH}) - 0.03 (r_{TL})$	0.115

Table 3.8: Statistical test results for carry-over effects from the original habitats tall wall and low wall with high and low sea urchin density for change in per cent total cover, numbers of species and diversity H' . UD = sea urchin density.

Parameter [change]	Carry-Over Effect for Original Habitat			
	Tall Wall		Low Wall	
	High UD	Low UD	High UD	Low UD
% Total Cover	$F_{1,39} = 1.10, p = 0.301$	$F_{1,39} = 0.68, p = 0.415$	$F_{1,39} = 0.17, p = 0.682$	$F_{1,39} = 0.52, p = 0.476$
No. of Species	$F_{1,39} = 0.85, p = 0.363$	$F_{1,39} = 0.07, p = 0.786$	$F_{1,39} = 0.71, p = 0.403$	$F_{1,39} = 0.12, p = 0.735$
Diversity H'	$F_{1,39} = 1.93, p = 0.173$	$F_{1,39} = 0.02, p = 0.885$	$F_{1,39} = 0.71, p = 0.404$	$F_{1,39} = 0.13, p = 0.717$

Table 3.9: Statistical test results of habitats after change-over for change in total cover in per cent, number of species, diversity H' . Shown is the effect of sea urchin density (UD) on tall walls and on low walls, the interaction and the move-effect (transfer + habitat after change-over). Further details see chapter two.

Parameter [change]	Effect			
	UD on Tall Wall	UD on Low Wall	Interaction	Move
% Total Cover	$F_{1,39} = 3.56, p = 0.067$	$F_{1,39} = 0.25, p = 0.619$	$F_{1,39} = 1.12, p = 0.297$	$F = 6.15, p < 0.01$
No. of Species	$F_{1,39} = 0.02, p = 0.879$	$F_{1,39} = 0.97, p = 0.330$	$F_{1,39} = 1.59, p = 0.215$	$F = 7.67, p < 0.01$
Diversity H'	$F_{1,39} = 0.06, p = 0.805$	$F_{1,39} = 0.24, p = 0.624$	$F_{1,39} = 1.67, p = 0.204$	$F = 7.24, p < 0.01$

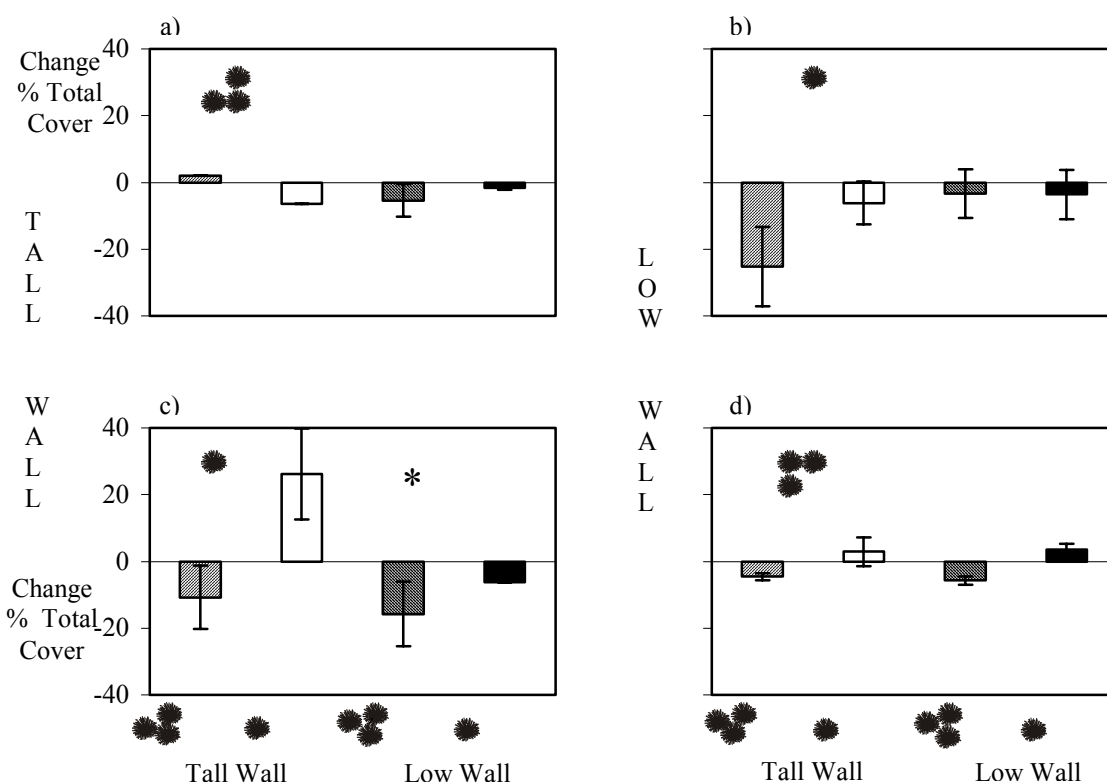


Fig. 3.20: Change of total cover in per cent (mean \pm SE) due to transfer and change of habitat (minus change of control assemblage) after transfer of assemblages to tall walls with high sea urchin density (∇) and low sea urchin density (\square) and to low walls with high (\blacktriangledown) and low sea urchin density (\blacksquare). Assemblages originated on a) tall walls with high sea urchin density, b) low walls with low sea urchin density, c) tall walls with low sea urchin density, d) low walls with high sea urchin density. A star (*) indicates that assemblages originating in the same habitat were significantly different from the control assemblage after change-over to different habitats.

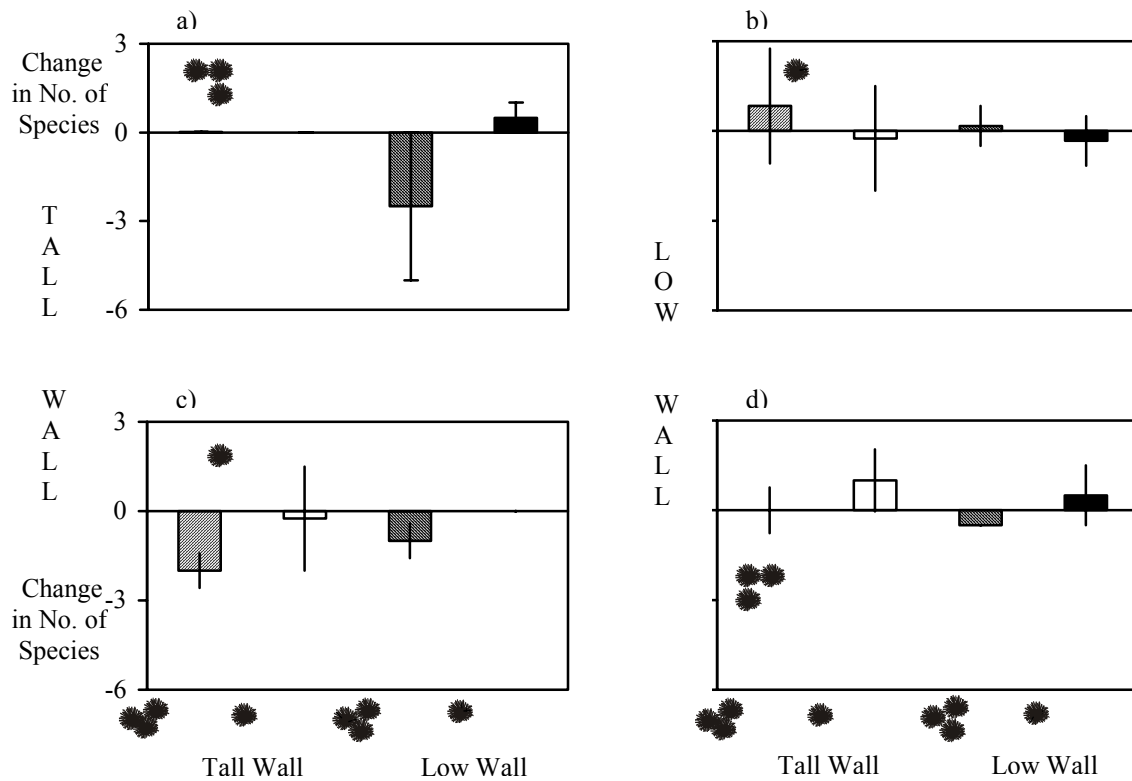


Fig. 3.21: Change in numbers of species (mean \pm SE) due to transfer and change of habitat (minus control assemblage) after transfer of assemblages to tall and low walls with high and low sea urchin density. Assemblages originated on a) tall walls with high sea urchin density, b) low walls with low sea urchin density, c) tall walls with low sea urchin density, d) low walls with high sea urchin density. Further explanation see fig. 3.20.

change-over and can be positive or negative; further details see chapter two) in percentage total cover, 15 % of the variation in change of numbers of species and 12 % of the variation in change of diversity. There was no carry-over effect of the habitats tall wall with high sea urchin density, tall wall with low sea urchin density, low wall with high sea urchin density and low wall with low sea urchin density for total cover in per cent, numbers of species and diversity (Table 3.8). The change in total cover, numbers of species and diversity was not significantly different between present habitats with high and low sea urchin density, neither on tall or low walls after change-over (= transfer to different habitat = present habitat; table 3.9). However, the change in total cover, numbers of species and diversity of assemblages that changed habitat was significantly different from the change in total cover, numbers of species and diversity of assemblages that remained in the original habitat indicating a transfer or an effect after change-over. Comparisons showed that this was mainly an effect of transfer (Fig. 3.20, 3.21, 3.22). Only change in total cover showed an effect of the present habitat; change-

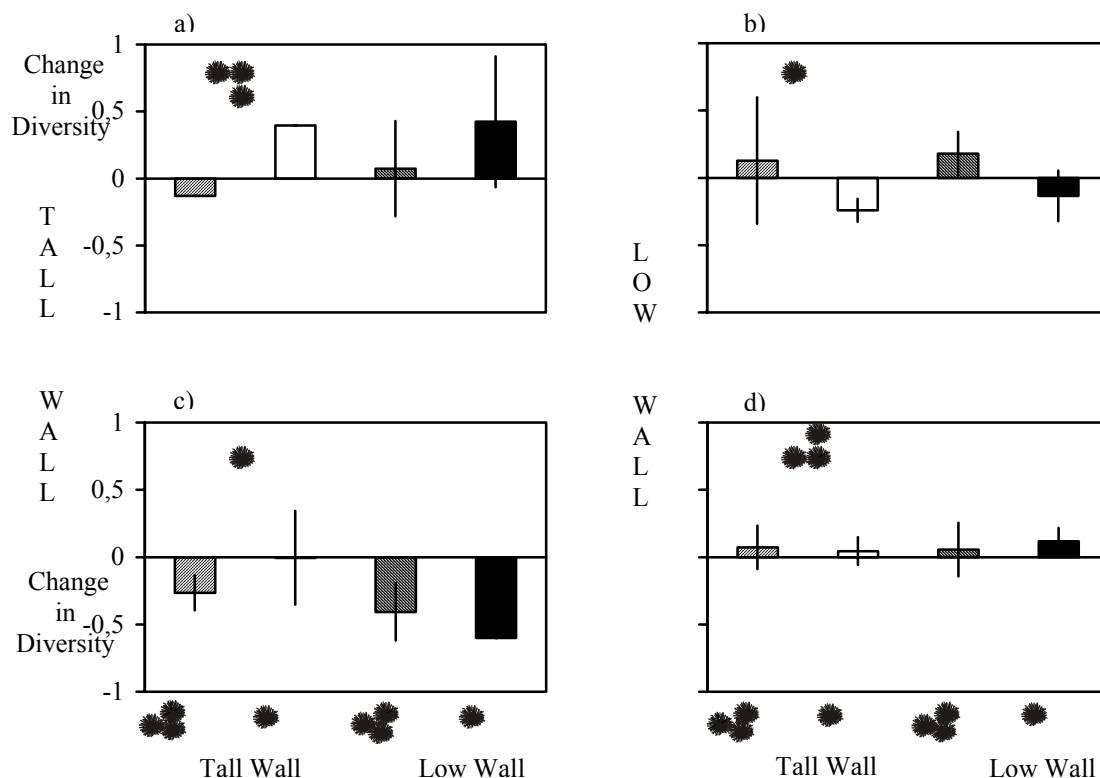


Fig. 3.22: Change in diversity (mean \pm SE) due to transfer and change of habitat (minus unmoved control) after transfer of assemblages to tall and low walls with high and low sea urchin density. Assemblages originated on a) tall walls with high sea urchin density, b) low walls with low sea urchin density, c) tall walls with low sea urchin density, d) low walls with high sea urchin density. Further explanation see fig. 3.20.

over to other habitats had a significantly negative effect on change in total cover of assemblages originating on tall walls with low sea urchin density (U-test, $p = 0.040$). The change in total cover after change-over was -2.1 times smaller, when habitat was changed (total cover decreased by $-12.25 \pm 5.31\%$) than when the assemblage remained on a tall wall with low sea urchin density (total cover increased by $26.13 \pm 13.63\%$).

A change in habitat did not significantly increase or decrease the rate of structural change of the assemblage (Fig. 3.23; U-tests $p = \text{ns}$, table 3.10).

Table 3.10: U-test results for the comparison of the rate of structural change of assemblages after change-over to different habitats with the rate of structural change of assemblages that remained in the original habitat.

Original Habitat			
Tall Wall		Low Wall	
High UD	Low UD	High UD	Low UD
$p = 0.602$	$p = 0.242$	$p = 1.000$	$p = 0.838$

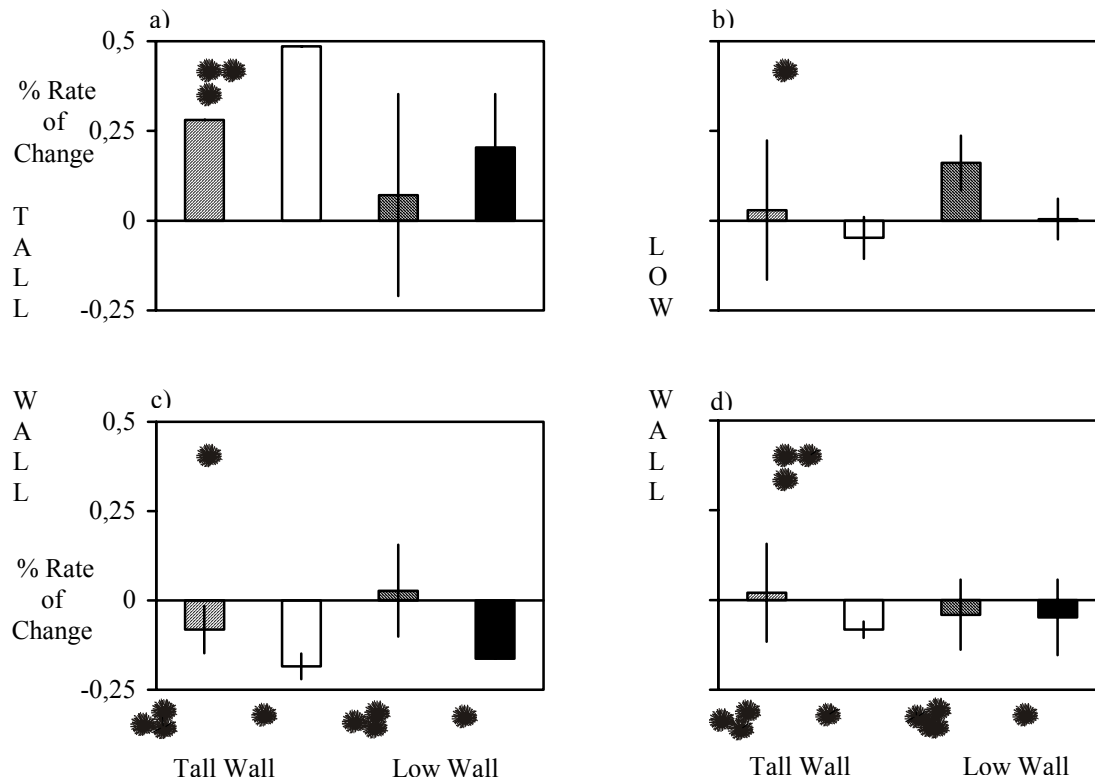


Fig. 3.23: Rate of change per day in per cent (mean \pm SE) of the assemblage (Bray-Curtis dissimilarity for every panel between original and present assemblage). Assemblages were transferred to tall and low walls with high and low sea urchin density. Assemblages originated on a) tall walls with high sea urchin density, b) low walls with low sea urchin density, c) tall walls with low sea urchin density, d) low walls with high sea urchin density. Further explanation see fig. 3.20.

Assemblages did not converge, when changed-over to the same habitat (Fig. 3.24). Only assemblages originating on low walls with high sea urchin density diverged from the original assemblage, when changed-over to different habitats (Fig. 3.25; U-test $p = 0.006$). The dissimilarity between assemblages remaining on low walls with high sea urchin density and assemblages that changed-over to another habitat increased 1.9 times from before change-over.

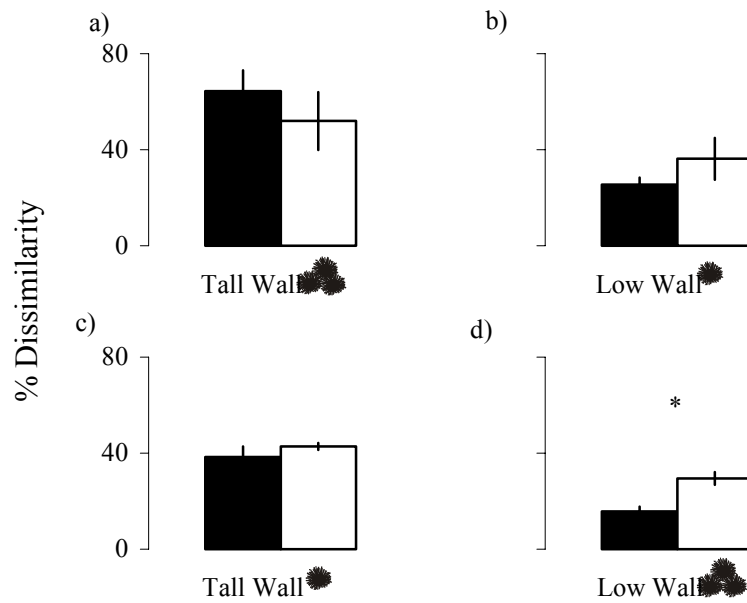


Fig. 3.24: Divergence of assemblages in percentage dissimilarity (Bray-Curtis, mean \pm SE) originating on a) tall walls with high sea urchin density, b) low walls with low sea urchin density, c) tall walls with low sea urchin density, d) low walls with high sea urchin density. Shown is the dissimilarity between assemblages before change-over (black column) and after change-over (white column). Dissimilarities were calculated between assemblages remaining in the habitat and assemblages that originated in the habitat, but changed-over to a different habitat. A star (*) indicates that dissimilarities of assemblages before and after change-over were significant different.

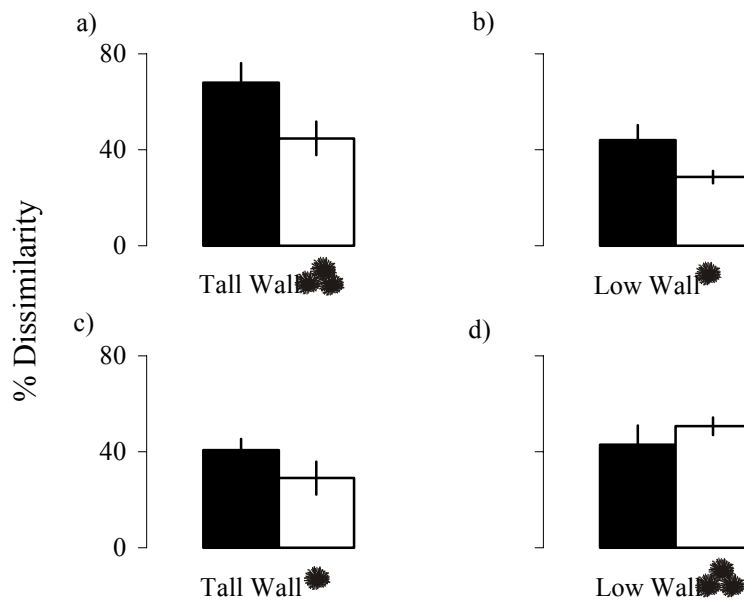


Fig. 3.25: Convergence of assemblages in percentage dissimilarity (Bray-Curtis, mean \pm SE) changed-over to a) tall walls with high sea urchin density, b) low walls with low sea urchin density, c) tall walls with low sea urchin density, d) low walls with high sea urchin density. Shown is the dissimilarity between assemblages before change-over (black column) and after change-over (white column). Dissimilarity was calculated between assemblages remaining in the habitat and assemblages that changed-over to the habitat. Dissimilarities of assemblages before and after change-over were not significant different.

4. Discussion

In this study, I investigated the processes that may have caused the differences in the structure of subtidal benthic assemblages on tall and low walls on a Rocky Reef in Eastern Australia. I described the structure and dynamic on tall and low walls by testing for differences between tall and low walls. I tested for differences in recruitment structure due to factors characteristic for a specific wall height and different sea urchin density and looked for differences in water motion on tall and low walls that may cause differences in larval and spore dispersal, settlement and feeding conditions. I assessed the differences in structure and dynamic of the assemblage in development caused by factors characteristic for a specific wall type and by different sea urchin density. Lastly, I tested for carry-over effects of the original habitat after change-over on assemblage structure, and if changes in the structure and dynamics of the assemblage are due to habitat effects after change-over and divergence and convergence of assemblages.

In this general discussion, I first recount the results and their interpretation. Then, I elucidate the importance of the sea urchin *Centrostephanus rodgersii* for the assemblage and what factors possibly determine its density and grazing performance. Next, I follow the development of assemblages on tall and low walls explaining how two alternative assemblages may develop.

The structure of the established assemblages on tall and low walls was very much affected by factors that are characteristic for a specific wall height. Low walls had reduced species numbers and diversity compared to tall walls. Total cover was only slightly reduced on low than on tall walls. Differences in the composition of the assemblage were primarily due to reduced abundances of the corallimorph *Corynactis australis*, the scleractine *Culicia* sp. and the colonial ascidian *Botrylloides leachi* as well as increased abundance of crustose coralline red algae on low compared to tall walls. The dominant grazer in the assemblage, the diadematid sea urchin *Centrostephanus rodgersii* was over four times more abundant on low than on tall walls. The rate of structural change on the walls was the same irrespective of height of wall. The composition of assemblages changed over time and the shorter the period between two sampling dates the higher the rate of structural change of the assemblage.

The one previous study that compared community structure of tall and low walls was done by Davis et al. (submitted). Their focus was to compare geographic differences in tall and low walls assemblages in the North Western Mediterranean, Spain, and South Western Pacific, New South Wales, Australia. One study site in Australia was Flinders Islet near Wollongong

(also my study site). They observed bigger colonies of invertebrates on tall than on low walls in Australia, also numbers of species were higher on tall walls. These findings correspond with my data showing that tall walls have a higher number of species than low walls. Low walls were dominated by crustose coralline algae in the study by Davis et al. (submitted) and my own. Correspondingly, I found no differences in total cover between tall and low walls, because in the absence of encrusting invertebrates crustose coralline algae occupied space on low walls and assemblages were assessed on photos inhibiting quantification of multi-layered growth. The sea urchin *Centrostephanus rodgersii* was more abundant on low than on tall walls in my study and Davis et al. (submitted) found higher biomass per square meter of the sea urchin on low compared to tall walls. They conclude that grazing may be the responsible factor for the differences in assemblage structure. Grazing by the sea urchin *Centrostephanus rodgersii* can create barrens on horizontal surfaces of Rocky Reefs in South Eastern Australia (e.g. Fletcher, 1987), but if the differences in sea urchin densities on vertical surfaces lead to different grazing pressure was not investigated by Davis et al. (submitted). The differences may not exclusively due to sea urchin grazing. Smith and Witman (1999), for example, demonstrated for the walls in a New Zealand fjord that differences in species diversity are not related to differences in sea urchin grazing, but are due to larval supply.

Structural change in time of the assemblage was smaller, when the investigation period was longer (twenty and twenty-two months, respectively), whereas assemblages changed ten times faster in the two months investigation period. The small rate of structural change over a long time period corresponds with studies by Sebens (1986) and Vance (1988), who both found for tall walls in the USA that they were occupied by the same set of species changing only relative frequency over several years. In my study, the rate of structural change was much greater, when the investigated time period was smaller. This may be due to fluctuations around an average rate of change that the assemblage structure nears the longer the period between two points in time.

Differences in water motion between tall and low walls may be responsible for differences in assemblage structure. However, the differences I found in water motion were so small that their relevance for the differences in assemblage structure is doubtful, but there may be differences in hydrodynamics on another level than measured by me (see below). Encrusting or massive growth forms as I found in my investigation, especially on tall walls, like sponges (e.g. *Pronax* sp., *Ircinia* sp.) and ascidians (e.g. *Herdmania momus*, *Botrylloides leachi*) are typical for strong or turbulent flows in Ireland, being more robust (Bell and Barnes, 2000). Passive filter-feeders like *Corynactis australis* may only survive in areas exposed to strong

water movement that allows sufficient feeding. The high abundance or exclusive presence of these species on tall in comparison to low walls may suggest that there are different hydrodynamic conditions at tall and low walls at my study site.

Recruitment on the walls was sometimes affected by factors that are characteristic for a specific wall height. On tall walls, recruitment covers then less area, is richer in species and more diverse than on low walls. Composition of the recruited assemblages was at times different on tall and low walls. The differences are mainly explained by diatom species 1, 2 and 4 and hydrozoan species 2. The effect of sea urchin density was even less often. High sea urchin density then results in decreased total cover of recruitment on the walls, numbers of species and diversity compared to low sea urchin density. There was once a habitat effect, when more species recruited on tall walls with high or low sea urchin density and on low walls with low sea urchin density than on low walls with high sea urchin density. Other interactions were not biologically relevant due to very small differences.

Generally, the same species recruiting on the panels were present on the walls, only dominances shifted. The established assemblage on tall walls consists predominantly of sponges, ascidians and cnidarians, whereas on low walls coralline algae dominate. On the recruitment panels, early successional species dominated, like diatoms, crustose coralline algae, hydroids, polychaetes and bryozoans, while sponge and ascidian recruits were extremely rare. The discrepancy is to be expected, since panels are new substrata. These early successional species can be found on walls also, but they may be poor competitors against species like sponges and ascidians (Kay and Keough, 1981), and therefore have either disappeared from the walls or can be found at newly disturbed sites, where succession was pushed again to an early stage. Diatoms are successful as new settlers since they are generally abundant in the plankton and settle passively on new substratum. They outcompete other new settlers, until the diatoms are overgrown or destroyed. In the invertebrate group, spirorbids especially may be extremely fit to colonize new substrata. When released from the adult, larvae are ready to settle and it takes less than ten days after settlement before first embryos are incubated (Vine and Bailey-Brock, 1984). Another thriving early colonizer is the bryozoan *Tubulipora* spp., whose larval life may be limited to minutes or seconds (Duggins et al., 1990). Hydroids of the family Campanulariidae are dominant early colonizers worldwide (e.g. Brault and Bourget, 1985). The group was important for the dissimilarity of assemblages being more abundant on tall than on low walls maybe due to unequal distribution of larvae. Crustose coralline red algae are early colonizers and are dominant in the assemblage on low walls, but they are not really important for differences in recruited assemblages, neither due to

factors characteristic for a specific wall height or sea urchin density. Their spores may be abundant in the plankton and the algae recruit uniformly on tall and low walls.

Effects of factors characteristic for a specific wall height on recruitment were not investigated in previous studies. Tall walls may be characterised by high diversity in recruitment. Smith and Witman (1999) reported high diversity of recruited species like the bryozoan *Tubulipora* sp., hydrozoans, serpulids and spirorbids recruiting on panels at a New Zealand fjord wall during a three-months study. The high diversity in recruitment was associated with areas of high species diversity. This corresponds with my study, where diversity of recruitment was higher on tall than on low walls, when there were differences. Established assemblages on tall walls are highly diverse compared to assemblages on low walls. High diversity areas in my study are therefore characterised by higher diversity in recruitment than low diversity areas. A reason for this may be a tight connection of wall specific larval pool with the specific larval output of the assemblage through weakly dispersing larvae (Graham and Sebens, 1996) as Ayre et al. (1997) showed for the local colonial ascidian *Botrylloides magnicoecum* near the study site.

These coherences may be important for recruitment into assemblages and therefore on panels also, since the panels are attached into assemblages, but do not explain differences in recruitment on tall and low walls irrespective of already established assemblages. A probably very important, if simple, explanation may be that tall walls have a greater settling surface than low walls due to extension in height. Greater settling surface should increase the probability of larvae meeting a surface to settle (Keough, 1983). More settling larvae may mean also a higher number of species and species diversity. Recruitment diversity may therefore be higher on tall than low walls. Rarer species may experience a strong reduction in recruiting numbers on low walls in comparison to tall walls or may miss the substratum completely.

Differences in recruitment between tall and low walls could, contrary to expectations, not be explained by differences in water motion between tall and low walls. Water motion was only very slightly higher on tall than on low walls, even at springtide, when for parts of fjord walls in New Zealand differences in water motion were found (F. Smith, personal communication); if these slight differences in water motion found by me are biologically important is unknown. The difference in water motion onto and along walls may or may not result in different larval pools by dispersing or aggregating larvae at walls, different settlement conditions in the passive phase for the larva by facilitating or inhibiting settlement or different feeding conditions, and thereby causing differing recruitment on tall and low

walls. The differences in flow may have been more pronounced, when measured only during the period of tidal change or during a storm event, which was unfortunately not possible, while a feasible increase in replication may not have led to significant differences (power-calculation).

In my experiments, total cover of recruits was once higher on low than on tall walls. Responsible for the difference is the diatom species 2. This diatom species may be more sensitive to light differences than other diatom species and may settle therefore preferably on low walls. On low walls, it may be that more light reaches the vertical surfaces of the walls, since a kelp canopy that is present on top of some parts of tall walls, is here absent (own observation). Unfortunately, it was not possible to measure radiation at the walls during this study, therefore this remains hypothetical.

Sea urchin density manipulations on tall and low walls showed that low sea urchin density can lead to an increase in total cover, species numbers and diversity of recruitment. Breitburg (1986) compared recruitment on ungrazed and grazed rocks. Grazing of the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* lowered abundances of recruiting species compared to recruitment on ungrazed rocks. Some species, like the polychaete *Vermeliopsis biformis* and the bryozoan *Cauloramphus spiniferum* even were excluded from recruiting by grazing. In the Caribbean, decreased densities of the sea urchin *Diadema antillarum* increased cover of algae, but also increased coral recruitment and diversity (Sammarco, 1980). As in my study, in both studies high densities of sea urchin reduced numbers of species and total cover of recruits. In some systems, density of sea urchins may not be important for recruitment patterns. In a New Zealand fjord, sea urchin density is not connected to diversity of recruits (Smith and Witman, 1999).

During development of the assemblages, differences between tall and low walls and high and low sea urchin density were quite small, but showed the same pattern as in the recruitment experiment and established assemblage. Numbers of species and diversity tended to be higher on tall than on low walls. Further, total cover and diversity tended to increase, when sea urchin density was low than when it was high. Composition of the assemblages during succession on tall and low walls were different, primarily due to the corallimorph *Corynactis australis*, the red algae *Ceramium* spp. and the bryozoan *Rhynchozoon* sp. being more abundant on tall walls and the bryozoan *Tubulipora* species 1 being more abundant on low walls. Rate of structural change was neither different on tall or low walls or when sea urchin density was high or low.

A major reason for the difference in assemblage composition may be that there were already differences between recruited assemblages on tall and low walls. These differences created in early succession (recruitment experiment) may have extended in time, but the species (mainly diatoms) having produced these differences in the early developing assemblage are now two years further in succession less important for differences. The major species causing differences in assemblage composition between tall and low walls had changed. The corallimorphan *Corynactis australis* was absent in the early assemblage. The red algae *Ceramium* spp. were already more abundant on tall walls in the early assemblage, but showed very low dissimilarity between wall habitats. The bryozoan *Tubulipora* species 1 was present, but not important for differences in the early assemblage. The bryozoan *Rhynchozoon* sp. was absent in the early assemblage. This shift in importance of species within the community indicates that early succession may have ended and the development is now after two years in another successional phase. Despite progressing succession, differences in composition of the assemblage still continue to exist. Growth into the developing assemblage (the panel) from the surrounding area by colonial species plays an important role for the differences in succession between tall and low walls. Contrary to solitary species, that invade new space via larvae, colonial species have more extensive facilities to invade (sexual, asexual, buds, fragments), especially via vegetative extension (Connell and Keough, 1985). Kay and Keough (1981) found that in cleared patches on pier pilings in South Australia 75 % of space invasion after twelve months happened by vegetative growth from the surrounding area. In their study, they demonstrated that sponges invaded almost exclusively via vegetative growth, whereas early colonists like bryozoans invaded via larvae, ascidians on the other hand used both methods. In my study, panels with developing assemblages on them were surrounded by the resident assemblage of tall and low walls. As I described for established assemblages on tall walls, they are very diverse with various colonial organisms, like sponges, ascidians and cnidarians. These species can invade the panel assemblages vegetatively and I found that all the sponge species had invaded from the surrounding area by growth. This was also true for the scleractinian *Culicia* sp.. On the other hand, the corallimorphan *Corynactis australis* invaded certainly from the surrounding area, but it is questionable, if it was by budding, more likely the species has crawling larvae that invade new space near the colony bit by bit, since individuals were not connected.

Sea urchin density and/or wall height (and therefore factors characterising a specific wall height) was changed during succession. Original habitats tall wall with high or low sea urchin density or low wall with high or low sea urchin density had no carry-over effect (effect of the

habitat before change-over, still persisting in the assemblage after change-over of habitat = formative effect) in total cover, number of species or diversity. The move of the assemblage affected total cover, number of species and diversity. This effect is probably a transfer effect of moving the panel or a wall effect in most cases. Only assemblages originating on tall walls with low sea urchin density decreased in total cover when habitat changed, whereas the in the habitat remaining assemblages increased in total cover. Assemblages originating at low walls with high sea urchin density diverged from assemblages remaining in the habitat, when habitat was changed.

When assemblages originating on tall walls with low sea urchin density change their habitat over to a habitat with high sea urchin density, total cover of the assemblage decreases. Figure 3.20 shows that when sea urchin density was high, total cover on tall walls was reduced by 10.75 (± 9.51) % cover and on low walls even by 15.75 (± 9.67) % cover, whereas when sea urchin density on low walls was low, total cover was less reduced, by 6.25 (± 0.00) % cover. This indicates that the negative effect of high sea urchin density on tall and low walls is stronger than the effect of low sea urchin density on low walls. The negative effect of high sea urchin density is due to higher grazing pressure on the assemblage than when sea urchin density is low. Sea urchins reduce total cover by grazing and bulldozing immediately after change-over from the tall wall - low sea urchin density habitat. In other studies similar effects of grazing on the assemblage were found, after grazers were introduced. Limpets reduced abundances and changed composition of algal and barnacle assemblages, when they were introduced into developing assemblages in the rocky intertidal in Oregon (Farrell, 1988). The toadfish *Opsanus tau* decreased numbers of species of developing assemblages in an estuary in Delaware, USA (Smedes and Hurd, 1981).

After change-over, only assemblages diverged that originated on low walls with high sea urchin density. This habitat is a naturally occurring habitat, and not manipulated. It may have a less strong carry-over effect (formative effect) than the other habitats, tall walls with high or low sea urchin density and low walls with low sea urchin density. The latter ones therefore might overshadow any effects caused by factors after change-over on the assemblage as indicated by a lack of divergence after these assemblages were transferred to different habitats. However, this is only true for immediately after change-over. It may be that a few months later these carry-over effects will not be detected anymore. Further sampling will be helpful here. So far, I can assume, that tall walls with low sea urchin density before change-over had the weakest carry-over effect on the assemblage. When this habitat type changes, succession may be re-directed. I conclude for this assemblage and in this successional phase,

the original habitat does not still shape total cover, number of species and diversity, after habitat changed. The lack of transfer of formative effects from the earlier assemblage to the later assemblage may indicate, that in rock wall assemblages in my study early colonizers are not important for later ones. However, formative effects that characterise a specific wall height and original sea urchin density, interactions of the original factor on total cover, number of species and diversity as well as formative effects on succession rate or composition of the assemblage cannot be excluded since they were not specifically analysed. Also, the fact that some assemblages did not diverge indicates that formative effects may be present, and therefore early colonizers may be important for the later assemblage after all.

I described in the previous part single processes and how they are influenced. In the following part, I demonstrate the complex ways by which the sea urchin *Centrostephanus rodgersii* may influence the structure of the community and by what sea urchin grazing may be determined.

Grazing by the sea urchin *Centrostephanus rodgersii* is an important community structuring factor, even when effects so far were less clear. The sea urchin is over four times more abundant on low than on tall walls. From this I draw the conclusion that high sea urchin abundance on low walls presumably means also high grazing intensity by the sea urchin on low walls, while low sea urchin abundance on high walls means low grazing intensity by the sea urchin. The two different sea urchin abundances developed due to the distinctive topographies of the walls. Low walls have a much higher number of crevices, fissures and ledges per area than tall walls (own observation, not quantified). These crevices serve as hiding places for the sea urchin during the day, since *Centrostephanus rodgersii* is a nocturnal forager to avoid predation (Fletcher, 1987; Andrew, 1993), especially from the Eastern Blue Groper *Achoerodus viridis* (Andrew, 1993; Gillanders, 1995; own observation). Less refuges from predation on tall walls therefore may mean higher predation on the sea urchins on tall walls and sea urchin density is reduced on tall walls. Moreover, less refuges may mean lower recruitment and immigration of sea urchins to the area, supported by Andrew (1993), who established that the availability of shelter is the cause for high sea urchin density in the barrens (horizontal surfaces) and therefore for the creation of the barrens habitat. Biological topography of the walls may be important, too. Low walls are dominated by crustose coralline red algae. Tall walls have a high cover of gelatinous or soft-bodied invertebrates like sponges, ascidians and cnidarians. The sea urchins can hardly attach themselves with their ambulacral feet to these biological surfaces on tall walls (Sebens, 1985; own observation). The calcareous surface on low walls on the other hand is not inhibiting attachment. Sea urchins on low walls

can forage almost everywhere, maybe exhibiting an activity radius of about 3 m as shown for horizontal surfaces (Fletcher, 1987), while sea urchins on tall walls are limited in their foraging to patches that are bare or covered by a calcareous organism, if they want a steady holdfast. The effect of biological topography may still be enhanced by water motion. I showed that water motion on tall walls tends to be slightly higher than on low walls. This little difference may be enough to break the hold of the sea urchin to the surface on tall walls more easily (Lissner, 1983; Sebens, 1985; Foster, 1987). The sea urchin may have to put more energy into holdfasting on tall walls than on low walls. When looking at bigger sized submarine canyons, so measured Cacchione et al. (1978) for the Hudson River submarine canyon only weak flows, but undercut bases of the walls indicate a down-canyon flow, that probably is only an episodic event. These episodic events can be so-called turbidity currents with very fast down-canyon flow caused by storms and high swell (Shepard and Marshall, 1978). Such events were never observed by me at the study site, but they cannot be excluded for causing higher flow on tall walls which often are part of canyons. An indication for a similar event at the study site may be the accumulation of coarse sediment and kelp fonds at the bases of tall walls after storms (own observation). I experienced from time to time very strong and deep easterly currents at the study site, which were not observed at the surface. They may have been caused by eddies originating from the East-Australian-Current-System and be connected with up- or down-welling events. However, I cannot explain how they can create differences in the flow field of tall and low walls.

Additionally to the limitation in refuges and activity radius and higher energy costs, suitable food for the sea urchin may be hard to reach on tall walls. Some species on walls are defended against grazing. Sponges at my study site are mechanical and/or chemical defended, like *Pronax* sp. and *Darwiniella australiensis*, both being abundant on tall walls (Wright et al., 1997; Fergusson, 2001). These sponges may even form escapes or grazing protected islands for other invertebrates which otherwise would be grazed on by sea urchins. An indication for refuge forming against sea urchin grazing at my study site is a similar situation that was found for the barnacle *Austrobalanus imperator* on low walls. This large barnacle is positively correlated with the total cover of invertebrates indicating that aggregations of the barnacle form a refuge for other invertebrates from grazing by the sea urchin (Davis and Ward, 1999). Crustose coralline red algae on low walls on the other hand offer a dominant, certainly feeding resistant (Ogden, 1976), but grazable substratum. Therefore, it is of benefit for the sea urchin to graze on low walls and this may increase sea urchin abundances there further. However, even when sea urchin densities would be the same on tall and low walls,

grazing intensities may not be. Even when sea urchin density is increased on tall walls (recruitment, immigration) to the density level of low walls, activity radius on tall walls may be still lower, lowering grazing intensity compared to the same sea urchin density on low walls, where grazing is almost unhindered. On the other hand, when sea urchin density is less than normal on low walls, grazing impact may still be greater than low sea urchin density on tall walls due to the bigger activity radius. Therefore, despite sea urchin density manipulations in my experiments, intensity of grazing may not have been determined by density but by the habitat type, tall or low wall, and effects subscribed to tall and low walls are actually artefacts (?) of sea urchin grazing intensity. Important when looking at this particular sea urchin species is also the inconsistency of effects, I observed. Grazing is sometimes important for the structure of the assemblage and sometimes not. This may be due to tall and low wall effects being actually indirect grazing effects, or more likely is that sampled areas were not always visited by sea urchins indicating patchiness of grazed areas in the habitats. This was also observed for stronglylocentrotid sea urchins (e.g. Breitburg, 1984).

In the following, I model how the single processes and effects fit together to explain how two different assemblages may develop on tall and low rock walls.

After space opens up on a tall wall and on a low wall, larvae will start to settle from the larval pool. The larval pool at tall walls may be different from the larval pool on low walls, mainly due to the species occupying the habitats. These habitats may control the structure of the assemblages that develop and may be even self-perpetuating: on tall walls, the dominant species, sponges, ascidians and cnidarians, may have only weakly dispersing, lecithotrophic larvae (Sebens, 1983; Haedrich and Gagnon, 1991; Todd, 1998; Osman and Whitlatch, 1998; Smith and Witman, 1999; for the local habitat see Ayre et al., 1997). Even having a long-living planktonic larval stage is no indication for far reaching dispersal (Keough, 1988). Graham and Sebens (1996) described a horizontal pattern of larval distribution away from vertical rock walls. They reckon that larvae that are ready to settle accumulate at invertebrate covered surfaces, since they found more larvae near invertebrate covered surfaces than near crustose coralline red algae covered ones. In high flow, larvae are better mixed and are found nearer at the wall than in low flow. The probability that a larva released at one wall reaches another may be very small. Therefore, the probability to get high diversity recruitment in a high diversity area and low diversity recruitment in a low diversity area may be high. Biological heterogeneity, as I found in form of high diversity on tall walls, may create eddies on the leeside of the sessile organism and entrap larvae passively (Eckman, 1990; Mullineaux and Butman, 1990; Miron et al., 1996; Walters et al., 1997; Wright and Boxshall, 1999),

increasing recruitment on tall compared to low walls. Assemblages on tall and low walls may attract or deter new settlers due to chemical cues. Attraction of recruits to other species or conspecifics is found in many species (e.g. Schmidt, 1982; Keough, 1983; Sebens, 1983; Stocker and Bergquist, 1987; Havenhand and Svane, 1989; Svane and Young, 1989; Davis and Campbell, 1996; Miron et al., 1996; Wright and Boxshall, 1999) and may be even to multispecies aggregations (Svane and Young, 1989; Bingham and Young, 1991; Osman and Whitlatch, 1995) as on tall walls. For recruitment on low walls, deterrence may be important in decreasing recruitment diversity. Low walls are dominated by crustose coralline algae. Algae of this group are often referred to as being deterrent to invertebrate larvae that want to settle (Sebens, 1983; Breitburg, 1984; Graham and Sebens, 1996; Degnan and Johnson, 1999) or avoid getting fouled by epithelial shedding (Keats et al., 1997). Breitburg (1984) showed in her recruitment study that serpulids and spirorbids and most bryozoans recruited less abundant on coralline covered rocks than on bare rocks. This resulted in less total cover on coralline covered surfaces. In another example, the ascidian *Herdmania curvata* has reduced settlement rates and metamorphosis when cultured with the crustose coralline red algae *Neogoniolithon brassica-florida*, *Hydrolithon onkodes* and *Lithothamnium prolifer* (Degnan and Johnson, 1999). The ascidian never settled on crustose coralline red algae, and larvae not having settled experienced general necrotic cell death. The few settled individuals near the algae were deformed. Crustose coralline red algae at the study site were never investigated concerning their deterrence to larvae, but may be deterrent to some new settlers, thereby reducing recruitment diversity, even on bare substrata nearby. This certainly needs further investigation.

Light conditions are an important settling cue for many larvae. Tall walls presumably are somewhat shaded by a canopy of the kelp *Ecklonia radiata* on top of these walls. Invertebrates like ascidians, spirorbids, cnidarians and barnacles prefer shaded habitats for settling (Crisp and Ritz, 1973; Young and Chia, 1984; Svane and Young, 1989; Svane and Dolmer, 1995; Saunders and Connell, 2000). Algae on the other hand need light for photosynthesis and therefore avoid shaded habitats as shown by me for the diatom species 2.

Grazing by the sea urchin *Centrostephanus rodgersii* may enhance the differences created through larval pool and attraction and deterrence further. Since grazing intensity is much higher on low walls, more species get grazed on, dislodged or mechanically damaged while the sea urchin crawls through, on low than on tall walls. Numbers of species and diversity is further reduced on low compared to tall walls where grazing intensity is much less. Recruiting species on low walls may have to be typical early colonizers that grow fast to maturity and

reproduce or form a calcareous skeleton to avoid grazing. Settling soft-bodied species like sponges, ascidians or cnidarians get removed immediately in this early phase of assemblage development without any grazing refuges. In early succession, recruiting species were typical early colonists like diatoms, bryozoans, hydroids, serpulids and spirorbids (Kay and Keough, 1980; Vine and Bailey-Brock, 1984; Brault and Bourget, 1985; Duggins et al., 1990) on low as well as on tall walls. However, assemblages are different possibly causing different species to recruit in further succession by facilitation, inhibition and tolerance (Connell and Slatyer, 1977).

After about two years in succession, assemblages on tall and low walls have arrived at a point, where crustose coralline red algae dominate in both habitats, maybe inhibiting later colonists (Connell and Slatyer, 1977). Assemblages are still different on tall and low walls, while having the same succession rates. Coralline red algae are less abundant on tall than on low walls, therefore maybe inhibiting less species there. On tall walls, species from the surrounding area, like the corallimorphan *Corynactis australis*, start now to invade the disturbed area. These species are mainly colonial or social living species. If colonial species invade not as larvae but as adults, they may be better competitors than crustose coralline red algae, whose competitive superiority is limited to larvae and new settlers (Breitburg, 1984). With time, crustose coralline red algae may therefore lose their competitive superiority gained through larval inhibition and fast growth on tall walls, where compound species are abundant. The ranking in importance of species has changed after two years succession and this points to a new successional phase. With more and more colonists that influence later colonists, more and more pathways open up for succession (Breitburg, 1985). Assemblages on low walls are still dominated by earlier colonists. For example, the early bryozoan *Tubulipora* species 1 was more abundant on low walls, while the later settling bryozoan *Rhynchozoon* sp. was more abundant on tall walls. Influencing factors that possibly differ on tall and low walls indicated for early succession, like larval pool, water motion, light conditions and grazing intensity of sea urchins, are still valid, but have less strong effects. This may be due to the strong inhibitory effect on new settlers by crustose coralline red algae that may be not affected by these factors and overshadow their effects. With time, on tall walls disturbed areas may be more and more invaded by surrounding species driving out crustose coralline red algae. Now, even recruitment of later colonists may be facilitated (Connell and Slatyer, 1977) by the compound species through attraction mechanisms and hydrodynamics. On low walls on the other hand, space invaders via vegetative growth only rarely surround the disturbed area, thereby decreasing the probability of the establishment of

colonial species. Crustose coralline red algae more and more further their dominance supported by the high grazing intensity of the sea urchins (Breitburg, 1984; Fletcher, 1987; Andrew and Underwood, 1993) that remove any recruits that settled despite inhibition. However, the benefits are mutual: inhibition of other recruits by crustose coralline red algae allows the sea urchin to keep its preferred feeding ground without limitation by soft-bodied invertebrates that impend movement and holdfast. Over time, some other species, like barnacles or grazing protected sponges, than crustose coralline red algae may get established since the grazing impact of sea urchins is variable (see above). However, this may only happen very rarely and in isolated patches (Davis and Ward, 1999).

In conclusion (Fig. 4.1), two possibly self-perpetuating assemblages develop, one on tall and one on low walls. Each assemblage has its own specific larval pool and therefore recruitment. The recruitment is further influenced by the wall specific sea urchin grazing intensity that also affects the developing and established assemblage. The wall specific sea urchin grazing intensity is determined by physical (refuges) and biological topography (established assemblage). Two different assemblages can persist in neighbouring areas. These two assemblages represent two alternative states (Lewontin, 1969; Sutherland, 1974) determined by their history and feedback mechanisms. It is clear from observations of the last ten years (personal communication A. Davis, D. Ward; own observation) that especially tall wall assemblages change only very minimal and almost invisible. This certainly does not

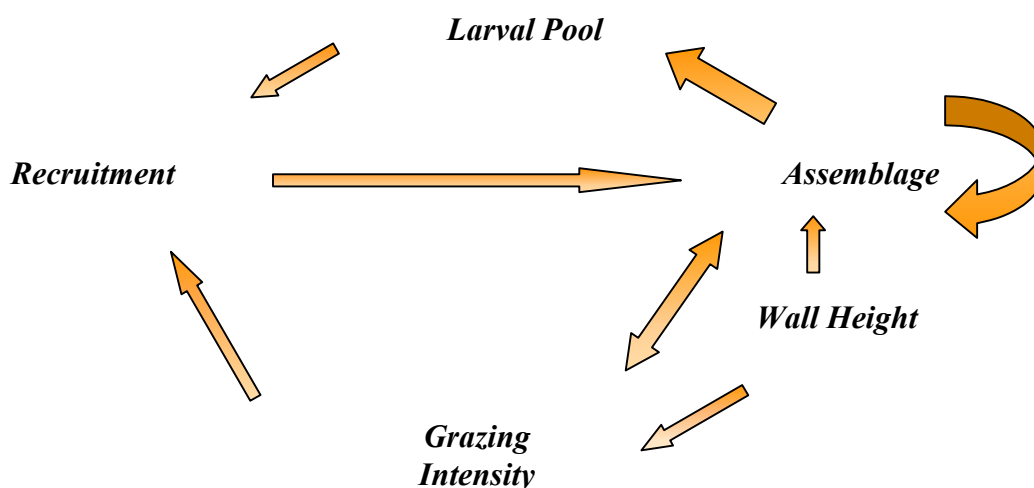


Fig. 4.1: Model of mechanisms and processes influencing assemblages on tall and low walls and leading to the development of two alternative assemblages. Each assemblage has its own specific larval pool and therefore recruitment. The recruitment is further influenced by the wall specific sea urchin grazing intensity that also affects the developing and established assemblage. The wall specific sea urchin grazing intensity is determined by physical (refuges) and biological topography (established assemblage). Further explanation see text.

allow me to make any statements about the long-time maintenance or stability of these states since I did not follow the assemblages for one generation (Sutherland, 1974). My findings point to self-perpetuation of these states, that are only possible in the particular habitat determined by wall height in this case, that cannot be easily changed (see above). Therefore, I assume the assemblages on tall and low walls are stable in the sense of stochastically narrow boundedness (Connell and Sousa, 1983; Kay and Butler, 1983; Keough and Butler, 1983; Crowley, 1992; Bingham and Young, 1995). However, there are differences in stability of these habitats. If during development of the assemblage the typical assemblage on a low wall would be suddenly under influences typical for an assemblage on a tall wall, the assemblage would switch immediately to an alternative state. For the switch, a decrease in sea urchin density is not enough; grazing intensity has to be lower. Since I did not follow the assemblage succession to an endpoint, I cannot safely say this assemblage would be the same as an assemblage always under the influence of these typical tall wall factors. I cannot exclude carry-over effects, or formative effects, that change the end result, and since carry-over effects for these two assemblages are presumably different, I cannot compare them at this stage. However, I can say that the assemblage switched to a different state from the original one. This fast switch of assemblages only on low walls may point to a hierarchy of stability states. Low wall assemblages are less stable than tall wall assemblages. It may be that in the long run the little invertebrate islands on low walls extend their area more and more since the sea urchin cannot graze on them and they overgrow the crustose coralline red algae, and so a different assemblage develops that is more diverse and pushes the barren state dominated by crustose coralline red algae into the background on the walls.

In this last part, I compare diversity in the different habitats and for different successional stages of the assemblages and compare my findings with the model by Menge and Sutherland (1987). Diversity in the established assemblage is highest on tall walls with low sea urchin density and lowest on low walls with high sea urchin density. This variation of diversity with predation and environmental factors is demonstrated in the experiments of recruitment and development. For both, older succession and recruitment, diversity was usually lowest when sea urchin density is high on low walls. Diversity is on a slightly higher level when sea urchin density is decreased or wall height is increased. Diversity is highest when sea urchin density is low on tall walls. This shows how with the decrease of the environment hostile to grazing and the increase of the density of the grazer, diversity decreases since the frequency and intensity of disturbances increases to a high level. With the increase of grazing hostile environment and the decrease in grazer density, diversity increases since frequency and

intensity of disturbances are at a lower level. I characterize the environment as moderate. Storms and swell usually originate in the south or southeast, therefore the study site is somewhat protected from the full force. Only in winter, storms may originate in southwest. In summer, when there is a cyclone in the north, swell may come from north to north easterly directions, thereby fully impacting on the study site, but this is rather rare. Recruitment at the study site is generally low (see recruitment experiment). The Menge and Sutherland model (1987) predicts for this case that diversity of sessile assemblages are equally influenced by environmental factors and predation. Competition between the sessile species is not important due to the low recruitment. As I showed above, established assemblages on tall and low walls are affected by wall height as environmental factor and sea urchin grazing. What distinguishes diversity on the walls may not be environmental stress working on the sessile assemblage, but the environment affecting sea urchins. As described above, grazing intensity is higher on low than on tall walls due to biological and geological topography. The more hostile the environment for the sea urchin, the less the assemblage gets disturbed and diversity is higher. On the other hand, the less hostile the environment for the sea urchin, the more the assemblage gets disturbed, diversity is lower. Environmental stress stays the same for the sessile assemblage irrespective of grazing level. However, the different grazing levels are explained by different environmental stress levels for the sea urchin.

I answered the central question of this study, why assemblages are different on vertical surfaces with different height at the Rocky Reef at Flinders Islet in the Western Tasman Sea, as far as it was possible by the experimental design and I improved the understanding of interactions in this particular Rocky Reef community. This may assist to explain similar patterns at Rocky Reefs in general, and set thinking to further research. It may help to protect this unique ecosystem with its high level of species diversity and value as nursery for fish and other species.

5. References

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Table A: Species present in the twelve recruitment experiments on tall and low walls with high and low sea urchin density. High UD = high sea urchin density; low UD = low sea urchin density. A plus (+) indicates the presence of the species.

	LOW WALL		TALL WALL	
	HIGH UD	LOW UD	HIGH UD	LOW UD
foraminifera	+	+	+	+
ciliata	+	+	+	+
diatoms				
diatom sp. 1	+	+	+	+
diatom sp. 2	+	+	+	+
diatom sp. 3	+	+	+	+
diatom sp. 4	+	+	+	+
diatom sp. 5	+			+
diatom sp. 6			+	
diatom sp. 7			+	
algae				
crustose coralline red algae	+	+	+	+
<i>Ceramium</i> spp.	+	+	+	+
rhodophyta sp. 3	+	+	+	+
rhodophyta sp. 4			+	+
rhodophyta sp. 5			+	+
rhodophyta sp. 6	+			
chlorophyta sp. 1	+	+	+	+
chlorophyta sp. 2	+	+	+	+
phaeophyta sp.1	+	+	+	+
phaeophyta sp.2	+	+	+	+
phaeophyta sp.3	+			
porifera				
porifera sp. 1		+	+	+
porifera sp. 2		+	+	+
cnidaria				
Fam. Campanulariidae				
<i>Stereotheca elongata</i>				+
hydroidea sp. 2	+	+	+	+
hydroidea sp. 3			+	+
hydroidea sp. 4				+
Fam. Campanulinidae				
<i>Aequorea aequorea</i>				+
Class Anthozoa				
<i>Corynactis australis</i>			+	
<i>Anthothoe albocincta</i>	+		+	
polychaeta				
<i>Pomatostegus</i> sp.	+	+	+	+
<i>Pileolaria lateralis</i>	+	+	+	+
<i>Hydroides elegans</i>	+	+	+	+
<i>Spirobranchus</i> sp.				+

	TALL WALL		LOW WALL	
	HIGH UD	LOW UD	HIGH UD	LOW UD
<i>Filograna implexa</i>				+
<i>Janua steurii</i>	+	+	+	
mollusca				
<i>Crassostrea commercialis</i>	+		+	+
mussels	+		+	+
cirripedia				
<i>Balanus trigonus</i>	+	+	+	+
<i>Austrobalanus imperator</i>	+	+	+	+
bryozoa				
<i>Tubulipora</i> sp. 1	+	+	+	+
<i>Tubulipora</i> sp. 2				+
<i>Lichenopera</i> sp.	+	+	+	+
<i>Conopeum tenuissimum</i>				+
<i>Baenia</i> sp.	+		+	
bryozoa sp. 6	+	+	+	+
bryozoa sp. 7			+	+
bryozoa sp. 8			+	
bryozoa sp. 9	+		+	
bryozoa sp. 10			+	+
bryozoa sp. 11				+
bryozoa sp. 12	+		+	
ascidia				
<i>Botrylloides leachi</i>	+	+	+	
ascidia sp. 2	+	+	+	+
misc				
misc 1	+	+	+	+
misc 2	+			+
misc 3				+
misc 4	+		+	+

Table B: Species present in developing assemblages on panels on tall and low walls with high and low sea urchin density in February and May 2002. High UD = high sea urchin density; low UD = low sea urchin density. A plus (+) indicates the presence of the species.

	LOW WALL		TALL WALL	
	HIGH UD	LOW UD	HIGH UD	LOW UD
diatoms				
diatom sp. 1	+	+	+	+
diatom sp. 2	+	+	+	+
algae				
crustose coralline red algae	+	+	+	+
<i>Ceramium</i> spp.	+	+	+	+
unidentified Chlorophyta	+	+		
porifera				
<i>Darwiniella australiensis</i>			+	
<i>Pronax</i> sp.			+	
porifera sp. 3(Mustard)			+	
cnidaria				
hydroids			+	+
<i>Corynactis australis</i>				+
<i>Culicia</i> sp.	+		+	
polychaeta				
<i>Pileolaria lateralis</i>		+		+
cirripedia				
<i>Balanus trigonus</i>	+	+		
bryozoa				
<i>Tubulipora</i> sp. 1	+	+	+	+
<i>Rhynchozoan</i> sp.	+	+	+	+
mobile species				
limpets	+			+

Table C: Species present in developing assemblages on panels on tall (TW) and low walls (LW) with high (HD) and low sea urchin density (LD) after change of treatment. A plus (+) indicates the presence of the species.

<i>Origin</i>	LW								TW							
	HD				LD				HD				LD			
	LW		TW		LW		TW		LW		TW		LW		TW	
<i>Residence</i>	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD
diatoms																
diatom sp. 1	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+
diatom sp. 2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
algae																
crustose	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
coralline red algae																
<i>Ceramium</i> spp.	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+
unidentified	+				+											+
Chlorophyta																
porifera																
<i>Callyspongia</i> sp.																+
<i>Chondrilla australiensis</i>												+				
<i>Darwiniella australiensis</i>												+				
<i>Hymedesmia</i> sp.												+				
<i>Pronax</i> sp.						+		+		+	+	+				
porifera sp. 3				+	+					+						
porifera sp. 4					+								+			+
cnidaria																
hydroids				+		+		+		+	+	+	+			+
<i>Anthothoe albocincta</i>								+								
<i>Corynactis australis</i>										+	+			+	+	+
<i>Culicia</i> sp.	+									+	+	+		+		+
polychaeta																
<i>Pileolaria lateralis</i>	+	+	+	+	+	+	+				+		+	+	+	+
<i>Pomatostegus</i> sp.									+	+				+		
cirripedia																
<i>Austrobalanus imperator</i>											+					
<i>Balanus trigonus</i>						+		+								
bryozoa																
<i>Tubulipora</i> sp. 1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Rhynchozoon</i> sp.				+	+		+	+		+	+	+	+	+		+
mobile species																
limpets	+					+	+							+	+	

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ERKLÄRUNG

Die von mir vorgelegte Dissertation mit dem Titel

‘‘Factors influencing structure and dynamics of subtidal assemblages on walls at a South Eastern Australian Rocky Reef’’

wurde – abgesehen von der Beratung durch die Betreuer – nach Inhalt und Form von mir eigenständig angefertigt, ferner hat meine Arbeit weder ganz noch zum Teil bei einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen, noch ist sie veröffentlicht worden oder wurde sie zur Veröffentlichung eingereicht.

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