Quantifying biotic interactions with inshore subtidal structures: comparisons between artificial and natural reefs

Thesis

Quantifying biotic interactions with inshore subtidal structures: comparisons between artificial and natural reefs

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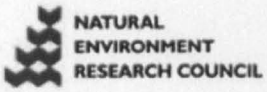

ABSTRACT

Artificial reefs have been deployed purposely worldwide to influence physical and biological processes around coastlines and in inshore waters; often to augment recreational diving and fishing, support environmental mitigation and habitat restoration and, more recently, for scientific research. The aims of this project were to develop standardised methods and protocols for use in artificial reef studies and to establish whether there were differences in the productivity and biotic interactions between artificial and nearby natural rocky reefs in Loch Linnhe, west coast of Scotland.

A comparative study was carried out to evaluate methods used in the assessment of subtidal epibiotic assemblage structure followed by a detailed study to compare epibiotic recruitment to artificial and natural reefs using PVC plastic recruitment panels. Predator exclusion cages were used to assess the effects of predation on epifaunal recruitment at different locations. Epifaunal biomass on concrete reef blocks and infaunal biomass in soft sediments surrounding the artificial reef complex was determined and an estimate made of relative productivity between the Loch Linnhe artificial reef modules and their receiving environment. Finally, the trophic dynamics of artificial and natural reefs were investigated through the use of stable isotope ratios.

These studies showed that post-settlement processes appear to be controlling differences in epifaunal recruitment to artificial and natural reefs in Loch Linnhe. Vertically orientated PVC recruitment panels, combined with galvanised wire mesh

predator exclusion cages, are recommended for use in comparative recruitment studies of subtidal artificial and natural reefs. It was also concluded that the Loch Linnhe artificial reef complex has increased the productivity to the local area and that the construction design of these artificial reefs would be a suitable option, with respect to the development of biological communities, for future artificial structures such as breakwaters.

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Chapter 1 General Introduction

1.1 Reefs

Reefs have been defined as "submarine, or exposed at low tide, rocky substrates and biogenic concretions, which arise from the seafloor in the sublittoral zone but may extend into the littoral zone where there is an uninterrupted zonation of plant and animal communities. These reefs generally support a zonation of benthic communities of algae and animal species including concretions, encrustations and corallogenic concretions" (Davies et al. 2001). Biogenic reefs are formed by the calcareous deposits of marine invertebrates such as corals and polychaetes. The best example of a biogenic reef is the Great Barrier Reef on the east coast of Australia; occupying an area of 345000 square kilometres it is the largest coral reef in the world and supports a highly diverse marine community. While reefs formed from biogenic concretions do exist around the UK coastline, in the form of the cold water coral reefs of *Lophelia pertusa* (Roberts 2002, Roberts et al. 2005) and shallow water serpulid reefs formed by *Serpula vermicularis* (Poloczanska et al. 2004), these are relatively uncommon. Biogenic reefs are also found in UK waters in the form of banks of horse mussel shells, *Modiolus modiolus* (Magorrian & Service 1998) and large aggregations of the polychaete *Sabellaria spinulosa* (Jones et al. 2000). However, the great majority of reef habitat in the UK, and indeed temperate latitudes as a whole, is in the form of rocky reefs. Formed by geological processes, these range from vertical rock walls to horizontal ledges, broken rock and boulder fields (Davies et al. 2001).

There are many reasons why subtidal reefs can support diverse biological

communities. The surface of a reef can provide a hard substratum suitable for the larvae and propagules of many epibiotic species to settle, mature and reproduce (Barnes & Hughes 1999). The habitat complexity offered by many reefs can provide mobile species with living space (Tait 1981), a means of escape from predators (Hixon & Beets 1993) and opportunity for nest building and the deposition of eggs (Moring & Nicholson 1994). The sessile and mobile reef-dwelling flora and fauna provide a readily available food source for many marine consumers (Johnson et al. 1994). Physical factors could also be important; reefs with high vertical relief can provide shelter from strong currents. Altered water currents around reefs can cause flocculation of plankton which is beneficial for suspension feeders (Bohnsack & Sutherland 1985), as well as localised effects on salinity and water temperature as the bottom waters are pushed up with currents moving over the obstruction (Lin & Su 1994). These cooler waters mix with the warmer waters above and this has been shown to attract gatherings of animals such as fish (Lin & Su 1994) perhaps in response to the flocculation of plankton resulting in increased food availability. All of these factors have been shown to contribute towards the success of natural reefs in supporting biologically diverse communities, and may also apply to artificial reefs (Bohnsack & Sutherland 1985).

1.2 Artificial reefs

An artificial reef is a "submerged structure place on the seabed deliberately to mimic some characteristics of natural reefs" (Jensen 1997). The primary goals of artificial reef deployments in coastal habitats have been to enhance the production of reef-associated species (such as macroalgae, invertebrates and fish), to alter spatial and temporal distribution patterns of target species and to increase the convenience or

efficiency of harvesting reef-associated species through the creation of new fishing sites (Moreno et al. 1994, Pratt 1994, Bohnsack et al. 1997, Relini & Relini 1997). Artificial reefs have also been used to influence physical processes around coastlines, in the form of breakwaters, and biological processes for environmental mitigation, habitat restoration, to protect an area from fishing effort and for recreational diving and fishing (Baine 2001).

1.2.1 Artificial reef design and construction materials

For centuries artisanal fishermen have used artificial structures to enhance catch rates. The first records of this are from Japan in the Kansei era (1789 – 1801). Following the realisation that fish aggregated around a sunken ship, which subsequently deteriorated to such an extent that the fish were no longer present in large numbers, local fishermen sunk large wooden frames mounted with sandbags, bamboo and wooden sticks to create their own artificial reefs close to their villages. Enhanced catches were noted around these structures leading to the construction of several hundred artificial reefs in the area (Ino 1974, Santos et al. 1997).

Purpose-built artificial reefs have been created in many shapes, sizes and materials. Traditionally artisanal reefs were built from low cost materials of opportunity (such as the example described above). More recently, materials of opportunity such as old vehicle tyres, washing machines, cars, aeroplanes, trains, and even warships have been used to create artificial reefs for recreational sport fishing and diving, particularly in the United States (Bohnsack & Sutherland 1985, Baine 2001).

Materials of opportunity provide an inexpensive substratum for the creation of

artificial reefs. Their use, however, has led to criticism that the deployment of reefs has been used as an excuse to legally dump waste materials in coastal environments which otherwise would be contrary to dumping regulations (Pickering & Whitmarsh 1996). This has not been helped by the poor management or planning in the construction of many artificial reefs and there are some striking examples in the literature. For example, two large artificial reefs made from tyres, bound together with polypropylene rope and tape, were constructed off the coast of Australia in the 1970s (Branden et al. 1994). Initially the reefs attracted, and retained, large numbers of fish and a diverse marine flora and fauna. However, within a few years both reefs were destroyed by storms which left thousands of loose tyres moving freely over the seabed (Branden et al. 1994). Another large tyre reef, consisting of between one and two million tyres, was constructed off the Florida coastline in the late 1960s (Sherman 2004). Again, since its deployment, storms and hurricanes have broken up the reef and by 2001 the tyres covered an area of 36 acres of seabed; double the initial size of the reef. The tyres continue to be transported across the seabed many tyres have also been washed up on shorelines. Hundreds of thousands of tyres have accumulated at natural reefs, damaging both the live corals and the coral reef habitat (Sherman 2004).

Artificial reefs are generally deployed in relatively shallow depths making them accessible to recreational divers and fishermen. It is, therefore, important that any structure placed on the seabed should have sufficient stability to withstand environmental processes such as storms, particularly when they are deployed on exposed coastlines.

Prime materials such as steel, concrete and fibreglass are rarely used in reef construction within Europe and America because of high purchasing costs. However, in countries such as Japan, Korea and Hong Kong, where the construction of artificial reefs has benefited from substantial governmental funding, these prime materials are frequently used (Pickering et al. 1998). Probably the greatest benefit in using these materials is that the reefs can be designed to be an appropriate size or shape depending on the purpose of the reef. For example, a reef deployed to prevent trawling in sensitive sea grass habitat could be designed to snag and rip trawl nets (e.g. Guillen et al. 1994).

1.2.2 Rigs to Reefs programme

The presence of oil and gas platforms has been shown to promote both epibiotic colonisation and macro-faunal attraction, thereby fulfilling some of the basic performance criteria of artificial reefs (Bull & Kendall Jr. 1994, Love et al. 1994, Sayer & Baine 2002). In the Gulf of Mexico, Southern USA, the red-snapper (*Lutjanus campechanus*) fishing industry appears to be benefiting from the presence of oil and gas platforms (Shipp 2005) and a large research programme is underway to investigate the relationship between these fish and these partly submerged structures. In 1986 the Louisiana Artificial Reef programme was created in response to the potential loss of productive habitat when platforms are removed as a result of the decommissioning process. The main objective of the programme was to take advantage of the fishing habitat opportunities offered by obsolete platforms (Shipp 2005). By 2004 there were 188 "reefed" platforms in the Gulf of Mexico representing about 8.4% of all decommissioned platforms (Shroeder & Love 2004).

The success of the "rigs to reefs" programme in the Gulf of Mexico has generated interest in adopting a similar policy in the North Sea (Sayer & Baine 2002). Currently OSPAR (Oslo Paris Convention) regulation 98/3, from the 1992 Convention for the Protection of the Marine Environment of the North East Atlantic, prohibits the disposal of offshore installations at sea (Anderson 2002, Sayer & Baine 2002). However, several commercially important fish species have been observed to associate with oil and gas platforms in the North Sea (Lokkeborg et al. 2002, Sayer & Baine 2002, Soldal et al. 2002) and the epibiotic colonisation of platform mooring structures and riser pipes includes species of conservation importance such as the cold water coral, *L. pertusa* (Roberts 2002, Gass & Roberts 2006). As a result, research has been carried out into the importance of these platforms in enhancing commercial fisheries in the North Sea.

Soldal et al. (2002) used hydroacoustic techniques to quantify the abundance of fish around platforms in the Ekofisk oil field and concluded that decommissioned platforms in the North Sea might be used effectively as artificial reefs. However, Cripps and Aabel (2002) carried out an environmental and socio-economic impact assessment and concluded that decommissioned platforms may be more useful when used to protect habitat or fisheries rather than used as part of a fisheries strategy. Sayer and Baine (2002) reviewed a number of studies and suggested that fish population estimates around platforms account for only a very small percentage of fish stocks in the North Sea (less than 1.3% for saithe (*Pollachius virens* (L.)) and less than 0.25% for cod (*Gadus morhua* (L.)) stocks).

Although the creation of artificial reefs from decommissioned platforms in the North

Sea may go some way toward protecting the numbers of fish currently recorded around active platforms, any positive benefit would have to be measured against the loss of fishery exclusion zones that would result at the cessation of extraction operations (Sayer & Baine 2002). The costs of decommissioning, combined with liability issues and differences in the receiving environment, suggests that a rigs to reefs programme in the North Sea is unlikely to occur on the same scale as that in the Gulf of Mexico, if at all.

1.3 Artificial reef research

Many European artificial reef programmes have been small (Wilding & Sayer 2002b), composed of small individual reefs or many small closely spaced units. However, Whitmarsh et al. (1995) predicted the minimum size of a commercial reef to support a viable lobster fishery in the UK would be 5000 tonnes. This is much larger than many experimental artificial reefs. The extrapolation of data from small to large (commercial scale) reefs may not be appropriate because of unforeseen scale effects (Wilding & Sayer 2002b); for example smaller reefs may not have the spatial scale required to identify processes regulating population size.

The majority of studies examining the effects of artificial reef construction in have also been relatively short term and have had little or no replication (i.e. in many studies just one reef has been examined, Grossman et al. 1997, Brickhill et al. 2005). Conclusions drawn from such investigations are, therefore, of limited scientific value. Many artificial reef studies have been descriptive or correlative but surprisingly few have been truly experimental (i.e. with controls, treatments, and replication) (Lindberg 1997, Brickhill et al. 2005). Lindberg (1997) suggested that

this may be a result of the fact that many reef experiments require co-operation from resource managers, reef builders and local anglers.

The great majority of man-made reefs in UK waters are in the form of breakwaters; built to alter the physical environment in order to protect coastlines from erosion and to provide shelter for ports and harbours. However, a few artificial reefs in the UK have been deployed for other purposes. The Torness artificial reef was constructed in 1984 from quarried rock derived from the construction of a nuclear power station (Jensen 1998). This reef has been the focus of some investigations into biological colonisation and both shellfish and fin-fishery potential. The first experimental artificial reef built in UK waters was constructed in 1989 in Poole Bay, Dorset, on the south coast of England. The reef was built primarily to assess the suitability of stabilized pulverised fuel ash (PFA) and flue gas desulphurization (FGD) gypsum combined with cement as a construction material for artificial reefs for fisheries enhancement purposes (Collins et al. 1994). The reef consists of a total of 50 tonnes of blocks (each block measuring 40 x 20 x 20cm) formed into eight conical units each 1m high by 4m diameter. The sinking of the *HMS Scylla* on the South Coast of England in March 2004 was the first deliberate sinking of a ship in UK waters to create a reef for recreational purposes. Currently this is the only permitted deliberate sinking of a vessel in UK waters for this purpose.

1.3.1 Loch Linnhe artificial reef complex

The Loch Linnhe artificial reef is a purpose-built experimental reef complex, designed to facilitate scientific research into the impacts and performance of a replicated suite of reef types, with the over-riding objectives of quantifying and

evaluating the economic potential for similar reefs deployed with target fisheries in mind (in this case the European Lobster, *Hommarus gammarus*; (Wilding & Sayer 2002a)). Construction of the reef complex started in August 2001 on the west coast of Scotland (grid reference 56°32 N 05°27 W; Figure 1.1) and it is expected that it will be completed by the end of 2006. The reef complex is sited in an area of silty sand overlain by cobbles and stones, in depths ranging from 10 to 30m (Wilding & Sayer 2002a). On completion the reef will comprise 42 reef modules made from up to 7000 tonnes of concrete blocks (Figure 1.2), and will cover an area of approximately 0.4km^2, making this one of the largest artificial reefs in Europe.

The reef blocks used in the construction of the Loch Linnhe reef complex are 21 x 21 x 42cm in size, and were made from granite dust mixed with low levels of cement and fly-ash, resulting in a substratum that has been shown to be both physically and chemically stable (Wilding & Sayer 2002b). Each discrete reef within the reef complex is termed a module. Half of the reef modules were constructed using simple reef blocks and half were constructed using complex reef blocks (Figure 1.3). The complex blocks have two voids in them to increase the potential structural complexity of the reef module. The blocks were manufactured by Foster Yeoman Ltd. at their Glensanda granite quarry situated on the Morvern peninsula, on the western shore of Loch Linnhe and were deployed onto the seabed using a crane from an anchored surface barge. Blocks were dropped onto a target buoy (Figure 1.4) and fell to the seabed where they randomly stacked to form conical reef modules approximately 3-4m high by 15-20m across with high structural complexity (Figures 1.5 and 1.6). A single deployment reef module consisted of approximately 4,500 reef blocks.

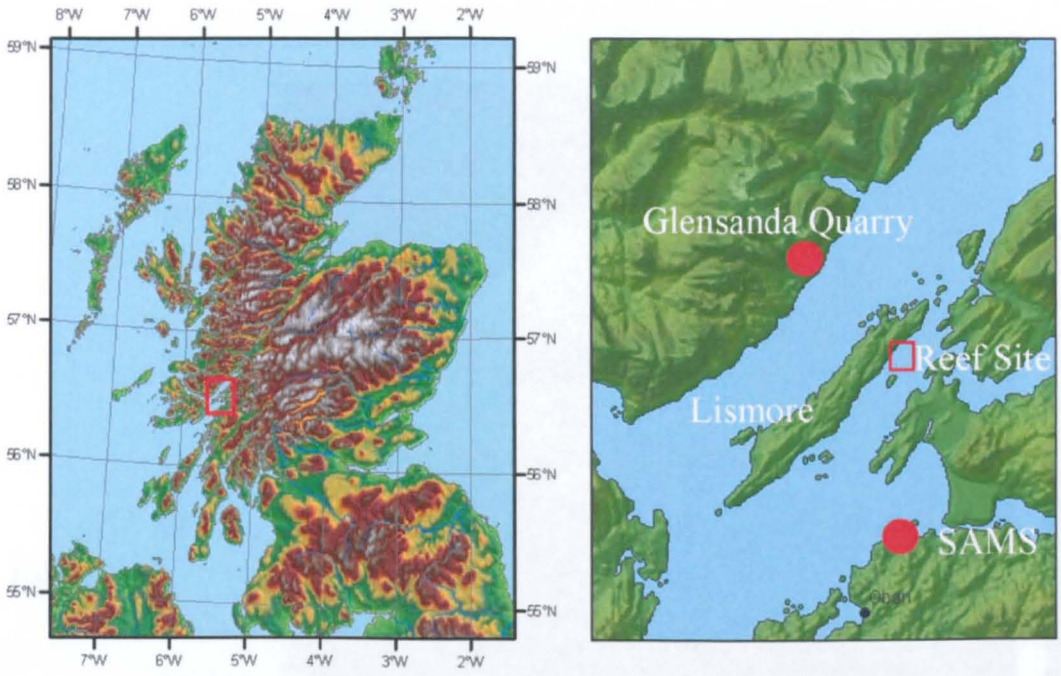

Figure 1.1 Location map of the Loch Linnhe artificial reef complex. The red box in Figure 1a shows the location and extent of the map shown in Figure 1b. The red box in Figure 1b shows the location and extent of the map shown in Figure 1.2.

The location for the Loch Linnhe artificial reef was selected for a variety of reasons. The site had to have shelter from the full force of storms, and the resulting swell from the Atlantic, and had to be readily accessible from both the Scottish Association for Marine Science laboratories in Dunbeg, near Oban, and Foster Yeoman's Glensanda Quarry on the Morvern Peninsular (see Figure 1.1). The reef also had to be sited in an area of soft sediment which was not part of an existing commercial fishery. Further requirements were that the artificial reef would be constructed in a range of depths, all within easy SCUBA range, with a range of sediment types and in a relatively high energy site in terms of tidal currents. The chosen site on the shores of Lismore Island in Loch Linnhe fulfilled all of these requirements.

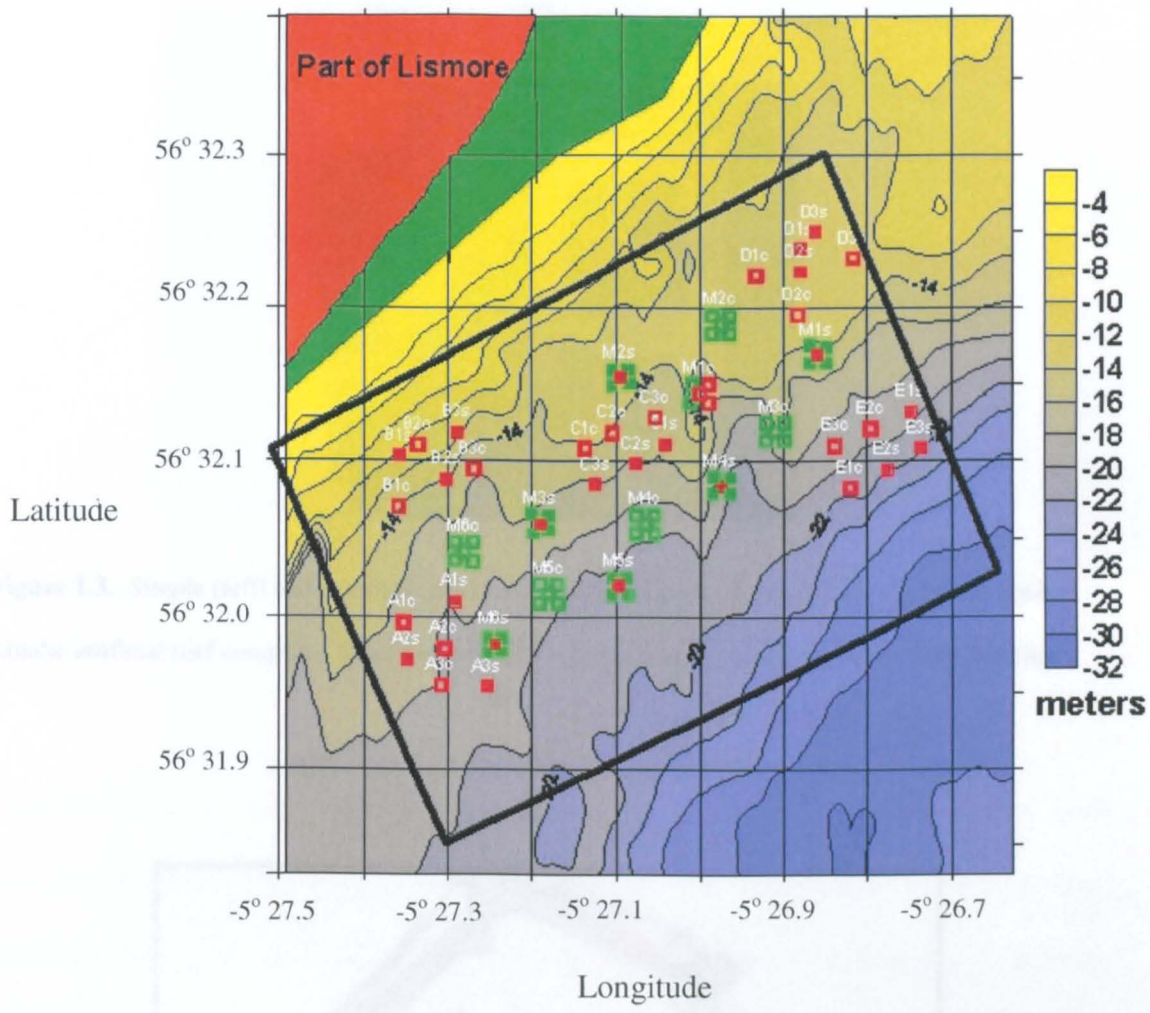

Figure 1.2 Layout of the Loch Linnhe artificial reef modules as of January 2006. Modules in red have been deployed. Modules in green are yet to be deployed. Complex reef modules are represented by "open" squares, and simple reef modules by "solid" squares. One square in the picture represents a single deployment of approximately 4,500 reef blocks.

Figure 1.3. Simple (left) and complex (right) reef blocks made at Glensanda quarry for the Loch Linnhe artificial reef complex. Blocks are 42 x 21 x 21cm. Image used courtesy of Tom Wilding.

Figure 1.4. Reef module deployment. Blocks are dropped onto a target buoy from a surface barge.

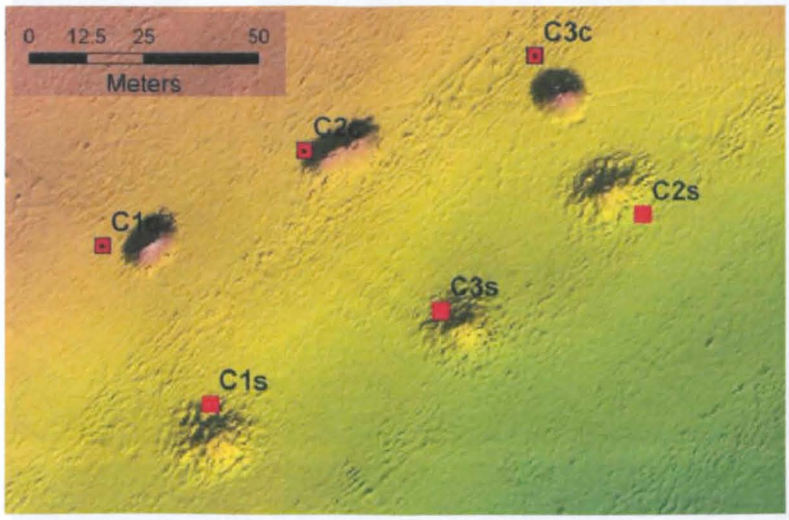

Figure 1.5. Multibeam sonar bathymetry images of a set of 6 reef modules. C1c, C2c and C3c are modules consisting of complex blocks, C1s, C2s and C3s are modules made from simple blocks.

Loch Linnhe is a large sea-loch used by the local community for a variety of both recreational and commercial activities. These include recreational SCUBA diving, fishing and sailing and commercial mussel farming (*Mytilus edulis* L.), salmon farming (*Salmo sala L.*) and creeling and trawling for prawns (*Nephrops norvegicus* L.) and crabs (*Cancer pagurus* L. and *Necora puber* L.). The natural rocky reefs in the area mostly consist of low relief bedrock with relatively low structural complexity and sustain seemingly high levels of grazing and predation by species such as the common starfish (*Asterias rubens* L.) and the edible urchin (*Echinus esculentus* L.) (*pers. obs.*). Kelp beds (*Laminaria saccharina* L. and *Laminaria digitata* L.) dominate the shallow subtidal reef habitat, the latter of which is a recognised indicator species for low energy or sheltered sites (Birkett et al. 1998).

a)

b)

Figure 1.6. Photographs of a complex reef module within the Loch Linnhe artificial reef complex, a) shortly after deployment and b) after 2 years of fouling.

1.4 Ecological functioning of artificial reefs

1.4.1 Fish and the attraction-production debate

The construction of many artificial reefs has been driven by the observation that fish aggregate around reefs (Carlisle et al. 1964) and the assumption that fish production is limited by habitat availability (Bohnsack 1989, Bohnsack et al. 1997, Grossman et al. 1997, Svane & Peterson 2001). In the early years of artificial reef use, high

densities and high catch rates of fish around the reefs were taken as proof of both increased productivity and evidence of fish populations being regulated by habitat limitation. More recently this assumption has been challenged by fishery scientists concerned that artificial reefs may be simply aggregating fish, making them easier to harvest (Lindberg 1997), leading to a debate as to whether artificial reefs increase productivity or simply attract mobile individuals from surrounding regions (Bohnsack et al. 1994, Pickering & Whitmarsh 1996, Carr & Hixon 1997). This is an important question not least because many mobile species found in high densities on reefs have the potential to become commercially valuable and are, therefore, also at risk of depletion from over-fishing (Bohnsack et al. 1997).

In the late 1980s, Bohnsack (1989) put forward two hypotheses concerning the efficacy of artificial reefs:

1) The production hypothesis: Artificial reefs provide additional critical habitat that increases the environmental carrying capacity and eventually the abundance and biomass of reef fishes

2) The attraction hypothesis: Artificial reefs attract fishes as the result of behavioural preferences but do not significantly increase total fish biomass.

It has been suggested that habitat limitation is key to the artificial reef controversy (Grossman et al. 1997). If habitat availability is limited then the introduction of new hard-bottomed habitat in the form of artificial reefs should increase fish production through increased foraging, increased nesting habitat for adult fish and reduced

mortality rates through the provision of resting habitat and refuge from predation (e.g. Hixon & Beets 1993, Relini & Relini 1997). Grossman et al. (1997) reviewed existing data on whether artificial reefs increase regional fish production and concluded that an increase in refuge availability may positively affect some reef fish. For example, they found that the abundance and distribution of corallivorous fish may have been limited by the amount of living coral habitat on a reef. However, they also stressed that this relationship does not always hold for noncorallivorous fish and that the majority of target species for sport or commercial fishing are noncorallivorous. Bohnsack et al. (1994) observed large numbers of newly-settled fish larvae on new reefs which then rapidly disappeared as a result of predation pressures. They went on to suggest that the provision of small shelter holes on artificial reefs could perhaps reduce this predation and enhance juvenile survival, implying that these juvenile fish may be habitat-limited. Unfortunately, despite the fact that many reefs have been created under the assumption that habitat is limiting, there is very little support for Bohnsack's production hypothesis in the literature.

In contrast, many recent studies have shown that fish populations are recruitment- rather than habitat-limited (e.g. Bohnsack et al. 1997, Grossman et al. 1997, Doherty & Williams 1998). Lindberg (1997) reasoned that before fishing pressures were so high, the existing natural habitat would have supported an abundance of reef fish at or near to carrying capacity. With many fish stocks reduced to levels below the carrying capacity of natural habitat as a result of anthropogenic exploitation, Lindberg (1997) argues that it is unlikely that hard-bottomed habitat is the dominant factor limiting population size and, therefore, rejects Bohnsack's production hypothesis. If recruitment is the dominant controlling factor in fish populations

around reefs then the addition of new artificial reefs and hard substratum will not increase regional fish productivity (Lindberg 1997). This would suggest that high densities of fish around artificial reefs are not a result of enhanced production but are a result of attraction from other areas in line with Bohnsack's attraction hypothesis. This is supported by Bohnsack (1994) who found that most of the fish resident on an artificial reef complex near the Florida coast colonised the reef as juveniles or adults having first settled in other areas. He also concluded that few individuals of high economic importance appeared to settle directly on the artificial reefs; instead they were either visitors or had become resident after first settling elsewhere (e.g. in seagrass beds).

The lack of support for the production hypothesis in the literature to date does not necessarily give credibility to the attraction hypothesis. Grossman et al. (1997) reviewed the effects of removing resident adults from the populations of several fish species, on the basis that if habitat is limiting then recruitment should increase as new individuals move in to replace those adults that have been removed, and concluded that there were a variety of mechanisms capable of limiting fish population size, including both recruitment and habitat availability. If, however, artificial reefs do prove to be little more than glorified Fish Aggregating Devices (FADs), structures suspended in the water column to concentrate populations of fish into an easily harvestable resource (e.g. Friedlander et al. 1994, Higashi 1994), then the enthusiasm with which artificial reefs are currently being created could cause serious harm to fisheries populations worldwide (Bohnsack 1989, Grossman et al. 1997).

1.4.2 Habitat complexity and attraction versus production

It is widely recognised that structural complexity influences the biological community associated with a habitat (e.g. Bohnsack & Sutherland 1985, Todd & Turner 1986, Barkai & Branch 1988, Sebens 1991, Potts & Hulbert 1994, Guichard & Bourget 1998, Svane & Peterson 2001, Bradshaw et al. 2003). Charbonnel et al. (2002) investigated the effects of the structural complexity of artificial reef units in the Mediterranean Sea and, although the study was severely limited by a lack of any replication, showed that increasing habitat complexity may be an effective way to increase species richness, abundance and biomass of fish assemblages associated with artificial reefs. A study by Carr and Hixon (1997) also demonstrated the importance of habitat complexity in the attraction-production debate. They compared fish assemblages on artificial and natural reefs in tropical latitudes and found natural reefs to have a greater number of individuals than artificial reefs. They concluded that this was a result of the greater structural complexity (variety of hole sizes) of the natural coral reefs despite the fact that the artificial reefs had both greater vertical relief and provided greater shelter availability (number of holes). Conversely, in temperate latitudes, Danner et al. (1994) recorded higher densities of rock fish recruits at artificial reefs than natural reefs.

The structural complexity of tropical coral reef habitat is generally greater than that of temperate rocky reef habitat and so while many inhabitants of coral reefs have been shown to be recruitment rather than habitat limited (Grossman et al. 1997) the same cannot be assumed of temperate reefs. This may be one explanation for the differences seen between results from the studies described above. Although few studies have compared fish assemblages on artificial and natural reefs the majority of

artificial reef research to date, across all disciplines, has been carried out in tropical or subtropical waters (Svane & Peterson 2001). This further emphasises the need for detailed temperate artificial reef studies.

1.4.3 Crustacea

To date, most attraction-production studies have focused on fish populations (see Svane & Peterson 2001), and there is little doubt of the importance of fish productivity in the management of marine systems worldwide. However, the importance of crustacean fisheries and other aspects of the reef ecosystem should not be overlooked.

Artificial reefs have been widely used to enhance crustacean fisheries (e.g. Herrnkind et al. 1997, Jensen & Collins 1997). Unlike fish farming (e.g. for Atlantic salmon, *Salmo salar* L.), attempts to hatchery-rear many species of crustacean have proved to be uneconomical because of the length of time it takes for individuals to reach market size (Jensen & Collins 1997). A study by Bannister et al. (1994) on the east coast of England showed *H. gammarus*, the common lobster (UK), to be site loyal as juveniles as well as adults, which suggests that this species could be suitable for ranching. Artificial reefs have been deployed in Canada, Israel, the USA and the UK specifically for lobster habitat with some success (Jensen & Collins 1997). Jensen and Collins (1997) found their reef to be a suitable long term habitat for *H. gammarus*, supporting individuals from all stages of the benthic life cycle, including berried females. Similarly, artificial tyre reefs in Israel have provided new and suitable habitat for the colonisation of the slipper lobster, *Scyllarides latus* (Latrielle) (Spanier et al. 1988) and in Florida concrete blocks have enhanced the survival and

local retention of the juvenile Caribbean spiny lobster, *Panulirus argus* (Latrielle) (Herrnkind et al. 1997). Studies have shown that many species of lobster are dependent on available crevices in their early life stages and that appropriately designed artificial shelters could enhance the survival and local production of these species (e.g. Spanier et al. 1988, Wahle & Steneck 1991, Herrnkind et al. 1997, Jensen & Collins 1997).

The attraction-production debate is also relevant to crustacean fisheries. Herrnkind et al. (1997) suggested that commonly deployed large structures or artificial reefs attract and concentrate lobsters and their predators, leading to greater exploitation of lobster populations by both natural predators and humans, similar to Bohnsack's attraction hypothesis for fish species (Bohnsack 1989). Jensen and Collins (1997), however, suggest that the dilution of the natural population through attraction to artificial habitats would only be an initial effect before all niches were occupied and that this could be minimised by careful siting of artificial reefs suggesting, therefore, that *H. gammarus* is habitat limited. Grossman et al. (1997) states that it is possible, based on the positive results obtained in small-scale studies, that artificial reefs could be used to increase local population sizes for reef species, in this case lobsters, that are clearly limited by refuge availability.

1.4.4 The attraction-production debate: current thinking

Research to date has suggested that the truth behind the attraction-production debate probably lies somewhere on the gradient between attraction and production, depending on the reef design, locality, or species being studied (Bohnsack 1989). This is summarised in Figure 1.7.

As with most artificial reef research, the study of how habitat affects production and attraction has been poorly dealt with and the many contributing factors have received little attention. For example, attraction to physical objects will be a component of any artificial reef development but the proportional effect could be expected to decline with increasing scale. Likewise, productivity is likely to be related to surface area which, in turn, is driven by the complexity of the reef and the scales of complexity. There will always be both attraction and production at artificial reefs but the relative proportions could be expected to change with scale, complexity and age of reef (Figure 1.8). Whereas the relationship with biomass may tend toward a linear relationship with scale, complexity may be non-linear.

1.4.5 Epifaunal fouling: settlement and recruitment

The surface of a reef, or any hard substratum in the marine environment, becomes colonised when the planktonic propagules of sessile organisms, which include many marine invertebrates and plants, settle from the water column and attach to a suitable substratum (Barnes & Hughes 1999). The resulting epibiotic communities that develop on the surfaces of reefs are composed predominantly of primary producers and primary consumers that form the basis of the food web. Taylor (1998) found the epifauna on rocky subtidal reefs studied in New Zealand to be the major consumers and nutrient recyclers amongst the reef-dwelling fauna. Epifaunal fouling also increases the heterogeneity and thus habitat diversity of a reef and, as a result, Relini and Relini (1997) suggest that the rate of fouling of an artificial reef can be correlated with reef productivity.

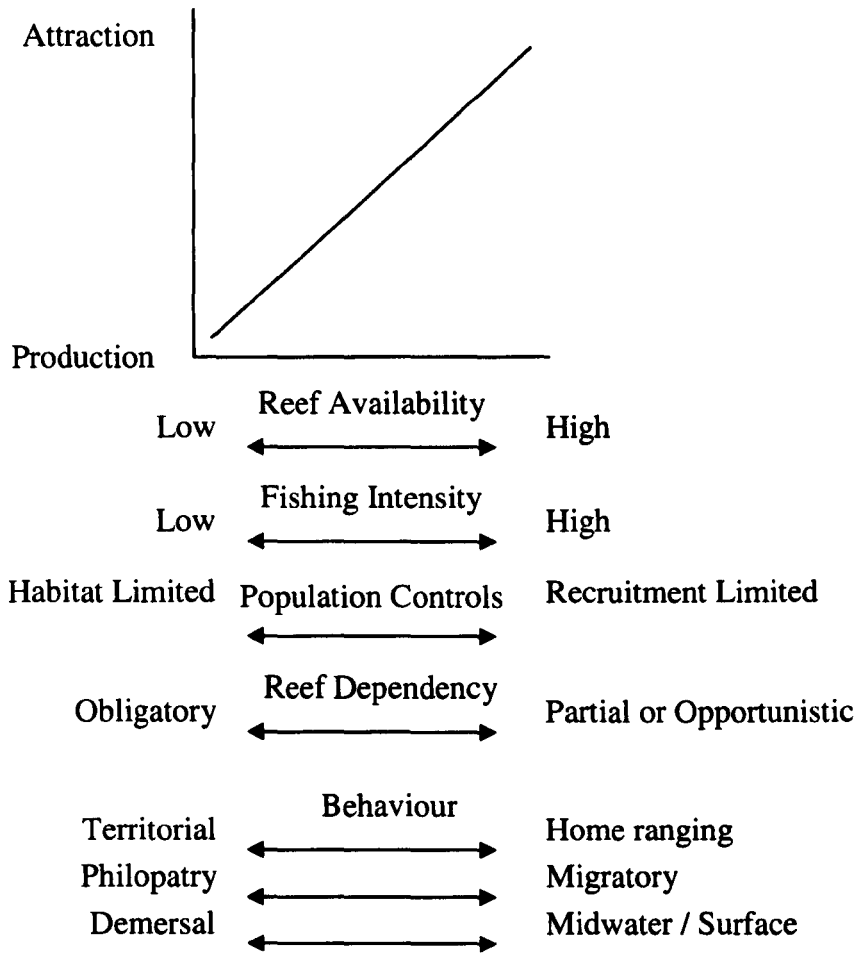

Figure 1.7. Gradients predicted to be important for attraction or production of fishes at artificial reefs (Bohnsack 1989).

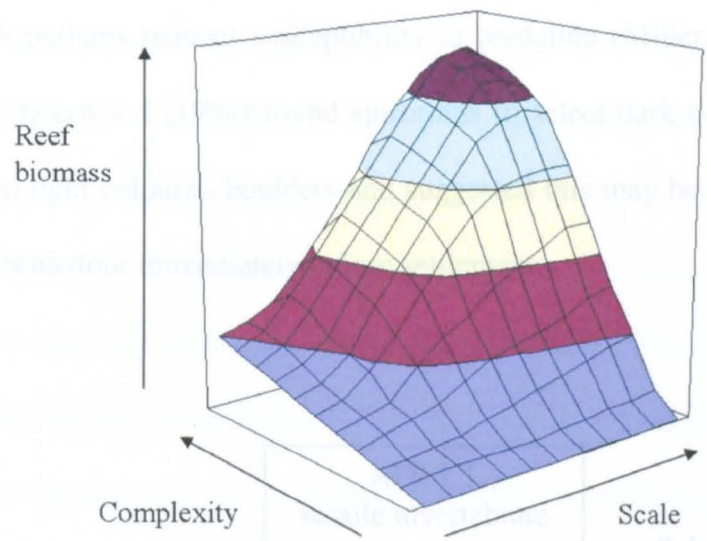

Figure 1.8 Proposed relationship between complexity, scale and reef biomass

The transient phase between the pelagic life of a propagule and the benthic existence of an adult is known as settlement (Abelson & Denny 1997). This has been defined more precisely by Connell (1985) as "the point when an individual first takes up permanent residence on the substratum. In sessile species this is when the planktonic propagule (larvae, spore etc.) has cemented itself to the surface". The life-cycle of a typical sessile marine invertebrate is shown in Figure 1.9.

Settlement is a complex process involving physical, chemical and biological cues, and fouling propagules have been shown to demonstrate the ability to select surface characteristics that will enhance their chances of survival (Crisp 1974, Richmond & Seed 1991, Morgan 2001, Brown et al. 2003). These include biological cues in the form of biofilms (Hurlbut 1991, Todd & Keough 1994, Wieczorek et al. 1995, Brown et al. 2001) as well as surface roughness/texture (Walters & Wethey 1996, Brown et al. 2003, Brown 2005) and colour (James & Underwood 1994). For

example, barnacles have been shown to have a preference for dimples on settlement plates which perhaps reduces susceptibility to predation (Miller & Carefoot 1989). James and Underwood (1994) found spirorbids to select dark coloured boulders in preference to light coloured boulders and suggested this may be a result of negative phototactic behaviour immediately before settlement.

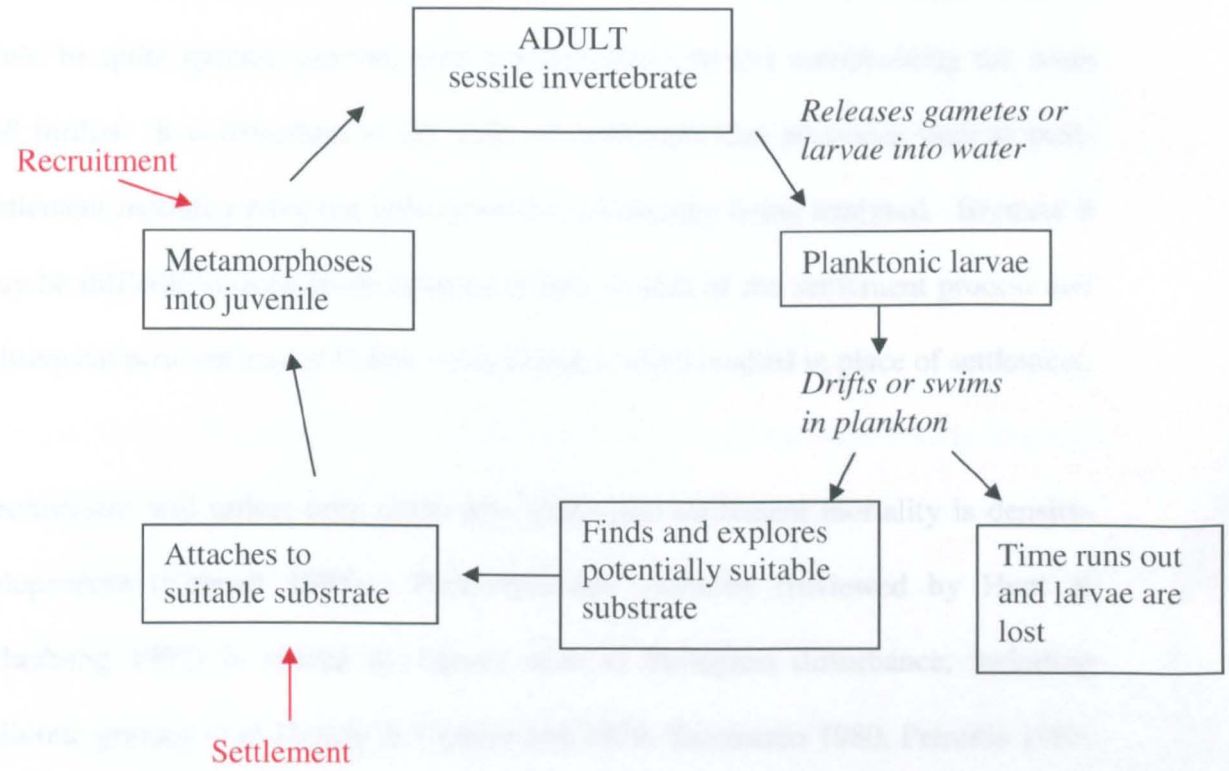

Figure 1.9. Life-cycle of a typical sessile marine invertebrate.

While these processes greatly influence the settlement of planktonic propagules to any substrata they can only affect settlement once the propagule has arrived at the settlement site. It has, thus, been suggested that the supply of larvae to an area is the critical first step in determining the structure of epibiotic assemblages, a concept termed supply-side ecology (Lewin 1986, Underwood & Keough 2001). This concept is discussed further in chapter 4.

The recruitment of sessile, epibiotic, organisms has been defined as "recently settled juveniles that have survived for a period of time after settlement" (Connell 1985), as shown in Figure 1.9. Recruitment thus combines settlement with early post-settlement mortality that has occurred on the substratum up to the time of the first census. There is some discrepancy in the literature over the time at which a settler ceases to be a settler and becomes a recruit, ranging from 24 hours (Davis 1988b) to 30 days (Caffey 1982). It seems likely that the time an individual remains a settler could be quite species specific, with environmental factors complicating the issue still further. It is important in the study of settlement that processes such as post-settlement mortality have not influenced the community being analysed. Because it may be difficult to distinguish between failure as part of the settlement process and subsequent post-settlement failure, recruitment is often studied in place of settlement.

Recruitment will reflect only settlement when post-settlement mortality is density-independent (Connell 1985). Post-settlement mortality (reviewed by Hunt & Scheibling 1997) is caused by factors such as biological disturbance, including epibiotic grazing (e.g. Denley & Underwood 1979, Sammarco 1980, Petraitis 1983, Miller & Carefoot 1989) and competition/overgrowth of individuals or colonies (e.g. Denley & Underwood 1979, Davis 1988a), and physical disturbance such as siltation (Kennelly 1991). Connell (1985) re-examined data from a number of studies and concluded that the use of densities of recruits (relatively easy to measure) to infer densities of settlers (difficult to measure) may be acceptable. It is, however, important to note that Connell (1985) reviewed studies of early recruitment rather than actual settlement. He found density-independent post-settlement mortality in all studies for which data was available for re-examination. Positive density-

dependence of early post-settlement mortality may result from density-dependent predation (Hurlbut 1991) or from a lack of suitable settlement sites (McShane 1991).

1.4.6 Methods used in recruitment studies

It is well known that established epifaunal invertebrates can exert inhibitory effects on settling larvae (e.g. Grosberg 1981, Connell & Keough 1985, Todd & Turner 1986) and, as discussed above, that recruitment will only reflect settlement when post-settlement mortality is density independent (Connell 1985). It is, therefore, necessary to use unoccupied habitat patches free of incumbents when investigating recruitment patterns. This can be achieved by scraping clean areas of natural substrata or through the use of artificial substrata.

The use of natural substrata in settlement studies is widespread, particularly amongst authors working in the intertidal zone (e.g. Sebens 1986, Carroll 1996, Bulleri 2005a, b). These authors all used cleared areas of natural substrata in their settlement/recruitment studies. To use natural substrata means that the study area is subject to the same biological, physical and chemical factors as the local surroundings, reducing the problems of trying to infer results from artificial substrata to the natural environment. However, in the subtidal environment experimental work is often conducted using SCUBA. In these cases the work time on the seabed is often restricted by decompression tables and scraping natural substrata *in situ* can be time consuming and is often impractical. Artificial substrata can offer a practical alternative where materials can be assembled on the surface prior to a dive.

The use of artificial substrata, or settlement panels, has many advantages over natural

substrata in settlement and recruitment studies. As discussed above, there are many biological, chemical and physical factors known to affect the settlement of marine propagules, so uniformity and replication of substrata used in experiments is of great importance.

Artificial substrata can be prepared to precise dimensions, with uniform surfaces and are easily replicated in large numbers (Turner & Todd 1993), giving researchers control over factors such as the size of area to be studied, the texture, colour and type of material to be used, and the freedom to position and orientate the study area as necessary. The provision of artificial recruitment or settlement panels also minimises the possibility of density dependent post-settlement mortality because of a lack of suitable settlement sites, and avoids problems of vegetative growth from organisms at the edge of cleared patches of natural substrata spreading into experimental areas.

With so many environmental factors known to affect settlement it is not surprising that substrate has been shown to be an important factor in the development of epifaunal assemblages (see work by Keough & Downes 1982, Keough & Downes 1986, Walters & Wethey 1996, Glasby 2000, Brown 2005). As a result, McGuinness (1989) has stressed that results from studies using artificial substrata can be extremely misleading if the effects of different substrata on biological recruitment are ignored. It is, therefore, important to determine to what extent it is possible to extrapolate from artificial to natural substrata (Glasby & Connell 2001) and, indeed, from natural to artificial substrata.

As well as issues relating to the choice of substratum to use in epifaunal recruitment studies there is also a wide range of techniques available for the assessment of epibiotic assemblage structure. These include *in situ* observations, photographic recording and subsequent image analysis and laboratory-based analyses (e.g. Jensen et al. 1994, Brown 2005, Bulleri 2005a) as well as measures such as abundance and percent cover (Reimers & Branden 1994, Brown 2005). Some of these techniques are better suited for use on either artificial or natural substrata and so it is very difficult to standardise methodologies across studies. For example, it is not possible to use laboratory-based analyses on many studies that use natural substrata and so either *in situ* observer counts or photographic methods are generally used to assess epifaunal assemblages on natural substrata. This variety of techniques employed in recruitment studies makes it difficult to interpret and compare results between studies.

1.4.7 Epifaunal recruitment and artificial reefs

Little attention has been given to epifaunal recruitment in the attraction-production debate. Svane and Peterson (2001) argue that the addition of hard substrata to the marine environment, such as an artificial reef, is primarily colonised by settling epibiotic larvae which otherwise would be lost. The addition of un-colonised hard substratum can, therefore, promote the development of fouling assemblages and increase the biomass of an area, provided that the added reef structures increase the total available area of hard substratum (Svane & Peterson 2001).

There are many recruitment and colonisation studies of artificial reefs and man-made structures in the literature. These studies generally fall into three categories:

monitoring of colonisation of artificial reefs (e.g. Cummings 1994, Falace & Bressan 1994, Foster et al. 1994, Nelson et al. 1994, Palmer-Zwahlen & Aseltine 1994, Pamintuan et al. 1994, Reimers & Branden 1994, Relini et al. 1994, Falace & Bressan 2002); comparisons between recruitment to different artificial substrata (e.g. Jensen et al. 1994, Qiu et al. 2003, Brown 2005); and comparisons between artificial and natural reefs (Butler & Connolly 1996, Connell & Glasby 1999, Glasby 1999a, Connell 2001, Glasby & Connell 2001, Bulleri 2005a, b, Perkol-Finkel et al. 2005). The vast majority of these studies on artificial reefs have monitored colonisation over time. Few studies have compared the colonisation on artificial reefs with that of local natural reefs or examined processes controlling the epifaunal recruitment to artificial reefs. These are issues that will be addressed in chapters 3 and 4.

1.5 Comparisons with natural reefs

Biological comparisons of artificial and natural reefs are difficult not only because of spatial variability in marine assemblages but also because of variability of factors such as age, size, isolation, depth and complexity of reefs (Carr & Hixon 1997). Many of these factors are known for artificial reefs but it is unlikely that the age of a natural reef will be known or can be determined. Artificial reefs are typically much smaller, younger and more isolated than their natural counterparts (Carr & Hixon 1997), making useful comparisons between reef types difficult. Many artificial reefs are constructed with the enhancement of fisheries in mind (see above) and they are accordingly often sited in areas lacking naturally occurring hard substrata. This makes the chances of finding a suitable natural reef for comparison even more unlikely.

Despite these difficulties it is important to make valid comparisons between artificial and natural reefs primarily to assess the differing potential contributions to system productivity but also to estimate potential economic returns of habitat manipulation compared with managing existing natural habitats. Even where natural reefs are present, the productivity of an area may be enhanced through the addition of new artificial hard substrata. Artificial reef studies would, therefore, be greatly enhanced by careful comparisons with natural reef systems, including detailed comparisons of the populations and assemblages of reef species that use artificial reefs with those on natural reefs and a determination of spatial scales over which artificial reefs act to attract or produce reef species (McGuinness 1989, Carr & Hixon 1997).

1.6 Structure of thesis

This NERC-funded thesis beings with a comparison of some frequently used methods and techniques available in the assessment of subtidal epibiotic assemblages. Some of these techniques are then used to investigate epifaunal predation pressures at the Loch Linnhe artificial reef complex and local natural rocky reefs. Seasonal recruitment is studied in order to investigate the epifaunal larval supply to artificial and natural reefs in Loch Linnhe which leads to a comparison of epifaunal recruitment at these different reef types.

Following this investigation into differences in epifaunal recruitment to artificial and natural reefs in Loch Linnhe, the epifaunal biomass on a simple and complex reef module are estimated and compared with the infaunal biomass per unit area of natural sea bed. This results in an assessment of the effects of habitat complexity on potential epifaunal production and on the potential net increase in epifaunal

production of an area as a result of artificial reef construction.

The study concludes with an investigation into the trophic dynamics of some key reef-dwelling taxa, on natural and artificial reefs in Loch Linnhe, using stable isotope analyses.

1.7 Aims

The aims of this project were:

1) to develop a standard protocol for methodology to assess the productivity of, and to quantify biotic interactions on, artificial and natural reefs

2) to establish whether there are differences in the productivity of artificial and natural rocky reefs in Loch Linnhe

Chapter 2 Evaluation of techniques used in the assessment of subtidal epibiotic assemblage structure

2.1 Introduction

The quantification of epifaunal fouling is an important aspect of artificial reef science. In order to make predictions on the development and productivity of biota attached to any hard substratum in the marine environment it is important to know how quickly the substratum is colonized by epifauna and what factors influence rates of colonization (Carr & Hixon 1997, Svane & Peterson 2001). The settlement of marine organisms is a complex process and larvae have been shown to select a settlement site based on environmental cues that include substratum type (Keough & Downes 1982, 1986, Walters & Wethey 1996, Glasby 2000); biological cues in the form of biofilms (Hurlbut 1991, Todd & Keough 1994, Wieczorek et al. 1995, Brown et al. 2001) and physical characteristics such as water movement (Todd & Turner 1986, Glasby & Connell 2001), rate of siltation (Pamintuan et al. 1994, Maughan 2001), light/shading (Pamintuan et al. 1994, Glasby 1999a,b, Maughan 2001) and surface orientation (Todd & Turner 1986, Glasby 2000, Glasby & Connell 2001). With so many known causes of variability in developing epifaunal assemblages it is essential that any method used in studies of this nature will provide a sensitive, accurate, and robust estimate of the assemblage structure.

A wide variety of techniques are routinely used in epifaunal studies to quantify assemblage structure. These include *in situ* photography and subsequent percent cover estimates from photographic images (Jensen et al. 1994, Moreno et al. 1994, Relini et al. 1994, Connell 1999, Glasby 1999a, Knott et al. 2004), *in situ* abundance

counts and estimates of percent cover (Danner et al. 1994, Jara & Cespedes 1994, Pamintuan et al. 1994, Chapman 2003, Bulleri 2005b), *in situ* surface scraping for biomass (Bombace et al. 1994, 1995), biomass determination in the laboratory (Qiu et al. 2003), abundance counts under a dissecting microscope in the laboratory (Nelson et al. 1994, Brown et al. 2003, Brown 2005), and percent cover in the laboratory (Nelson et al. 1994, Reimers & Branden 1994, Relini et al. 1994). However, despite the variety of techniques that have been used to determine the extent of epifaunal fouling there has been little comparative evaluation of or between the techniques used.

The efficiency of some percent cover techniques has been compared in the intertidal environment using a variety of *in situ* and image analysis methods (Foster et al. 1991, Meese & Tomich 1992, Dethier et al. 1993, Pech et al. 2004). In some cases visual estimation of percent cover was more accurate than random point quadrat techniques (Dethier et al. 1993). However, if photoquadrats were employed, then the degree of cover for a specific organism and the number of taxa present were always underestimated (Foster et al. 1991, Pech et al. 2004). Meese and Tomich (1992) found that no method was significantly better than others for estimating percent cover of an organism when it occurred in very low abundances and they recommended electronic digitizing of outlines of organisms on photographic images as being the most repeatable of the methods evaluated. However, none of these studies evaluated the sensitivity of the methods employed when examining how representative percent cover was of the assemblage structure, or how robust the techniques were when repeatedly undertaken in different ways (e.g. *in situ*, in the laboratory, or using image analysis). No studies of this nature have been undertaken

in the subtidal environment.

This chapter presents results from a study designed to evaluate a variety of sampling methods in order to compare their accuracy in determining the degree and type of subtidal epifaunal fouling. Substratum type has been shown to be an important factor in epibiotic colonisation (Keough & Downes 1986, Walters & Wethey 1996, Glasby 2000, Brown 2005) and so two substrata were used in this experiment in order to test the relative sensitivity of the techniques described below. The substrata used for fouling were concrete reef blocks, identical to those used in the construction of the Loch Linnhe artificial reef complex (Sayer & Wilding 2002, Wilding 2006) and PVC plastic. PVC was selected because it has been shown to support a different epifaunal assemblage to the concrete reef blocks (Brown 2005).

2.2 Materials and methods

The experimental design consisted of 12 concrete blocks (40 x 21 x 22cm) and 12 PVC panels (16.5 x 22cm) deployed, using SCUBA, in Dunstaffnage Bay (west coast of Scotland, 56°27.10N 5°26.16W) in a water depth of approximately 7 metres below chart datum. The concrete blocks were arranged in a line on the seabed; the PVC panels were fixed, using cable ties, to a galvanised pipe support frame approximately 50cm above the seabed (Figure 2.1). The PVC panels were arranged in two rows of six panels on the frame. For both the concrete blocks and PVC panels, experimental surfaces were orientated vertically and all faced the same direction with respect to tidal flows. The concrete blocks at PVC panels were deployed on the 15th August 2003. Analysis of the developing assemblages on both PVC panels and concrete blocks was carried out in mid-January 2005.

The epifaunal communities within a 14.5cm x 10cm experimental area on each block/panel were photographed *in situ* using a Nikonos V amphibious camera with close-up frame (19.5cm x 14cm), Fuji Velvia slide film (50 ASA) and strobe in order to minimise parallax error and to standardise scale. One photograph was taken on each PVC panel and concrete block. Once photographed, the epifauna within the same 14.5 x 10cm experimental area of each of the 12 PVC panels and 12 concrete blocks was quantified *in situ* for abundance, frequency and percent cover (see techniques below).

a)

b)

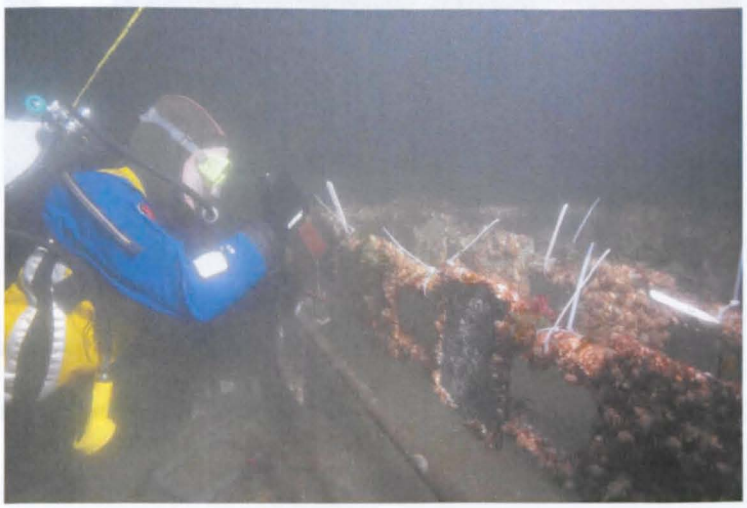

Figure 2.1 Photographs of a) artificial reef blocks and b) PVC panels *in situ*.

Six PVC panels and six concrete blocks were randomly selected for *in situ* scraping for biomass. A metal scraper was used to remove all the epibiota from the 14.5cm x 10cm experimental area of each PVC panel or concrete block (Figure 2.1b and Figure 2.2). Samples were scraped into sealable plastic bags. Mobile animals (e.g. nudibranchs) were removed prior to scraping.

a)

b)

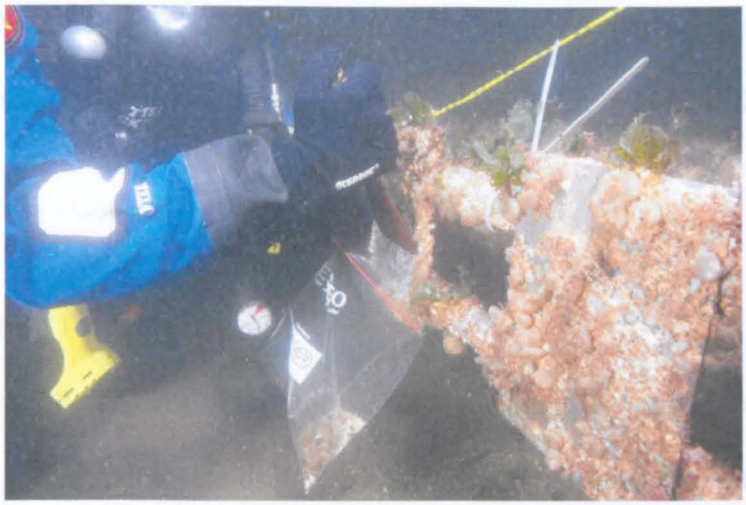

Figure 2.2. Scraping epifaunal biomass into sealable plastic sample bags, from a) a concrete block and b) a PVC panel, *in situ* using a metal scraper.

The remaining six PVC panels and six concrete blocks were lifted to the surface

taking care not to disturb the sessile assemblages on experimental surfaces. PVC panels were recovered by hand using SCUBA. Concrete blocks were secured into plastic crates on the seabed using SCUBA and lifted by winch to a surface vessel. Once recovered, the experimental substrata were immediately taken back to the laboratory. All substrata were kept in flowing seawater prior to examination under a boom-mounted low power stereo light microscope (Wild M5, Figure 2.3). Assemblages on the PVC panels and concrete blocks were analysed for abundance, frequency and percent cover using the techniques described below before being scraped clean for biomass determinations. All data collection was carried out by the same observer.

2.2.1 Sampling site – "Methods"

For the purpose of this study "method" refers to the location where the sampling was carried out. Therefore, in this study three methods were compared: (1) *in situ*-based underwater analysis using SCUBA, (2) laboratory-based analysis using a microscope and (3) image-based analysis of photographic images, taken *in situ*, with the aid of a computer.

2.2.2 Analysis – "Techniques"

For the purpose of the present study "technique" refers to the way data was collected from the panels. The abundance of individuals of each taxon was counted following the technique employed by Brown (2005). Counts were made within the 14.5cm x 10cm experimental area of each of the six PVC panels and concrete blocks with the aid of an analysis grid with 100 equal squares delineated using monofilament. Fouling organisms were identified to the lowest possible taxon using authoritative

keys. Distinct colonies of encrusting species, such as colonial ascidia and encrusting and erect bryozoa, were also counted. Motile species were recorded but not included in the analysis. Abundance counts were carried out both *in situ* and in the laboratory.

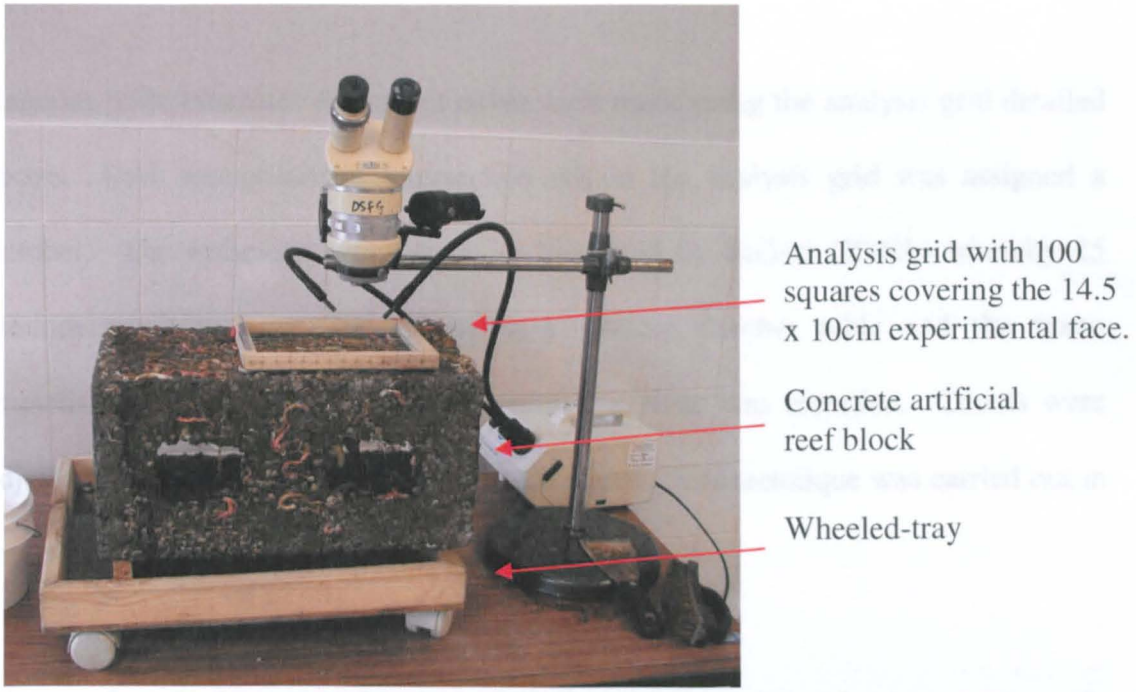

Figure 2.3 Concrete block on a wheeled-tray under a binocular microscope.

The same analysis grid was used to calculate the frequency of each taxon within each 14.5cm x 10cm experimental area. Taxon frequency was a presence/absence count of each taxon within each grid square of the analysis grid and so a measure was made of the percentage of squares in which at least one individual of a given taxon was observed. The technique used here was similar to that used by the U.S. Fish and Wildlife Service (2004). One individual could be counted as being present in more than one grid square. Frequency counts were made both *in situ* and in the laboratory.

Visual estimates of percent cover were made, as per the method used by Dethier et al. (1993), with the use of the analysis grid detailed above. Each taxon present

within the experimental area was assessed for percent cover, where one grid square was equal to one percent of the total area. Part filled squares and small organisms were estimated to a minimum resolution of 0.1 percent. Visual estimates were carried out *in situ* and in the laboratory.

Random point estimates of percent cover were made using the analysis grid detailed above. Each monofilament intersection within the analysis grid was assigned a number. The technique was similar to that used by Bulleri (2005b) whereby 25 random numbers were selected using a random number table and the taxon immediately beneath each selected intersecting point was recorded. Counts were adjusted to calculate percent cover for each taxon. This technique was carried out in the laboratory but not *in situ*.

Biomass from both concrete blocks and PVC panels was removed using a scraper. In the laboratory, additional sampling was made using forceps to remove small organisms missed by scraping and those that had buried into crevices on the surface of blocks (such as the bivalves *Hiatella arctica* (L.) and *Mytilus edulis* (L.)). All biomass samples, from *in situ* and laboratory methods, were placed into pre-weighed foil trays and crucibles, re-weighed for estimates of wet weight and then dried to a constant weight at 50°C before being ashed in a muffle furnace for 12 hours at 450°C.

Slides from the *in situ* photographic surveys were scanned and then imported into imaging software where each image was cropped to leave the same 14.5cm x 10cm experimental area used in the other methods. 100 equal squares were digitally

superimposed onto the image in order to undertake the same estimation techniques as described above.

The method/technique combinations evaluated in the study are summarised in Table 2.1.

Table 2.1. Method/technique combinations evaluated in this study

		Technique				
		Abundance	Frequency	Percent cover grid	Percent cover random point	Biomass
Method	In situ	X	X	X		X
	Laboratory	X	X	X	X	X
	Image	X	X	X	X	

2.2.3 Data analysis

Biomass data were tested for normality using the Anderson-Darling test and for equal variances using Levene's test (Dytham 2003). As a result, data were log transformed prior to univariate statistical analysis. Differences in biomass estimates collected using different methods and from different substrata were tested using a two way ANOVA (model: orthogonal, factors fixed) (Underwood 1997).

Community structures on concrete blocks and PVC panels were assessed using multivariate statistical methods within the PRIMER software package (Clarke & Warwick 2001). The fouling assemblage structure on concrete blocks and PVC panels identified by each method using each technique was assessed by non-parametric Multi-Dimensional Scaling (nMDS) ordination using the Bray Curtis similarity measure. These data were log (x+1) transformed prior to multivariate analysis to minimise bias caused by very abundant taxa. Analysis of similarity

(ANOSIM, Clarke 1993) was performed to test the significance of differences in epibiotic fouling on the two substrata for each method/technique combination.

A second stage nMDS ordination, and subsequent ANOSIM test, was performed to compare the ordinations generated by each method/technique combination. The nature of the groupings identified in the second stage ordination was further explored using the similarity percentage programme (SIMPER, Clarke & Warwick 2001) specifically to determine the characterising species for each method/technique combination evaluated.

Tests for equal variance and normality were carried out on all taxonomic data using Levene's test and the Anderson-Darling test respectively and data were transformed where necessary (square root, log (x+1) or fourth root transformations) in order to conform to the assumptions made by univariate parametric tests. One-way ANOVAs with Fisher's paired test were performed to test the effect of substratum on the abundance or cover of each selected taxon for each method/technique combination. Where transformation failed to remove heterogeneous variances a non-parametric Kruskall Wallis test was carried out instead of ANOVA.

2.3 Results

2.3.1 Biomass

Significantly greater biomass was recorded on PVC panels compared with concrete blocks when analysed for both dry weight and ash free dry weight ($p < 0.001$, Figure 2.4). No significant difference in biomass weight was found between estimates made *in situ* and in the laboratory ($p > 0.05$, Figure 2.4).

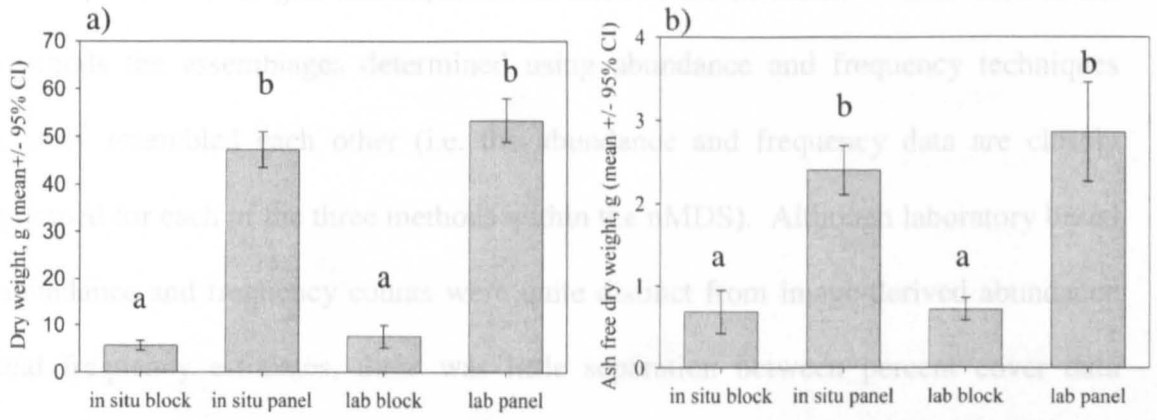

Figure 2.4. Estimates of the biomass of epifaunal settlement on PVC panels and concrete blocks as measured by a) dry weight and b) ash-free dry weight, using both *in situ* and laboratory methods (n = 6 in each case). Different letters above bars show significant differences ($p < 0.05$). Identical letters above bars show non-significance ($p > 0.05$).

2.3.2 Taxonomic data

For each method/technique combination tested, significant differences existed between the epifaunal assemblage structures that had developed on the two substrata used in this study ($p < 0.01$, ANOSIM, Table 2.2). The method/technique combinations with the lowest R values were 'laboratory percent cover random point' and 'image percent cover random point'. This indicates that the random point technique was less sensitive than abundance, frequency or percent cover grid techniques in discriminating between the assemblages on the two substrata.

To establish whether there were any overall differences in patterns observed using the different method/technique combinations a second stage resemblance matrix was created and an nMDS was plotted (Figure 2.5). The second stage nMDS plot indicated that the percent cover random point technique produced data that were distinct from the other techniques (Figure 2.5). There was a high degree of similarity

in the percent cover grid technique for all three of the methods. Within each of the methods the assemblages determined using abundance and frequency techniques closely resembled each other (i.e. the abundance and frequency data are closely grouped for each of the three methods within the nMDS). Although laboratory based abundance and frequency counts were quite distinct from image-derived abundance and frequency estimates, there was little separation between percent cover data collected in the laboratory and those from image analysis. Data collected *in situ* were more closely clustered and distinct from those collected using other methods but the difference was not significant ($p > 0.05$, ANOSIM results, Table 2.3).

Table 2.2. ANOSIM results, R* values with significance (%) in brackets, of comparisons of epifaunal assemblage structure on the two substrata using all method/technique combinations. Test factor = substratum (PVC panel *vs.* concrete block). All method/technique combinations had a significant difference between assemblages on PVC panels and concrete blocks ($p < 0.01$).

	Abundance	Frequency	Percent cover grid	Percent cover random point
In situ	0.920 (0.1)	0.911(0.1)	0.937(0.1)	
Laboratory	1.000 (0.2)	0.933(0.2)	0.906(0.2)	0.752(0.1)
Image	0.955 (0.1)	0.835(0.1	0.948(0.1)	0.799(0.1)

* The R statistic (Global R) can be used as a comparative measure of the degree of separation between the sites (Clarke & Warwick 2001), in this case concrete and PVC plastic with values that tend toward the maximum of 1.0 indicating the highest degree of separation.

The main characterising taxa identified from the SIMPER analysis were barnacle, solitary ascidian, calcareous tube worm, erect bryozoan, green algae, and red algae (Table 2.4). These species were selected for further univariate analysis, both for their characterising nature and for their range of structural function within assemblages. Univariate analysis was also carried out on the number of species/taxa present per unit area of substratum (S) (see section 2.3.3 below).

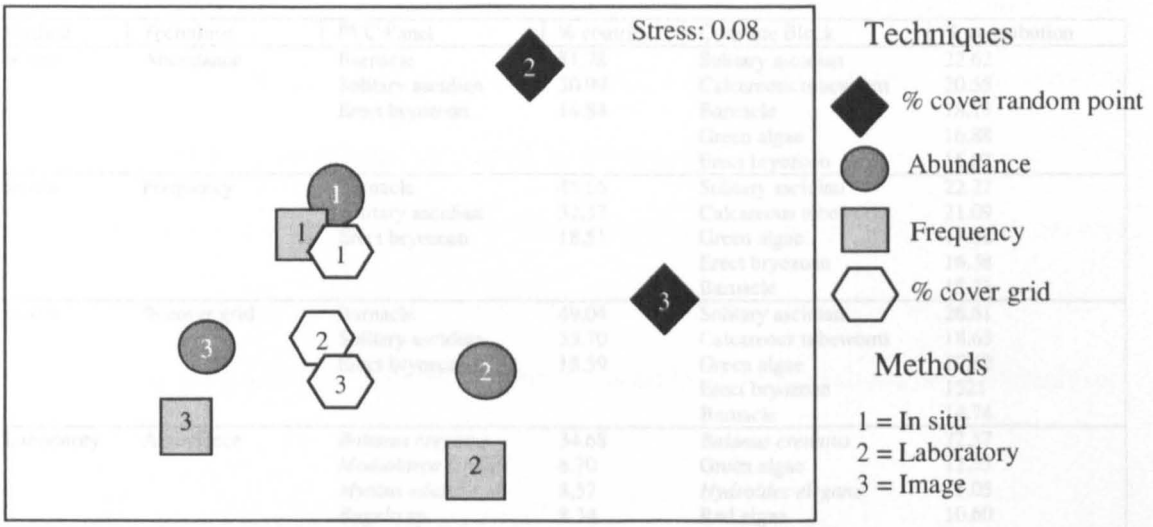

Figure 2.5. Second stage nMDS ordination showing the similarity of data generated by different methods and techniques. Each point on a second stage nMDS plot reflects a primary resemblance matrix. Primary resemblance matrices used to generate this plot contained data comparing the assemblages on PVC and concrete for each method/technique combination.

Table 2.3. Percentage dissimilarity between methods and techniques as determined by second stage ANOSIM

METHOD	*In situ*	Laboratory	
Laboratory	24.15		
Image	38.93	10.46	
Global R = 0.227 (6.6%)			
TECHNIQUE	Abundance	Frequency	% cover grid
Frequency	-14.8		
% cover grid	-18.5	-3.7	
% cover random point	66.7	58.3	66.7
Global R = 0.12 (24.2%)			

Table 2.4. The characterising species for each site/method combination as determined by percentage contribution (SIMPER analysis).

Method	Technique	PVC Panel	% contrib.	Concrete Block	% contribution
In situ	Abundance	Barnacle	51.78	Solitary ascidian	22.62
		Solitary ascidian	30.99	Calcareous tubeworm	20.55
		Erect bryozoan	14.84	Barnacle	18.19
				Green algae	16.88
				Erect bryozoan	16.07
In situ	Frequency	Barnacle	45.16	Solitary ascidian	22.27
		Solitary ascidian	32.37	Calcareous tubeworm	21.09
		Erect bryozoan	18.51	Green algae	17.32
				Erect bryozoan	16.38
				Barnacle	15.21
In situ	% cover grid	Barnacle	49.04	Solitary ascidian	26.61
		Solitary ascidian	33.70	Calcareous tubeworm	18.63
		Erect bryozoan	15.59	Green algae	17.62
				Erect bryozoan	1521
				Barnacle	14.74
Laboratory	Abundance	*Balanus crenatus*	34.68	*Balanus crenatus*	22.57
		Modiolarca tumida	8.70	Green algae	12.55
		Mytilus edulis	8.57	*Hydroides elegans*	11.05
		Bugula sp.	8.34	Red algae	10.60
		Anomiidae	6.61	*Bugula* sp.	9.93
		Ascidiella aspersa	5.72	*Pomatoceros triqueter*	8.99
Laboratory	Frequency	*Balanus crenatus*	19.01	*Balanus crenatus*	13.72
		Bugula sp.	10.89	Green algae	12.58
		Mytilus edulis	9.95	Red algae	11.26
		Modiolarca tumida	9.06	*Bugula* sp.	11.25
		Ascidiella aspersa	8.23	*Hydroides elegans*	10.55
		Anomiidae	7.28	*Ascidiella aspersa*	9.33
Laboratory	% cover grid	*Balanus crenatus*	47.14	Solitary ascidian	25.26
		Solitary ascidian	27.38	*Balanus crenatus*	19.43
		Bugula sp.	11.55	Green algae	18.29
		Red algae	5.10	*Bugula* sp.	14.10
				Calcareous tubeworm	11.85
				Red algae	11.08
Laboratory	% cover random	Balanus crenatus	45.89	Bare	26.11
		Bare	25.66	Solitary ascidian	20.55
		Solitary ascidian	24.16	*Balanus crenatus*	16.09
				Green algae	13.56
				Pomatoceros triqueter	10.97
				Bugula sp.	5.19
Image	Abundance	Barnacle	45.93	Green algae	20.03
		Solitary ascidian	23.22	Calcareous tube worm	19.00
		Erect bryozoan	17.76	Solitary ascidian	18.21
		Green algae	5.14	Barnacle	17.80
				Erect bryozoan	13.68
				Red algae	10.17
Image	Frequency	Barnacle	35.64	Solitary ascidian	20.03
		Solitary ascidian	28.47	Green algae	18.83
		Erect bryozoan	20.35	Calcareous tube worm	18.35
		Green algae	6.19	Barnacle	15.23
				Erect bryozoan	14.44
				Red algae	9.98
Image	% cover grid	Barnacle	46.46	Solitary ascidian	30.47
		Solitary ascidian	33.76	Green algae	19.87
		Erect bryozoan	12.57	Calcareous tube worm	16.12
				Barnacle	11.99
				Erect bryozoan	10.89
				Red algae	7.06
Image	% cover random	Barnacle	39.17	Bare	29.66
		Bare	22.88	Solitary ascidian	26.55
		Solitary ascidian	22.39	Green algae	13.04
		Erect bryozoan	15.10	Calcareous tube worm	12.65
				Barnacle	7.11
				Erect bryozoan	6.34

No laboratory data were available for those concrete blocks and PVC panels that had been scraped *in situ*, so all taxonomic data from these panels (*in situ* and image analysis) were removed from analysis to create a balanced dataset. Data used for univariate analysis, therefore, consisted of abundance, frequency and percent cover grid techniques carried out *in situ*, in the laboratory and from images, and percent cover random point technique data from laboratory and image analysis, for the 6 concrete blocks and 6 PVC panels that were taken back to the laboratory for analysis.

2.3.3 Comparison between methods

Mean abundance, frequency and percent cover estimates for the characterising taxa on PVC plastic and concrete blocks are shown in Figure 2.6. It is apparent from Figure 2.6 that laboratory-based estimates were often greater than those determined either *in situ* or from images. Statistical tests were not carried out to investigate the differences in mean values because the data were not independent.

Abundance, frequency, percent cover grid and percent cover random point of both barnacle, calcareous tube worm and green algae were significantly different between PVC and concrete for all three methods used ($p < 0.05$, Table 2.5 and Appendix I).

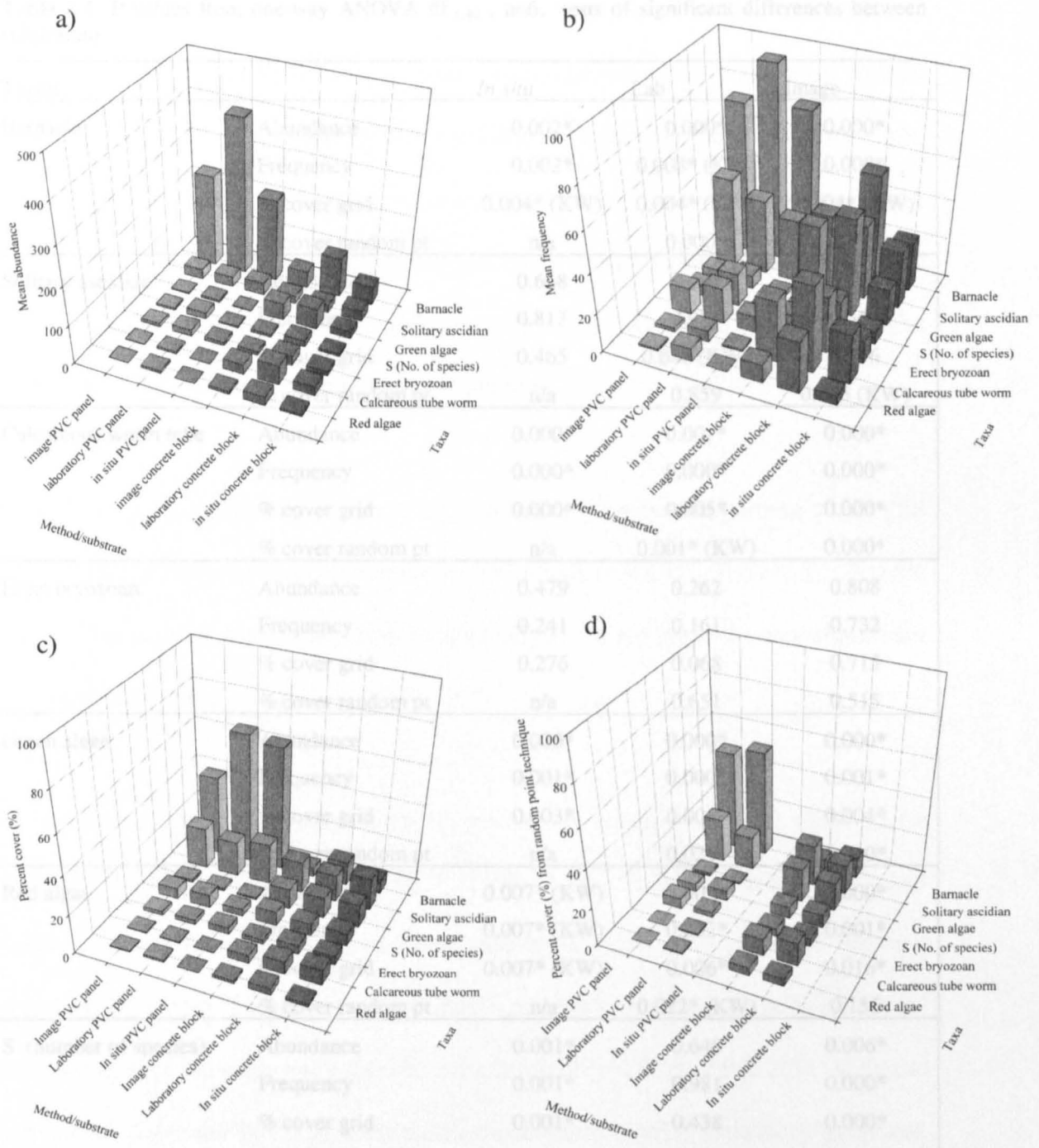

Figure 2.6. Abundance (a), frequency (b), percent cover grid (c) and percent cover random point (d) estimates of characterising taxa on PVC plastic and concrete blocks using different methods.

Table 2.5 P values from one-way ANOVA df $_{1,10}$, n=6, tests of significant differences between substratum.

Taxon		*In situ*	Lab	Image
Barnacle	Abundance	0.002*	0.000*	0.000*
	Frequency	0.002*	0.008* (KW)	0.000*
	% cover grid	0.004* (KW)	0.004* (KW)	0.004* (KW)
	% cover random pt	n/a	0.000*	0.000*
Solitary ascidian	Abundance	0.668	0.497	0.466
	Frequency	0.813	0.985	0.561
	% cover grid	0.465	0.688 (KW)	0.376
	% cover random pt	n/a	0.859	0.935 (KW)
Calcareous worm tube	Abundance	0.000*	0.001*	0.000*
	Frequency	0.000*	0.000*	0.000*
	% cover grid	0.000*	0.005*	0.000*
	% cover random pt	n/a	0.001* (KW)	0.000*
Erect bryozoan	Abundance	0.479	0.262	0.808
	Frequency	0.241	0.161	0.732
	% cover grid	0.276	0.068	0.715
	% cover random pt	n/a	0.651	0.515
Green algae	Abundance	0.000*	0.000*	0.000*
	Frequency	0.001*	0.000*	0.001*
	% cover grid	0.003*	0.001*	0.004*
	% cover random pt	n/a	0.021*	0.010*
Red algae	Abundance	0.007* (KW)	0.005*	0.000*
	Frequency	0.007* (KW)	0.002*	0.001*
	% cover grid	0.007* (KW)	0.006*	0.016*
	% cover random pt	n/a	0.022* (KW)	0.156
S (number of species)	Abundance	0.001*	0.640	0.006*
	Frequency	0.001*	0.981	0.000*
	% cover grid	0.001*	0.438	0.000*
	% cover random pt	n/a	0.001*	0.034*

An asterisk (*) indicates significance at $p<0.05$. (KW) indicates a Kruskall Wallis test used as variances were not homogeneous after transformation. Full ANOVA and Kruskall Wallis tables can be found in Appendix I.

There were no significant differences between substrata for either solitary ascidian or erect bryozoan abundance, frequency, percent cover grid or percent cover random point (not assessed *in situ*) ($p > 0.05$ in all cases, Table 2.5). There was, however, a

large degree of variation in the extent of the non-significance between methods and techniques. For example, laboratory-based determinations of erect bryozoan percent cover grid data between substrata had a p value of 0.068 whereas laboratory-based determinations of erect bryozoan percent cover random point had a p value of 0.651 (Table 2.5). With the exception of percent cover random point, laboratory-based determinations for erect bryozoan had smaller p values (closer to the critical alpha value) than either *in situ* or image analysis methods.

Red algae had significantly different abundance, frequency and percent cover grid values when substrata were compared for all methods ($p < 0.05$, Table 2.5). Percent cover random point determined from image analysis for red algae was not significant between substrata ($p > 0.05$, Table 2.5).

In situ and image-based measures of 'S' (number of species) were all significantly different between substrata ($p < 0.05$, Table 2.5). However, laboratory-based measures made using all three of these techniques were non-significant between substrata ($p > 0.05$, Table 2.5). Conversely, percent cover random point measures assessed in the laboratory were significantly different ($p < 0.05$, Table 2.5). With the exception of percent cover grid estimates on concrete blocks, laboratory-generated values of 'S' were always greater than those generated *in situ* or from image analysis for both substrata (Figure 2.7).

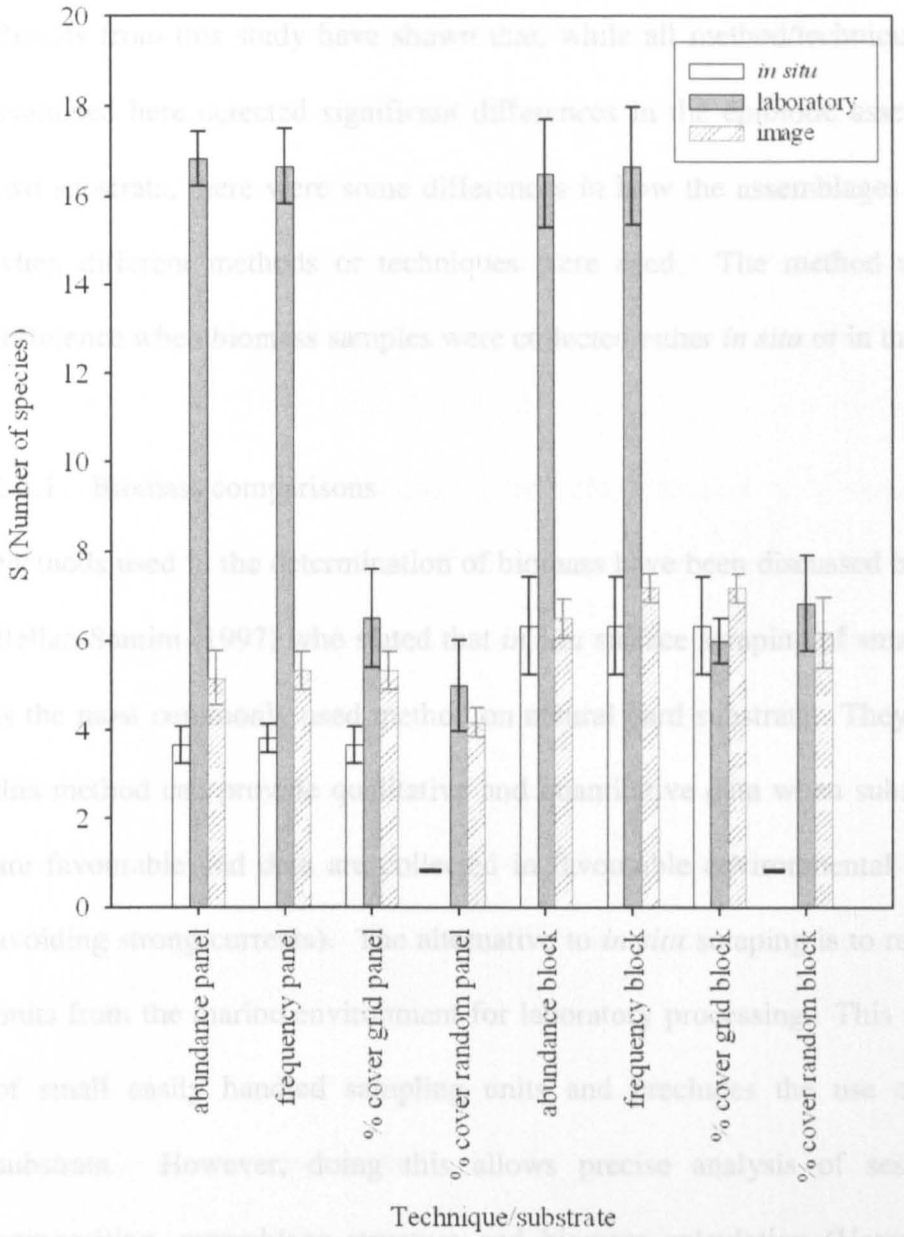

Figure 2.7. Mean S (number of species) with 95% confidence intervals generated for different methods and techniques on the two experimental substrata. No data were gathered *in situ* using the percent cover random point technique (indicated by a dash '—').

See Appendix I for full ANOVA and Kruskall Wallis results tables.

2.4 Discussion

Results from this study have shown that, while all method/technique combinations evaluated here detected significant differences in the epibiotic assemblages on the two substrata, there were some differences in how the assemblages were described when different methods or techniques were used. The method used caused no difference when biomass samples were collected either *in situ* or in the laboratory.

2.4.1 Biomass comparisons

Methods used in the determination of biomass have been discussed by Harmelin and Bellan-Santini (1997) who stated that *in situ* surface scraping of small defined areas is the most commonly used method on natural hard substrata. They concluded that this method can provide qualitative and quantitative data when substratum features are favourable and data are collected in favourable environmental conditions (e.g. avoiding strong currents). The alternative to *in situ* scraping is to remove sampling units from the marine environment for laboratory processing. This requires the use of small easily handled sampling units and precludes the use of most natural substrata. However, doing this allows precise analysis of sessile epibenthos composition, assemblage structure and biomass calculation (Harmelin & Bellan-Santini 1997).

Results from the current study found no significant difference in biomass (ash free dry weight or dry weight) between samples collected *in situ* or in the laboratory although the level of non-significance was very small and so deserves further consideration. There are many difficulties when sampling underwater. For example, low density plant and animal tissue can float away while sampling and dense

material, such as calcareous tubes and barnacle shell parts, can, and were observed to, fall to the seabed during collection. More material would, therefore, be expected to be lost when sampling *in situ* than in laboratory conditions. The marginal non-significance level for differences in dry weight determinations between *in situ* and laboratory methods may be caused primarily because of the difficulty with sampling barnacles and calcareous tube worms in the subtidal environment.

Qiu et al. (2003) used biomass of individual taxa as a measure of community development. The separation of taxa for biomass determinations following the scraping of epibiota from any hard substratum is difficult, especially when small encrusting organisms, such as bryozoa, or strongly attached organisms, such as calcareous worms and barnacles, are present. In the present study it was possible to separate ascidia from the rest of the assemblage but it was not possible to accurately differentiate between other encrusting organisms and so a measure of total biomass was used.

2.4.2 Taxonomic comparisons

The two substrata used in this study differed in the assemblage they supported to a greater extent compared with the findings of a previous fouling study using these materials in Dunstaffnage Bay (see Brown 2005). Assemblages were so different between substrata that all methods and techniques used in the present study clearly showed an effect of substratum on epifaunal development. The use of a second stage nMDS plot to compare the matrices for each method/technique combination permitted a direct method of comparing results from techniques which use different measures, such as percent cover and abundance counts, that otherwise cannot be

directly compared. It is also a useful approach when comparing methods because it is not necessary to standardise on taxonomic resolution for each method/technique combination as is essential for statistical tests such as ANOVA. For example, the use of a second stage analysis allowed techniques carried out in the laboratory, where many taxa were identified to species level, to be compared with *in situ* techniques where taxa were identified to group level.

There are many advantages and disadvantages of the methods evaluated in this study. *In situ* counts, while time consuming in the field, eliminate the need to take samples back to the laboratory for analysis and so experiments can be carried out on either natural or artificial substrata. *In situ* analysis is also often non-destructive which allows for time-series data to be collected and makes it a sensible choice of method when working in sensitive or protected areas. One of the greatest disadvantages of *in situ* sampling is the length of time required in the field. This is a particular problem in the subtidal when SCUBA is being used for data collection. *In situ* sampling is also potentially very crude compared with other methods as analysis is dependent on the observer being able to identify taxa by eye. In this way many small taxa can be overlooked, misidentified or underrepresented.

While laboratory-based sampling can be time consuming and requires the use of a microscope, time needed for working in the field is kept to a minimum (i.e. the collection of recruitment panels is a quick and simple task compared with *in situ* counting). If it is not possible to analyse samples immediately upon collection, or if samples cannot be kept alive in running water until the time of analysis, then panels can be preserved (e.g. Todd & Turner 1986, Qiu et al. 2003). Laboratory counts

under a microscope give a detailed account of the entire assemblage structure including small taxa which can be easily overlooked *in situ*. The disadvantage of laboratory-based sampling is that artificial substrata must often be used in order to allow samples to be removed from the experimental site. This can create problems with respect to extrapolating data and processes from artificial to natural substrata (McGuinness 1989, Glasby & Connell 2001).

The greatest advantages of photographic sampling and subsequent image analysis are that it is non-destructive and permanent records are generated which mean that samples can be re-examined at a later date if necessary (Bowden 2005). However, while the resolution of photographic images can be excellent it is often difficult, or impossible, to confidently identify taxa to genus or species level. Photographic sampling also only gives a two dimensional view of the assemblage being examined and so information could potentially be lost when assemblages are multi-layered.

All methods evaluated in this study were performed using a variety of techniques. Estimating the abundance of organisms in an assemblage gives a measure of the number of individuals of a taxon present within a specified area. An estimate of percent cover gives a measure of the area covered by a taxon in a specified area. Frequency counts give a measure of the spread of a taxon in a specified area. This means that large taxa present in small numbers will be represented to a greater extent in data collected using percent cover or frequency estimates than abundance estimates. Conversely, small taxa present in large numbers will be represented to a greater extent in abundance counts than in percent cover estimates. It is not surprising, therefore, that different techniques can provide different views of the

same assemblage structure. This problem is highlighted by a study conducted in Australia by Knott et al. (2004) who found a non-significant difference in assemblage structure between natural reefs and concrete breakwalls using a measure of percent cover but a significant difference in assemblage structure at the same sites using presence/absence data.

Measures of percent cover, either using some form of random point or visual estimate, are amongst the most frequently used techniques in the determination of epibiotic assemblage structure (e.g. Foster et al. 1991, Dethier et al. 1993). Multivariate analysis has shown the random point technique used in this study to be quite distinct from the other techniques assessed, perhaps because of poor sensitivity when it comes to detecting small taxa with low abundance. This finding is in agreement with a study by Dethier et al. (1993) who showed visual estimates of percent cover to be more repeatable and more sensitive than random point estimates. It is worth noting that in the current study only 25 intersecting points were used to assess assemblage structure. The number of points used to estimate percent cover has been shown to affect the sensitivity of the technique (Dethier et al. 1993), showing that increasing the number of points up to 100 improved the accuracy and decreased the variability of random point estimates. It is, therefore, possible that a study using 100 random points would have identified less distinct differences in an assemblage structure than the 25 random points used in the current study. However, Dethier et al (1993) concluded that a prohibitively large number of points would be needed to distinguish even moderate differences in percent cover values.

Percent cover estimates are frequently used as measures of community structure in

recruitment studies because of difficulties in differentiating between individuals of many seaweed and colonial animal species (Foster et al. 1991). Studies that use abundance counts as measures of assemblage structure often exclude colonial organisms, such as hydroids and encrusting bryozoans and colonial ascidians, from analysis of the data because of the difficulty in quantifying their abundances. Frequency counts are not often used in marine epifaunal studies but have been, and still are, used in terrestrial studies (e.g. Greig-Smith 1964, Britt 2005) where similar problems of distinguishing between individuals exist. Results from multivariate analysis in the current study suggest that, where the presence of colonial species prevents the use of abundance counts, the use of frequency counts may give a more similar estimate to abundance data than percent cover estimates in the assessment of epibiotic communities.

The close clustering of the percent cover grid points in the multivariate analysis suggests that this technique may be more robust between methods than either the abundance or frequency techniques evaluated here. The abundance and frequency techniques were more disperse showing that they may not be as repeatable between methods as the percent cover grid technique.

Multivariate analysis also showed the *in situ* method for all techniques to be more closely clustered than the other methods and very similar to each other. While this could suggest that it is more robust and accurate than the other methods evaluated, laboratory-based data were generated through detailed analysis under a low power microscope and so it can, perhaps, be assumed that data gathered in this way reflect the most accurate assessment of the assemblage. Data generated *in situ* were quite

distinct from laboratory-generated data on the nMDS plot in the current study which suggests that the reason for the clumping may not be caused by the robustness of the method but instead may be a result of a lack of sensitivity of the *in situ* method.

With the exception of the percent cover random point method, univariate analyses in the present study showed little effect of method or technique when looking for differences between substrata for most of the characterising species used in the evaluations. However, it is worth noting that this was not the case for the number of species (S). Laboratory-based abundance, frequency and percent cover techniques suggested no significant difference in the number of species on the two substrata evaluated. *In situ*- and image-based analysis using the same techniques all suggested a significant difference in the number of species on PVC plastic and concrete blocks. With the exception of percent cover grid estimates on concrete blocks, values of 'S' generated in the laboratory were always greater than those generated *in situ* or from image analysis for both substrata. While it cannot always be assumed that higher values mean a more accurate method or technique, Bowden (2005) makes a sensible suggestion when comparing photographic techniques that, on the basis that what is not present is not counted, there is logic in assuming that the higher estimate in each case will be the more accurate. As discussed above, it can also be assumed that laboratory-based data could reflect the most accurate assessment of the assemblage, at least in terms of numbers of individuals and species present.

The use of 'S' simply gives a measure of the number of species (or taxon) present in a given area. No other diversity indices were used in this study as it was not possible to generate this information from percent cover or frequency estimates as these

measures do not give an indication of the actual number of individuals present. However, this difference between methods for 'S' suggests that when diversity indices are required for an investigation that the choice of method used is important.

Although not statistically tested, because of non-independence of data, a significant interaction may have been present between method and substratum for barnacles counted both *in situ* versus laboratory and for laboratory versus image analysis methods. This may be because the lower numbers of barnacles present on concrete, as opposed to PVC, made counting more accurate using less sensitive methods such as *in situ* and image analysis. There also appeared to be a significant interaction between laboratory and image analysis methods for calcareous tube worm. The increased number of barnacles on the PVC panels may also have affected the ability to accurately detect calcareous tube worms using image analysis. This indicates that factors such as substratum may have a significant bearing on the relative accuracy of the sampling method employed; which is another complicating factor when attempting to compare the findings between studies that have used different sampling strategies.

Epifaunal fouling has been shown to be an important aspect of subtidal community ecology (Relini & Relini 1997, Taylor 1998). It is, therefore, important that factors influencing the rate of colonisation are understood when making predictions on the development and productivity of reefs (Carr & Hixon 1997, Svane & Peterson 2001), particularly with respect to comparisons between reef types (e.g. natural and artificial reefs) or reef location. The choice of methods to employ when studying epifaunal recruitment or colonisation may be limited by field conditions or the type of substrata

being studied. However, many recruitment studies lend themselves to the use of small, easily handled, sampling units such as settlement panels. Their use generates the freedom to use any of the methods and techniques evaluated in this study. The variation in estimates caused by the choice of method/technique combination used could potentially be generating inaccurate or non-comparable estimates of epifaunal assemblage structure.

The variety of techniques employed in colonisation studies makes it difficult to interpret and compare results between studies (e.g. Relini & Relini 1997, Qiu et al. 2003). Time taken for analysis using different methods and techniques was not recorded in the present study. However, it is acknowledged that in some studies the accuracy of estimate may have to be compromised by operational considerations. Nevertheless, the use of so many different methods and techniques in epifaunal studies undoubtedly confounds the problems of identifying important ecological processes and makes comparisons between different studies almost impossible. In future studies that aim to assess subtidal epifaunal recruitment, abundance or frequency counts made in the laboratory would be more likely to generate the most accurate estimates. When biomass estimates are needed, laboratory-based epifaunal scraping should be used in preference to *in situ* sampling, whenever possible.

As a result of the findings from this study, laboratory-based abundance counts, together with laboratory-based biomass determinations, will be used in the assessment of epibiotic assemblages in the following chapters.

Chapter 3 Predation pressures on developing epifaunal assemblages at artificial and natural reefs

3.1 Introduction

Predation has been shown to be an important factor affecting the development of community assemblages (Sebens 1986, Barkai & Branch 1988, Turner & Todd 1991, Brown & Swearingen 1998, Guichard & Bourget 1998, Connell & Anderson 1999, Bulleri et al. 2000, Osman & Whitlatch 2004, Bulleri 2005b). When carrying out large scale spatial and temporal settlement studies where settlement is to be inferred from recruitment it is, therefore, necessary to know whether predation pressures are consistent across experimental sites in order to be able to draw useful conclusions from the data. This may be particularly important when experimental sites have known differences; for example when epifaunal recruitment to artificial and natural reefs is to be compared (see chapter 4).

Biological communities have been shown to differ with both the age (Perkol-Finkel et al. 2005) and the habitat complexity (Bohnsack & Sutherland 1985, Barkai & Branch 1988, Sebens 1991) of a reef. It is, therefore, important to assess predation pressures at artificial and natural reef sites when measuring epifaunal recruitment, where age and complexity of the reefs may differ (Rose 2005). To simply quantify the abundance of predators does not give any indication of the actual effects of predation on the developing epifaunal communities. To quantify mobile predators is also problematic in highly complex habitats such as artificial reefs; with their many nooks and crannies offering shelter to animals and making them difficult for an observer to find. Known differences in complexity between study sites could,

therefore, be expected to introduce inaccuracies when comparing predator abundance between sites.

3.1.1 Assessing predation pressures

Two techniques are used frequently in the assessment of the effects of predation on epifaunal assemblages; removal of predators by hand or the exclusion of predators through the use of fences or cages. The repeated removal of predators by hand is time consuming and can only be effective if the target predators are slow-moving. For example, Bulleri et al. (2000) manually removed limpets from artificial and natural midlittoral reefs. The advantage of this method is that the experimental area with predators removed is subject to the same environmental conditions as the control areas.

There have been many studies using cages to look at the effects of predation on species and/or community structure (e.g. Arntz 1977, Schmidt & Warner 1984, Jensen & Jensen 1985, Menge et al. 1986, Barkai & Branch 1988, Kennelly 1991, Menge 1991, Petraitis 1991, Turner & Todd 1991, Steele 1996, Brown & Swearingen 1998, Connell & Anderson 1999, Osman & Whitlatch 2004) with varying success. For example, Barkai and Branch (1988) successfully used cages to demonstrate that predation by a rock lobster was causing distinct differences in the epibenthos of two closely situated islands off the west coast of South Africa. However, Schmidt and Warner (1984) used cages to isolate the various effects of predation and concluded that the effects of caging were more influential in their study than the effects of predation.

Previous studies have shown that the use of predator exclusion cages can cause changes in the physical environment over experimental surfaces. These changes are known as cage artefacts and include altered hydrodynamics, increased siltation and/or a reduction in light intensity (e.g. Hulberg & Oliver 1980, Schmidt & Warner 1984, Barkai & Branch 1988, Kennelly 1991, Guichard & Bourget 1998). As discussed in chapter 1, planktonic propagules and larvae are known to be able to select settlement sites based on a variety of physical, chemical and biological cues, that will enhance their chances of survival (Crisp 1974, Richmond & Seed 1991, Morgan 2001, Brown et al. 2003). The presence of cage artefacts thus has the potential to affect epibiotic settlement on experimental surfaces (e.g. Bulleri 2005b) making it difficult to determine whether differences in assemblage structure between caged and uncaged treatments are a result of the effects of predation or cage artefacts.

The control of cage artefacts in studies using predator exclusion cages is often done through the use of partial cages (Olafsson et al. 1994, Moksnes 2002); cages with holes or missing parts to enable predators access to experimental surfaces, while still being exposed to cage artefacts. Through the use of partial predator exclusion cages it should be possible to differentiate between the effects of predation and cage artefacts.

3.1.2 This study

In order to determine the effects of predation on epibiotic recruitment at artificial and natural reef sites in Loch Linnhe, recruitment panels were employed with and without predator exclusion cages. The main potential predators of epifaunal

recruitment in the study area are the starfish *Asterias rubens* (L.) and the sea urchin *Echinus esculentus* (L.) (*pers. obs.*).

The common starfish, *A. rubens,* is the most common starfish in the NE Atlantic, occurring on every type of substratum. In shallow waters it is known to form dense aggregations that move slowly along coastlines feeding voraciously (Begon et al. 1986, Figure 3.1). The diet of *A. rubens* consists of bivalves, polychaetes, other echinoderms and small crustacea, especially barnacles (Mortenson 1927, Hayward & Ryland 2003).

Figure 3.1 A dense aggregation of *A. rubens*. Photograph taken at the Loch Linnhe artificial reef complex at a depth of 16m.

The edible urchin, *E. esculentus*, is common in the infralittoral fringe on rocky substrata on all British coasts, especially in depths of 10 to 40m (Begon et al. 1986, Hayward & Ryland 2003). It is a large urchin, growing to approximately 180mm in diameter (Figure 3.2) and is omnivorous, feeding mostly on kelp, *Laminaria* spp.,

and a variety of minor animals including Bryozoa and barnacles (Mortenson 1927, Hayward & Ryland 2003).

Figure 3.2. Photograph of *E. esculentus* on reef module M1c within the Loch Linnhe artificial reef complex. The white barnacle scars show where predators have grazed the concrete reef blocks.

Other potential predators include reef-dwelling fish such as corkwing and rockcook wrasse (*Crenilabrus melops* (L.) and *Centrolabrus exoletus* (L.)) that graze heavily on encrusting fauna (Sayer et al. 1996). The nudibranch, *Onchidoris bilamellata* (L.), is also present in the area and has been observed in large numbers on artificial reefs in Loch Linnhe (*pers. obs.*). This nudibranch species is common in the intertidal and shallow sublittoral rocky coasts to 20m and feeds on barnacles (Hayward & Ryland 2003).

The aims of this study were to identify the effects of predation on epifaunal recruitment at artificial and natural reefs sites in Loch Linnhe and to establish

whether there are significant proximity-to-reef effects on predation.

Null hypotheses tested:

1. H_0: There are no effects of reef type on the effects of predation on epifaunal recruitment.

2. H_0: There are no effects of distance from reef on the effects of predation on epifaunal recruitment.

3.2 Materials and methods

3.2.1 Sites

Twelve sites were chosen in and around the Loch Linnhe artificial reef complex at a depth of approximately 15m; 3 natural rocky reef sites, 3 artificial reef modules, 4 off-reef sites 100m distant from the reef (2 distant from natural reefs, 2 distant from artificial reefs), and 2 control sites at a greater distance from any reef (see Table 3.1 for site information and Figure 3.3 for location map).

Many factors have been shown to influence the settlement of subtidal communities including depth (Dobretsov & Miron 2001) and tidal regimes (Maughan & Barnes 2000). Therefore, sites were selected to be as similar as possible with respect to environmental parameters.

The three artificial reef modules used in this study were chosen for their similar depths, importantly within easy SCUBA range, and for their similar deployment dates (reef age). A1 and A3 were deployed within a month of each other (A1 deployed 23/04/2002; A3 deployed 02/06/2002). A2 was used as a third site as the

depth of the reef was similar to A1 and A3 even though it was deployed more recently (09/08/2002 to 13/03/2003). Modules A1 and A3 both consisted of simple reef blocks and A2 was constructed of complex blocks.

Table 3.1 Recruitment study site information.

Site code	Site name	Site type	Latitude	Longitude	Depth
N1	Black Island N _ 0m	Natural on-reef	56° 31.606 N	5° 27.203 W	12.5m
N2	Black Island S _0m	Natural on-reef	56° 31.000 N	5° 28.426 W	17m
N3	Gregs	Natural on-reef	56° 28.655 N	5° 30.950 W	14m
N1 OFF	Black Island N _ 100m	Natural off-reef	56° 31.639 N	5° 27.287 W	15m
N2 OFF	Black Island S _ 100m	Natural off-reef	56° 31.031 N	5° 28.356W	17m
A1	M2s _ 0m	Artificial on-reef	56° 32.170 N	5° 27.100 W	15m
A2	M1c _0m	Artificial on-reef	56° 32.162 N	5° 26.972 W	16m
A3	M1s	Artificial on-reef	56° 32.180 N	5° 26.865 W	15m
A1 OFF	M2s _ 100m	Artificial off-reef	56° 32.163 N	5°27.191 W	16m
A2 OFF	M1c _ 100m	Artificial off-reef	56°32.202 N	5° 27.020 W	16m
C1	Control 1 (Lismore)	Off reef	56° 32.050 N	5° 27.504 W	15m
C2	Control 2 (Gregs)	Off reef	56° 29.719 N	5° 30.567 W	15m

As for the artificial reef sites, natural reef sites were selected for similarity of physical and environmental parameters such as depth. However, site selection was complicated because of commercial fishing activity in the area. Because recruitment panels were being placed on soft sediment next to the rocky reefs, and left for many months, it was important that the sites chosen were not regularly trawled by local fishermen. This, along with the close proximity to the artificial reef sites, was the primary reason for selecting the three natural reef sites (Table 3.1).

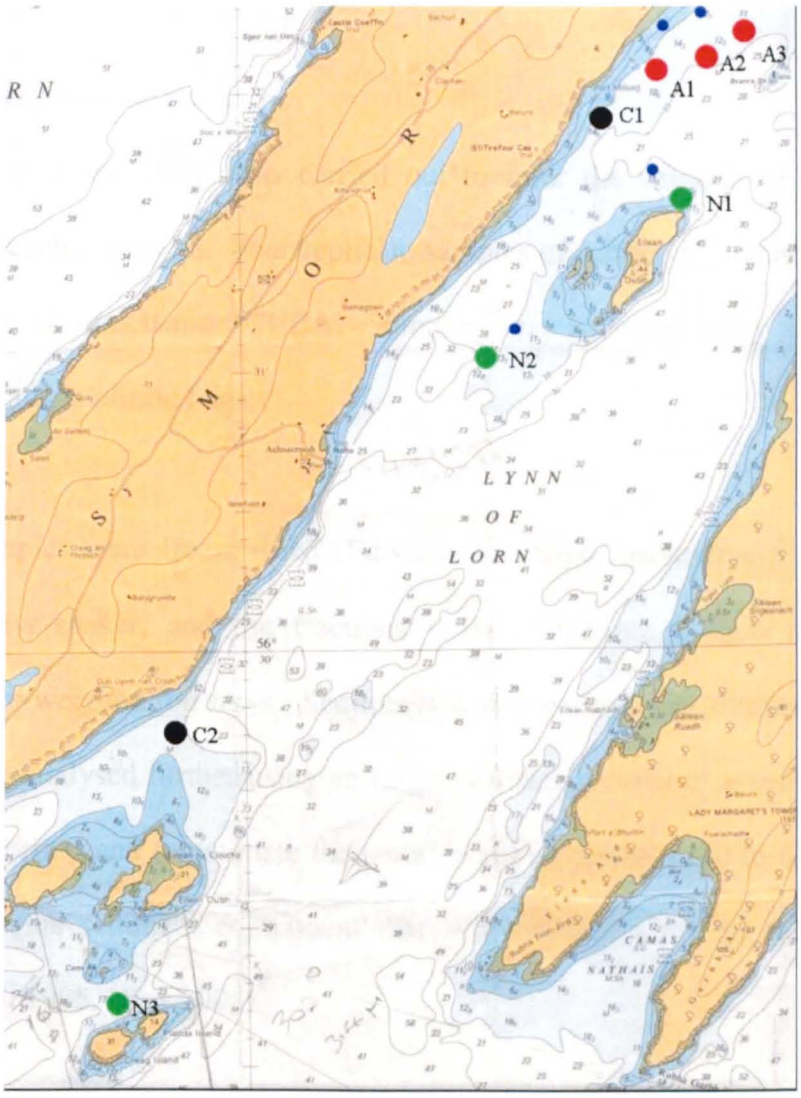

Figure 3.3 Chart showing approximate location of recruitment sites in Loch Linnhe. Artificial reef sites are shown in red, Natural reef sites in green, off-reef sites in blue and control sites in black. Refer to Table 3.1 for further information. Chart used with permission from the Hydrographic Office.

The four off-reef sites were 100m from each of four reefs (2 natural, 2 artificial). Care was taken to ensure that no other reefs of any kind were within 100m of the off-reef sites. Sites were selected to have similar depths to the natural and artificial reef study sites. The control sites were chosen for their greater distance away from any reef structure (natural or artificial), but having similar site characteristics with respect to tidal regime and depth to the reef sites used in the study. It was also important to

select sites not exposed to regular fishing and trawling activity.

3.2.2 Particle size analysis

Particle size analysis (PSA) was carried out to infer the strength of tidal water movement at each study site. Four replicate samples of surface sediment were taken at each of the 12 sites using SCUBA. Samples were collected using a trowel and placed into sealable plastic bags.

Sediment samples were freeze-dried (Edwards Modulyo freeze-dryer), sorted in a bench-top sieve-shaker, and the fractions (<1mm, 1-2mm, 2-4mm and >4mm) weighed in pre-weighed foil trays. Sediments with a particle size smaller than 1mm diameter were analysed further using an LS230 Coulter counter to assess the degree of sediment sorting and to estimate the sortable silt component (10 to 63 microns), which is the fine sediment component that is winnowed away by tidal currents (McCave et al. 1995, Hass 2002).

3.2.3 Recruitment panels

Extruded PVC plastic recruitment panels used in this study were the same as those used in chapter 2 and were made from 3mm thick Trodivur EN extruded PVC (Amari Plastics Plc.). PVC was chosen as the artificial substrata for use in this study as it has a uniform surface, is relatively inexpensive, is easy to cut and it is lightweight and, therefore, easy to handle underwater. PVC has also been shown to be a good substratum for use in settlement/recruitment studies with respect to epibiotic fouling on the west coast of Scotland (Brown 2005).

Panels were arranged in arrays of 4 replicate panels, attached in a vertical plane to a PVC frame (Figure 3.4) using cable ties. The PVC frame was constructed from 22mm grey PVC pipe. Frames were hammered into the soft sediment at the edge of each reef leaving the panels suspended approximately 15cm above the seabed. Each panel dimension was 16.5 x 22cm. This size was chosen to allow the epifaunal recruitment to panels to be photographed using a Nikonos amphibious camera with a 35mm close-up frame (19.5 x 14cm). Panels at all sites were aligned parallel to the prevailing tidal flow to expose the experimental surface of the panels to the full tidal current. This recruitment panel design was also used in the recruitment study presented in chapter 4.

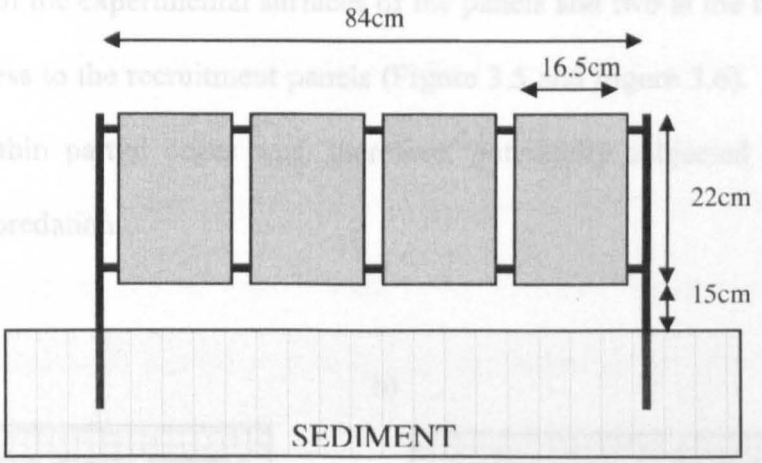

Figure 3.4. Diagram of PVC recruitment panels on PVC frame.

Prior to deployment all recruitment panels were engraved with an identifying number on the back surface. The PVC panel frames were also engraved with a code to identify reef site and treatment. White plastic garden labels were attached to each frame to make identification easier underwater; especially important for those panels subjected to heavy fouling.

Timing of deployment has been shown to affect the assemblage structure that develops on recruitment panels (Nandakumar 1996) and so panels in this experiment were all deployed within a two week period (14/07/03 to 01/08/03).

Predator exclusion

Predator exclusion cages were made from 13mm galvanised wire mesh, with cage dimensions of 92cm long x 25cm wide x 45cm high (Figure 3.5). Cages were designed to be wide enough to be stable and to provide sufficient space for large epifaunal organisms, such as the solitary ascidian, *Ascidiella aspersa* (Müller), to grow unrestricted. Partial cages were used to control for any cage artefacts. These were identical to the full cage, but with $20cm^2$ holes cut near the base of the cage (one in front of the experimental surfaces of the panels and two at the back) to allow predators access to the recruitment panels (Figure 3.5 and Figure 3.6). The epifauna on panels within partial cages was, therefore, potentially subjected to both cage artefacts and predation.

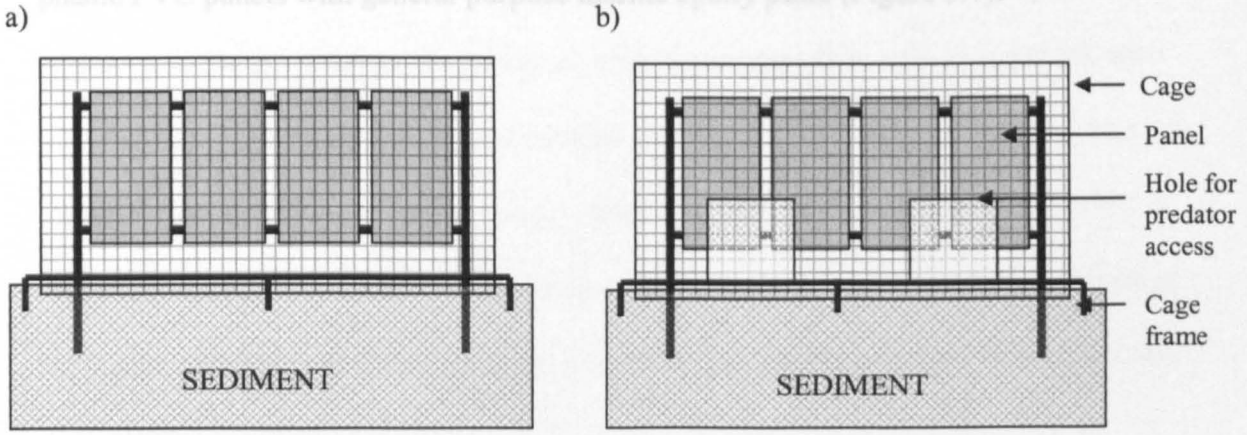

Figure 3.5 Diagram of recruitment panels with a) predator exclusion cage and b) partial cage showing the holes in the cage to allow predators access to panels.

Cage frames were constructed from PVC piping to make the cages sturdy enough to withstand tidal currents and the impact of drifting kelp. Cable ties were used to secure the edges of the cages and to attach the PVC support frames to the cages (Figure 3.5 and Figure 3.6). Fouling on cages has been shown to increase cage artefacts (Kennelly 1991) and so cages were cleaned as often as possible, using SCUBA and a scouring sponge, to remove fouling, particularly by hydroids. Cages were replaced when necessary.

Measuring cage artefacts

The effect of the presence of a cage on water flow across recruitment panels was assessed in this study using plaster clods (Doty 1970, Glasby 1999b). Clods were made with quick-set plaster (John Winter and Co. Ltd., Super Yellow dental plaster) using a cylindrical PVC plastic pipe mould resulting in a clod 50mm high with a diameter of 43mm. The initial dry weight of clods used in this study was 125g ± 3g. Those clods deformed with air bubbles were rejected as the air pockets could affect the dissolution rates. Clods were weighed and measured before being glued to plastic PVC panels with general purpose marine epoxy paste (Figure 3.7).

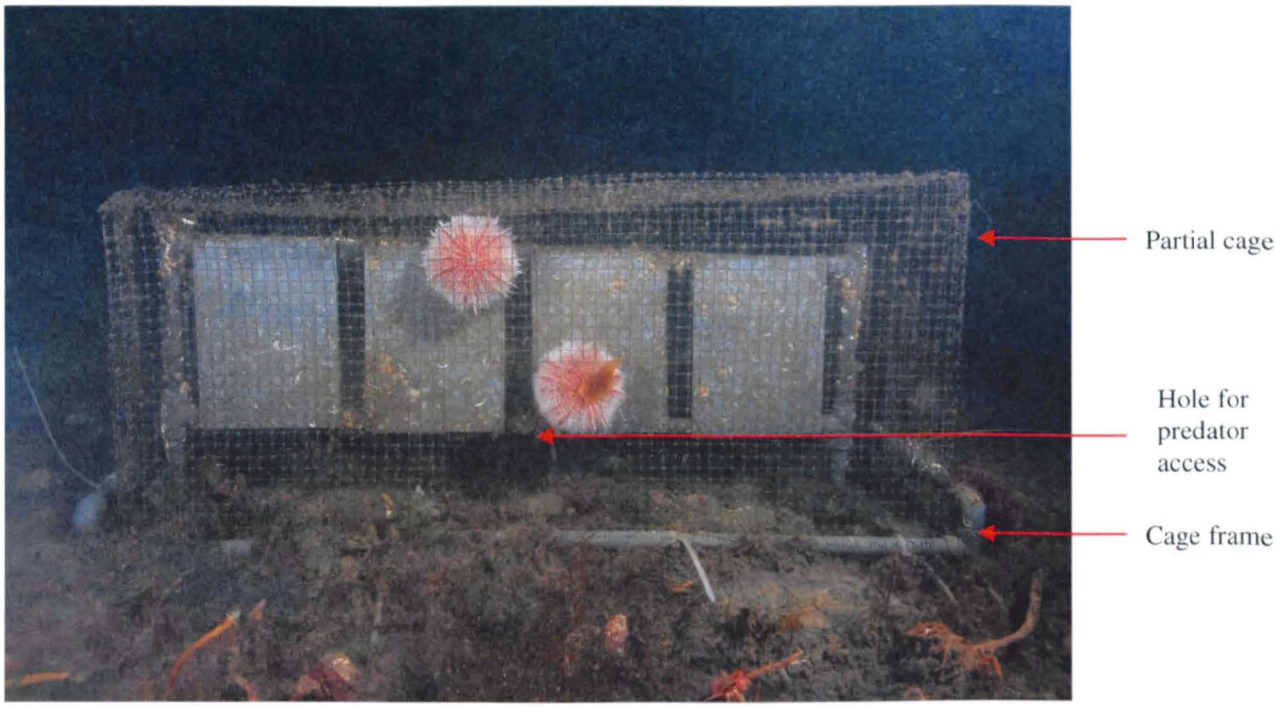

Figure 3.6. Photograph of PVC recruitment panels with partial predator exclusion cage. Note the presence of two urchins (*E. esculentus*) on panels inside the partial cage.

Five replicates of each treatment (caged, partially-caged and open recruitment panels) were placed in 7m of water (Chart Datum) for seven days in Dunstaffnage Bay (West coast of Scotland, 56°27.10N 05°26.16W) close to the Scottish Association for Marine Science. Clods on panels inside cages, partial cages and open panels were arranged in a random grid layout approximately two metres apart. All panels and cages were aligned parallel to the prevailing current. Weight loss of clods has been shown to be linear until dissolution has reduced the clod to approximately 30 percent of its original weight (Jokiel & Morrissey 1993). Clods in the present study were, therefore, left to dissolve *in situ* for just one week to prevent too much weight loss.

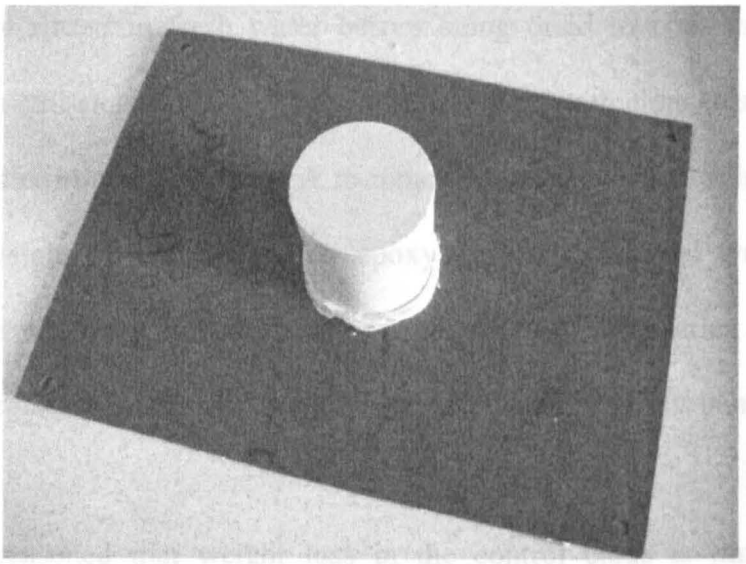

Figure 3.7. Plaster clod attached to a PVC panel prior to deployment.

Five control clods were placed in still seawater in an aquarium tank for seven days to calculate the diffusion of plaster in calm water. Temperature and salinity have been shown to affect the dissolution rate of plaster (Jokiel & Morrissey 1993) and so these were kept as similar as possible to the conditions faced by the experimental clods in Dunstaffnage Bay. Jokiel and Morrissey (1993) also showed that 20 litres is the minimum size of calibration tank that should be used for a 50g plaster clod. If too small a tank is used the calibration water becomes saturated resulting in a slowing of dissolution of plaster clods over time.

Five clods were calibrated simultaneously in the same tank, and so approximately 625g of plaster was present at the start of the calibration. The calibration tank used in this study held 1700 litres ($1.7m^3$) which was far in excess of the volumes required to prevent impedance of clod dissolution (Jokiel & Morrissey 1993). The dissolution of clods in the calibration water can, therefore, be assumed to have been constant over time.

All clods were rinsed in fresh water before being dried to constant weight and weighed whilst still attached to the PVC panels. Panels with clods were then placed in turbulent water in an aquarium tank to remove/dissolve all plaster in order to get an accurate weight of the panel with epoxy glue. The actual weight of clod remaining after one week's deployment was calculated by subtracting the weight of the panel and epoxy from the total weight of the clod attached to its panel.

Doty (1970) reasoned that weight loss in the control clods is limited only by diffusion and so the ratio of weight loss in the experimental clods to weight loss in the calm water "control" clods can be used as an index describing the magnitude of diffusing enhancement caused by water motion. This diffusion factor (DF), calculated by dividing the mean weight loss of the control clods by the mean weight loss of experimental clods, was used in this study to assess cage artefacts with respect to water flow.

3.2.5 Sampling protocol

Recruitment panels were deployed in August 2003 at all 12 sites (3 artificial, 3 natural, 4 off-reef and 2 control) and left to foul *in situ* for 15 months until October 2004. Three panel treatments (each with 4 panels on a single frame) were deployed at each site; caged, open and partially-caged.

All panel arrays and cages were deployed and recovered using SCUBA. Panels were recovered from the seabed in collection frames made from 1.5 inch PVC pipe. Care was taken to protect the experimental surfaces of the panels from accidental scraping. Panels were kept submerged in a tank of seawater onboard the research vessel until

they could be transferred into seawater tanks in an aquarium back at the laboratory.

All panels were first photographed in the aquarium using Fuji velvia slide film, a Nikonos amphibious camera and 35mm close-up frame (19.5 x 14cm) and strobe. Epifaunal community analysis was then conducted using a boom-mounted binocular stereo microscope. A wooden counting frame with 100 grids, delineated using monofilament, was used to count sessile organisms which were identified to species level where possible. The frame was designed to fit exactly over the panels and to cover the outside 15mm of each edge. Taxa in this edge area were excluded from the abundance counts to control for edge effects (Todd & Turner 1986).

Biomass was determined by scraping all epibiota from the experimental surface of the panels into pre-weighed crucibles. Solitary and colonial ascidians were weighed separately. All crucibles were dried at 50°C to constant weight before being ashed in a muffle furnace overnight at 450°C.

3.2.6 Data analysis

Biomass data were tested for normality using the Anderson-Darling test and for equal variances using Levene's test (Dytham 2003). The effect of treatment at the different reef types was tested using one-way ANOVAs with Fisher's pairwise comparisons.

Community structures on recruitment panels subjected to different cage treatments were assessed using multivariate statistical methods within the PRIMER software package (Clarke & Warwick 2001). Non-parametric Multi-Dimensional Scaling

(nMDS) ordinations and analysis of similarity (ANOSIM, Clarke 1993) were used to assess differences between treatments at different sites. Data were log (x+1) transformed prior to multivariate analysis to minimise bias caused by very abundant taxa.

Characterising species were identified using the SIMPER procedure (PRIMER, Clarke 1993). The abundances of the characterising species were assessed for differences between treatment types at each reef type using non-parametric Kruskall Wallis pairwise comparisons because of heterogeneous variances in the data.

The developing epifaunal assemblages were compared between treatments in this study and not between reef types. This enabled the assessment of predation on epifaunal assemblages at each of the reef types (artificial, natural, artificial off-reef, natural off-reef and control). Comparisons will be made between the epifaunal assemblages at artificial and natural reefs in chapter 4.

3.3 Results

3.3.1 Particle Size Analysis

Sediment samples from all sites were dominated by the 0-1mm particle size fraction (Table 3.2), ranging from approximately 62 to 87 percent by weight. The 1-2mm fraction was the most variable between sites, ranging from approximately 3 to 30 percent by weight. The 2-4mm fraction was the least represented fraction ranging from approximately 1 to 12 percent by weight. The greater than 4mm sediment fraction accounted for 1 to 18 percent by weight of the sediments.

Table 3.2. Sediment size fractions by percentage weight for each study site.

Reef	>4mm	2-4mm	1-2mm	0-1mm	Mean grain size (mm)
N1 ON	8.46	9.00	11.76	70.78	1.14
N2 ON	9.77	5.96	8.05	76.22	1.07
N3 ON	1.01	7.17	29.74	62.08	1.01
N1 OFF	7.55	5.14	6.88	80.44	0.96
N2 OFF	10.67	5.51	6.20	77.62	1.07
A1 ON	9.94	3.05	6.90	80.11	0.99
A2 ON	7.15	5.46	11.26	76.12	1.00
A3 ON	11.50	12.23	13.35	62.92	1.34
A1 OFF	13.59	6.12	6.88	73.42	1.20
A2 OFF	18.55	4.67	7.23	69.54	1.34
C1	15.40	4.07	4.19	76.34	1.18
C2	7.03	1.67	3.63	87.37	0.82

Frequency distribution curves of the 0-1mm fraction (Appendix II) showed that sediments collected from all twelve sites were either bimodal or poorly sorted with little variation between sites except for N3 ON reef site which, while still poorly sorted, had a higher percentage of coarse grains.

The mean grain size, calculated using the percentage weight of each fraction, of the 12 sites used in this study ranged from 0.82mm at C2 to 1.34mm at A3 ON and A2 OFF reef sites (Table 3.2). Using the Hjulstrom curve (Figure 3.8) the mean grain size range of sediments analysed in this study show that the mean flow velocity at the sites is in the range of approximately 0.09 to 0.11m sec^{-1}.

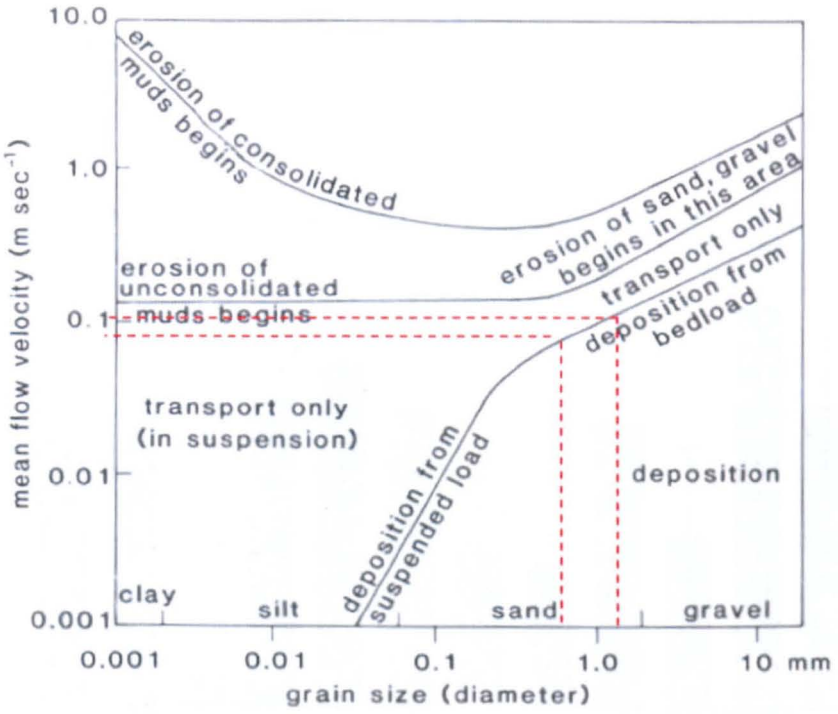

Figure 3.8 Schematic representation of relationship between current velocity and sediment erosion, transport and deposition (Hjulstrom's diagram, deduced experimentally from flows of 1m depth) (Tucker 1991). The dotted red lines show the range of mean flow velocities of sediments in this study.

Figure 3.9 shows the mean sortable silt fractions at the twelve sites used in this study. While there were obvious differences between certain sites, for example N3 ON had a lower sortable silt fraction by volume than any other site, no significant differences were found between reef types (natural, natural off-reef, artificial, artificial off-reef, control) (One-way ANOVA with 95% Fisher's pairwise comparisons, $p > 0.05$; Table 3.3).

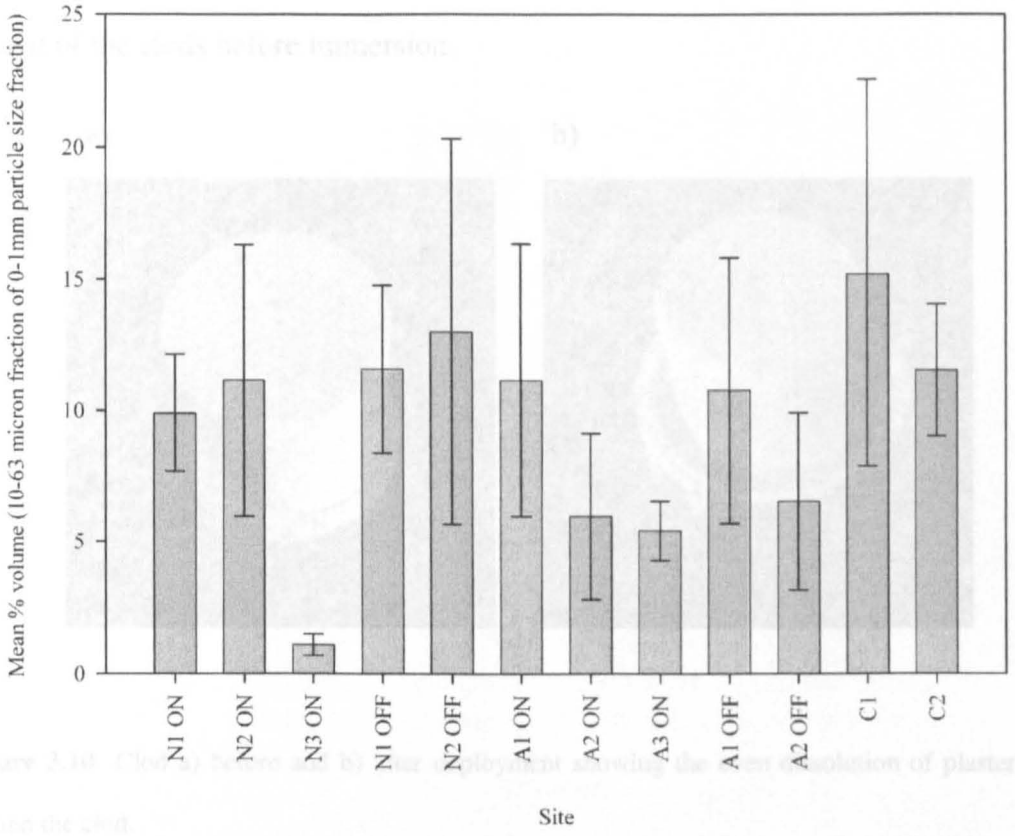

Figure 3.9 Mean sortable silt (10-63 micron fraction of the 0-1mm sediments) by volume. Error bars show 95% confidence intervals (n = 4).

Table 3.3. ANOVA table for tests for differences in sortable silt fraction between reef type (natural on-reef, natural off-reef, artificial on-reef, artificial off-reef, control).

Source	DF	SS	MS	F	P
Reef type	4	72.2	18.1	1.31	0.354
Error	7	96.6	13.8		
Total	11	168.8			
S = 3.7115	R-Sq = 42.78%	R-Sq (adj) = 10.09%			

3.3.2 Cage artefacts

Figure 3.10 shows a photograph of a typical clod before and after submersion. It can be seen that the dissolution of the clod appears to be uniform around the circumference of the clod. Following one week of immersion the maximum weight

loss of clods was 60.4g. This represents approximately 50 percent of the average weight of the clods before immersion.

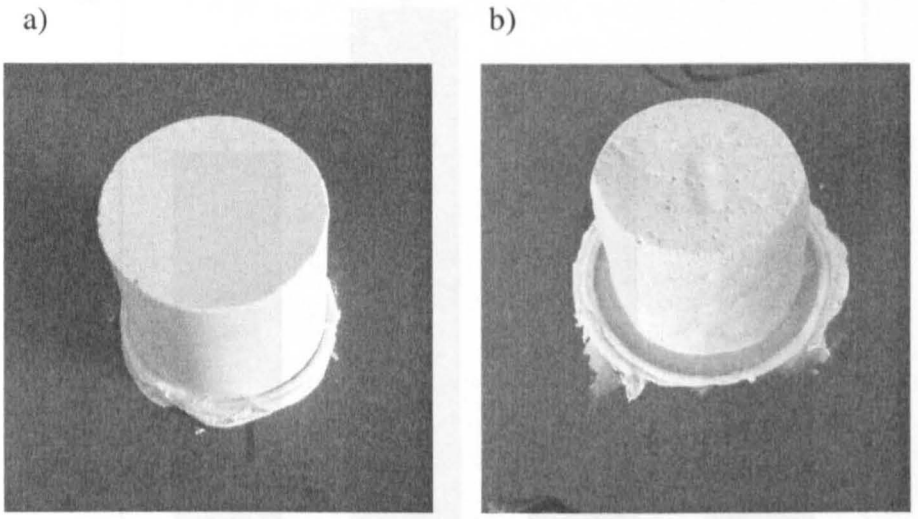

Figure 3.10 Clod a) before and b) after deployment showing the even dissolution of plaster from around the clod.

The mean weight loss of clods on open, caged, partially-caged and control panels after one week of immersion in Dunstaffnage Bay (aquarium tank for control panels) is shown in Figure 3.11. Clods on open panels had the greatest weight loss. Partially-caged and then caged panels had the next greatest weight loss, followed by control panels with the least weight loss.

The DF ratios in this study ranged from 1.76 for caged clods to 2.36 for open clods (Table 3.4). The percentage loss of water velocity across panels inside cages and partial cages was calculated using the DF values. It can be seen that there was little difference between the water flow across clods inside cages or partial cages, but that these had approximately 25 percent less water movement across them than clods attached to open panels (Table 3.4).

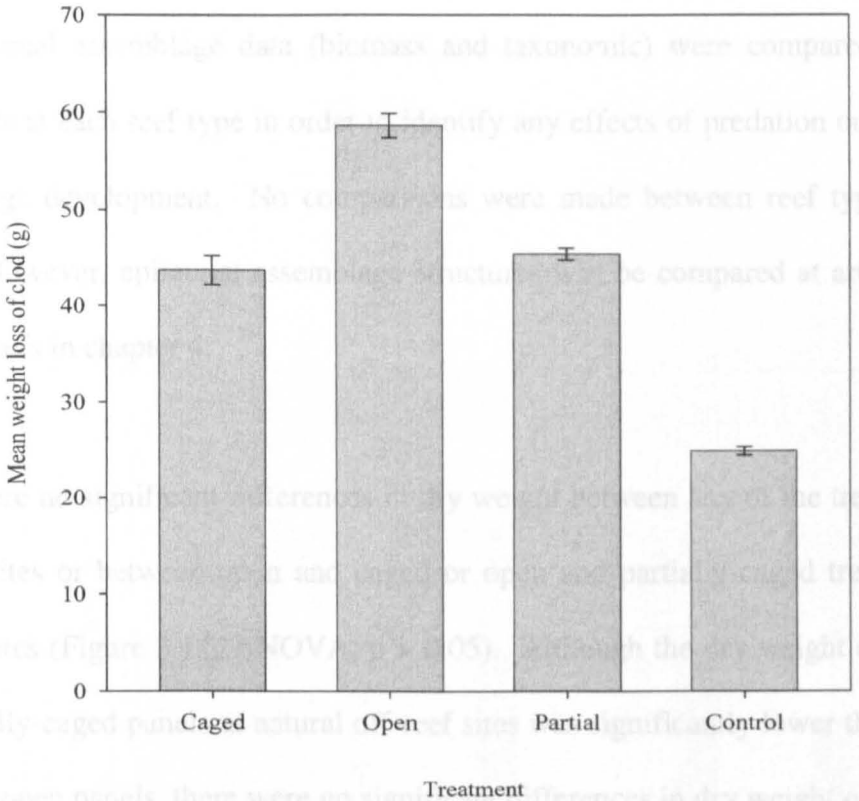

Figure 3.11 Mean dry weight loss of clods with 95% CI after 7 days of dissolution (n = 5 in each case).

Table 3.4 DF ratios of clods (mean weight loss of control clods ÷ mean weight loss of experimental clods) and percentage of maximum water current velocity across clods at different treatments.

Treatment	DF ratio	% of maximum water current velocity on clods
Caged	1.76	75%
Open	2.36	100%
Partial	1.82	77%

3.3.3 Biomass

All epifaunal assemblage data (biomass and taxonomic) were compared between treatments at each reef type in order to identify any effects of predation on epifaunal assemblage development. No comparisons were made between reef types in this study. However, epifaunal assemblage structures will be compared at artificial and natural reefs in chapter 4.

There were no significant differences in dry weight between any of the treatments at control sites or between open and caged or open and partially-caged treatments at natural sites (Figure 3.12; ANOVA, $p > 0.05$). Although the dry weight of biomass on partially-caged panels at natural off-reef sites was significantly lower than that on caged or open panels, there were no significant differences in dry weight of epifaunal biomass between open and caged treatments at natural off-reef sites (Figure 3.12; ANOVA, $p > 0.05$). However, at both artificial and artificial off-reef sites the dry weight of epifauna on caged panels was significantly greater than the dry weight of epifauna on either open or partially-caged panels (Figure 3.12; ANOVA, $p < 0.05$). No significant differences were found in dry weight of epifauna between open and partially-caged panels at artificial or artificial off-reef sites (Figure 3.12; ANOVA, $p > 0.05$). Full ANOVA tables for biomass data are given in Appendix II.

There were no significant differences in ash free dry weight on panels between treatments at control sites, natural sites or natural off-reef sites (Figure 3.13; ANOVA, $p > 0.05$). As for the dry weight data, there was a significantly greater ash free dry weight of epifauna on caged panels than open or partially-caged panels at both artificial and artificial off-reef sites (Figure 3.13; ANOVA, $p < 0.05$). There

were no significant differences in ash free dry weight of epifauna between open and partially-caged panels at artificial or artificial off-reef sites (Figure 3.13; ANOVA, $p > 0.05$).

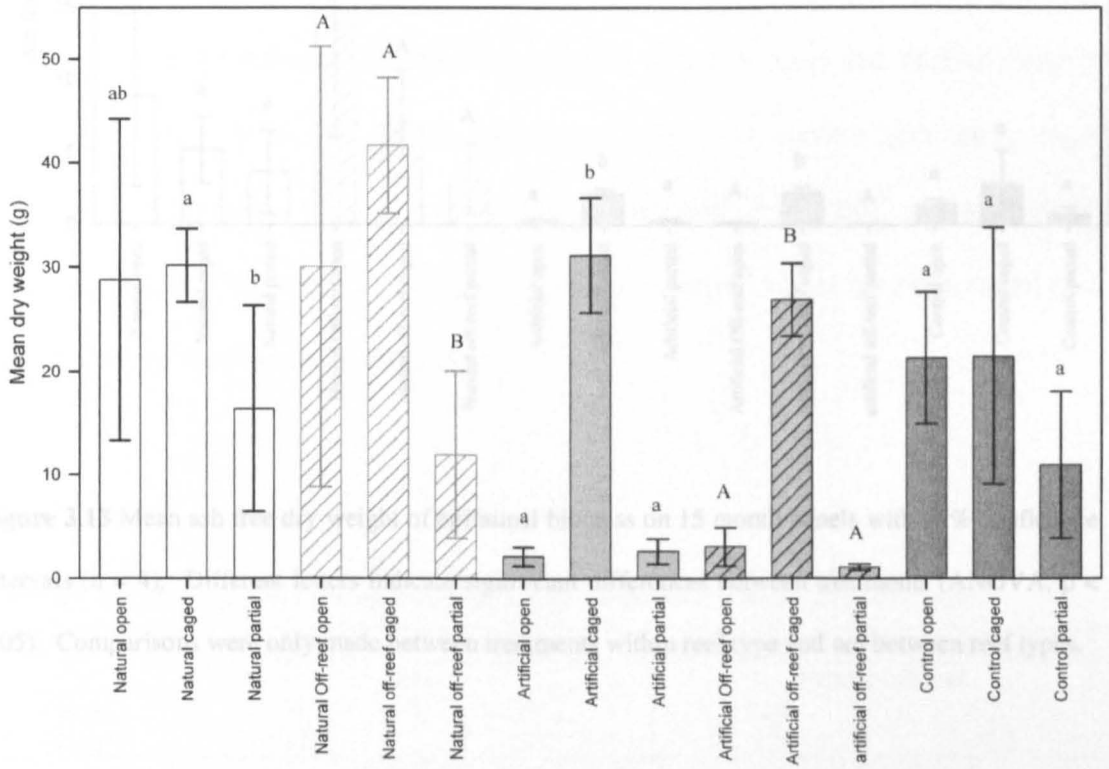

Figure 3.12 Mean dry weight of epifaunal biomass on 15 month panels with 95% confidence intervals (n = 4). Different letters indicate significant differences between treatments (ANOVA, $p < 0.05$). Comparisons were only made between treatments within reef type and not between reef types.

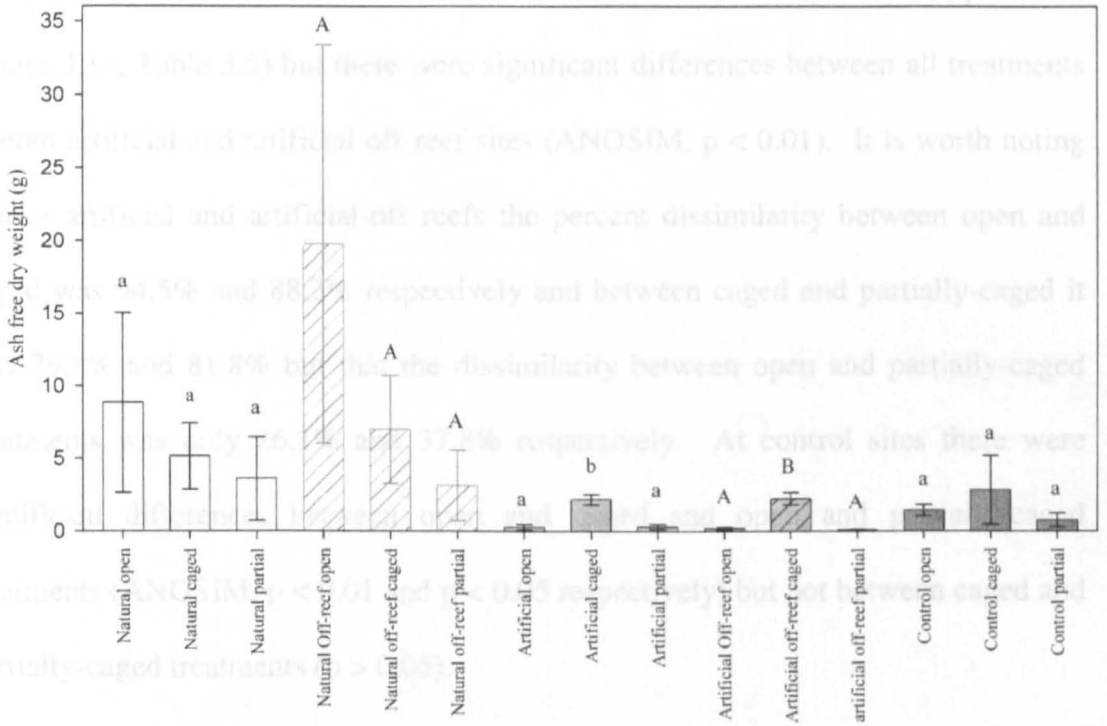

Figure 3.13 Mean ash free dry weight of epifaunal biomass on 15 month panels with 95% confidence intervals (n = 4). Different letters indicate significant differences between treatments (ANOVA, $p < 0.05$). Comparisons were only made between treatments within reef type and not between reef types.

3.3.4 Multivariate analysis of taxonomic data

It can be seen in Figure 3.14 that data points at natural and natural-off reefs were clustered according to site; i.e. the three treatments were separated as points were clustered into three and two groups respectively with each group containing all three treatments. However, at artificial and artificial off-reef sites data points were clustered according to treatment rather than site. It can also be seen that the caged data points are more distinct than open or partial data points in these plots (Figure 3.14c and d).

No significant differences were found between the epibiotic assemblages on panels from different treatments at the natural or natural off-reef sites (ANOSIM, $p > 0.05$, Figure 3.14, Table 3.5) but there were significant differences between all treatments at both artificial and artificial off-reef sites (ANOSIM, $p < 0.01$). It is worth noting that at artificial and artificial-off reefs the percent dissimilarity between open and caged was 94.5% and 88.2% respectively and between caged and partially-caged it was 79.8% and 81.8% but that the dissimilarity between open and partially-caged treatments was only 26.1% and 37.8% respectively. At control sites there were significant differences between open and caged and open and partially-caged treatments (ANOSIM, $p < 0.01$ and $p < 0.05$ respectively) but not between caged and partially-caged treatments ($p > 0.05$).

Table 3.5 ANOSIM results showing dissimilarities (%) between treatments at all reef types.

	Open	Caged	Open	Caged
	Natural		Natural off-reef	
Caged	6.5		12.4	
Partial	11.2	7.2	9.5	9.0
	Artificial		Artificial off-reef	
Caged	94.5**		88.2**	
Partial	26.1**	79.8**	37.8**	81.8**
	Control			
Caged	33.4**			
Partial	22.3*	4.9		

** significant at $p<0.01$, * significant at $p<0.05$

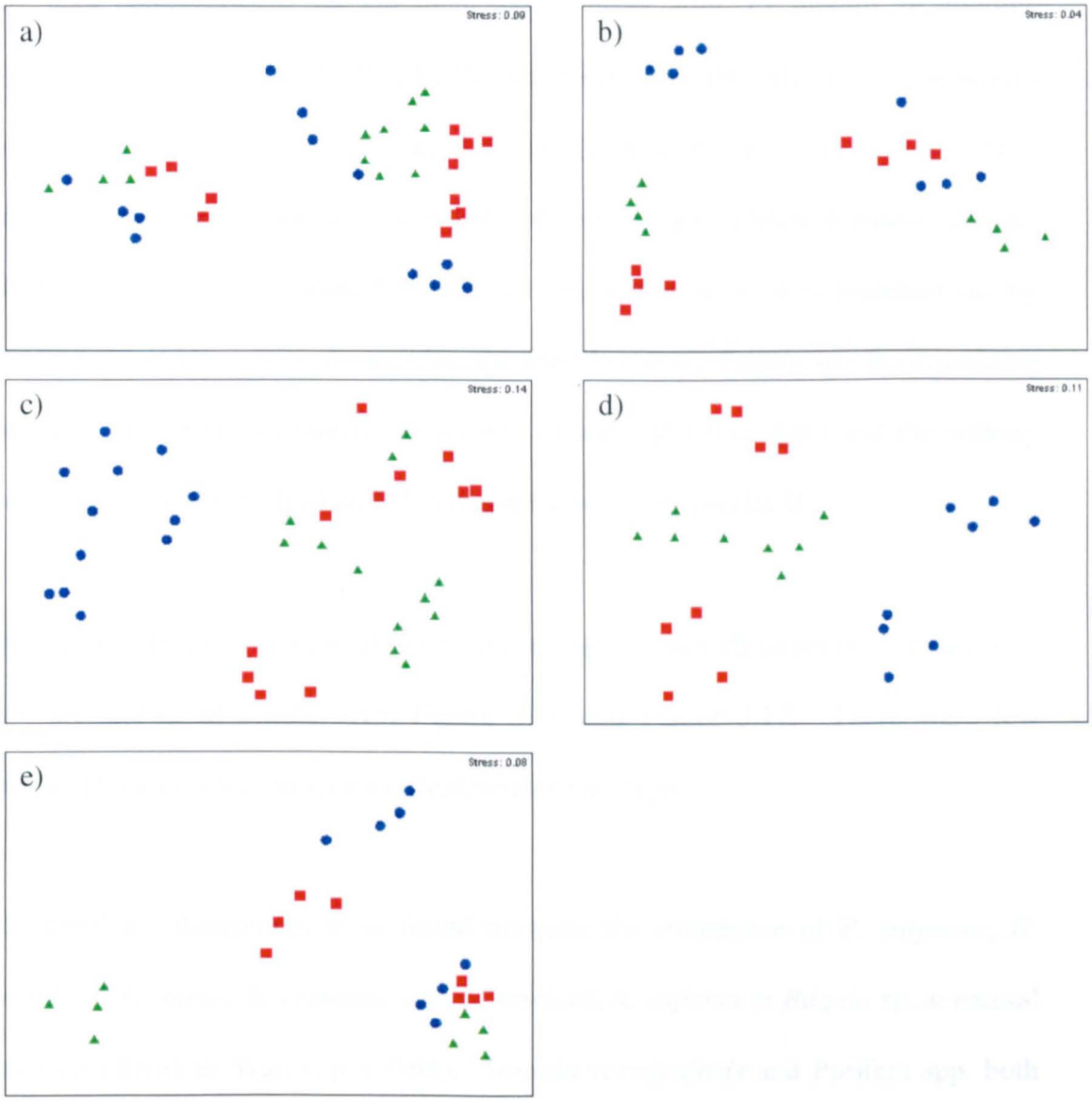

Figure 3.14 nMDS plots for the 15 month data; a) Natural, b) Natural off-reef, c) Artificial, d) Artificial off-reef, e) Control. Factor = treatment; ▲ Open, ● Caged, ■ Partial.

3.3.5 Univariate analysis of taxonomic data

The taxa characterising the epifaunal assemblages after 15 months of fouling, identified using SIMPER (PRIMER, Clarke 1993), were the calcareous tube worms *Pomatoceros triqueter* (L.), *Hydroides elegans* (Haswell), *Serpula vermicularis* (L.), *Filograna implexa* (Berkeley) and sinistral spirorbids; the barnacle *Balanus crenatus* (Bruguière) and its scar (left behind when an animal dies or is knocked off by grazers); the saddle oyster, Anomiidae; the erect bryozoan *Bugula* sp.; the encrusting byrozoan *Fenestrulina malusii* (Audouin); sponges (Porifera spp.) and the solitary ascidian *A. aspersa*. Full SIMPER tables are given in Appendix II.

The mean abundance of each of these taxa on panels from all treatments at each reef type are shown in Figure 3.15, Figure 3.16 and Figure 3.17. There were few consistent patterns within species, treatment or reef type.

No significant differences were found between the abundance of *P. triqueter*, *H. elegans*, *B. crenatus*, *B. crenatus* scar, *F. implexa*, *A. aspersa* or *Bugula* sp. at natural reef sites (Kruskall Wallis, $p > 0.05$). *Serpula vermicularis* and Porifera spp. both had a significantly lower abundance on open panels than partially-caged panels at natural sites (Kruskall Wallis, $p < 0.05$, Figure 3.15 and Figure 3.17) but no significant difference between open and caged or caged and partially-caged treatments ($p > 0.05$). There was a significantly greater abundance of Anomiidae on caged panels than open panels at natural sites (Kruskall Wallis $p < 0.05$, Figure 3.16) but no significant difference between open and partially caged or caged and partially-caged panels ($p > 0.05$). *Fenestrulina malusii* had a greater abundance on open than caged panels at natural sites (Kruskall Wallis, $p < 0.05$, Figure 3.17) but no

significant difference between open and partially-caged or caged and partially-caged panels ($p > 0.05$). There was a greater abundance of sinistral spirorbids on open and partially-caged panels than on caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference between open or partially-caged panels ($p > 0.05$).

At natural off-reef sites *P. triqueter* and *H. elegans* both had a significantly higher abundance on caged than open or partially-caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference between open or partially-caged panels ($p > 0.05$). No significant differences in abundance between panel treatments were found for *S. vermicularis*, sinistral spirorbid, *B. crenatus* scar, Anomiidae, *A. aspersa*, Porifera spp., *F. malusii* or *Bugula* sp. at natural off-reef sites (Kruskall Wallis, $p > 0.05$, Figure 3.15, Figure 3.16 and Figure 3.17). There was a significantly lower abundance of *B. crenatus* on open panels than either caged or partially-caged panels at natural off-reef sites (Kruskall Wallis, $p < 0.05$, Figure 3.16) and no significant differences between caged and partially-caged panels ($p > 0.05$). There was a significantly greater abundance of *F. implexa* on caged panels than on partially-caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.16) but no significant difference between open and caged or open and partially-caged panels ($p > 0.05$).

No significant differences in abundance between panel treatments were found for *P. triqueter*, *S. vermicularis*, sinistral spirorbid or *A. aspersa* at artificial reef sites (Kruskall Wallis, $p > 0.05$, Figure 3.15 and Figure 3.17). *Balanus crenatus*, *F. implexa*, Porifera spp. and *Bugula* sp. all had significantly greater abundances on caged panels than open or partially-caged panels at artificial reef sites (Kruskall

Wallis, $p < 0.05$, Figure 3.16 and Figure 3.17) but no significant difference between abundances on open and partially-caged panels ($p > 0.05$). There was a significantly lower abundance of *B. crenatus* scars on caged than open or partially-caged panels at artificial reef sites (Kruskall Wallis, $p < 0.05$, Figure 3.16). A significantly greater abundance of Anomiidae was found on partially-caged panels than open panels at artificial sites (Kruskall Wallis, $p < 0.05$, Figure 3.16) but no significant differences between caged and open or caged and partially-caged panels ($p > 0.05$). *Hydroides elegans* had a significantly greater abundance on open than caged panels at artificial sites (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference between partially-caged and open or partially-caged and caged panels ($p > 0.05$). *Fenestrulina malusii* had a significantly greater abundance on partially-caged than open panels which, in turn, had a significantly greater abundance than caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.17).

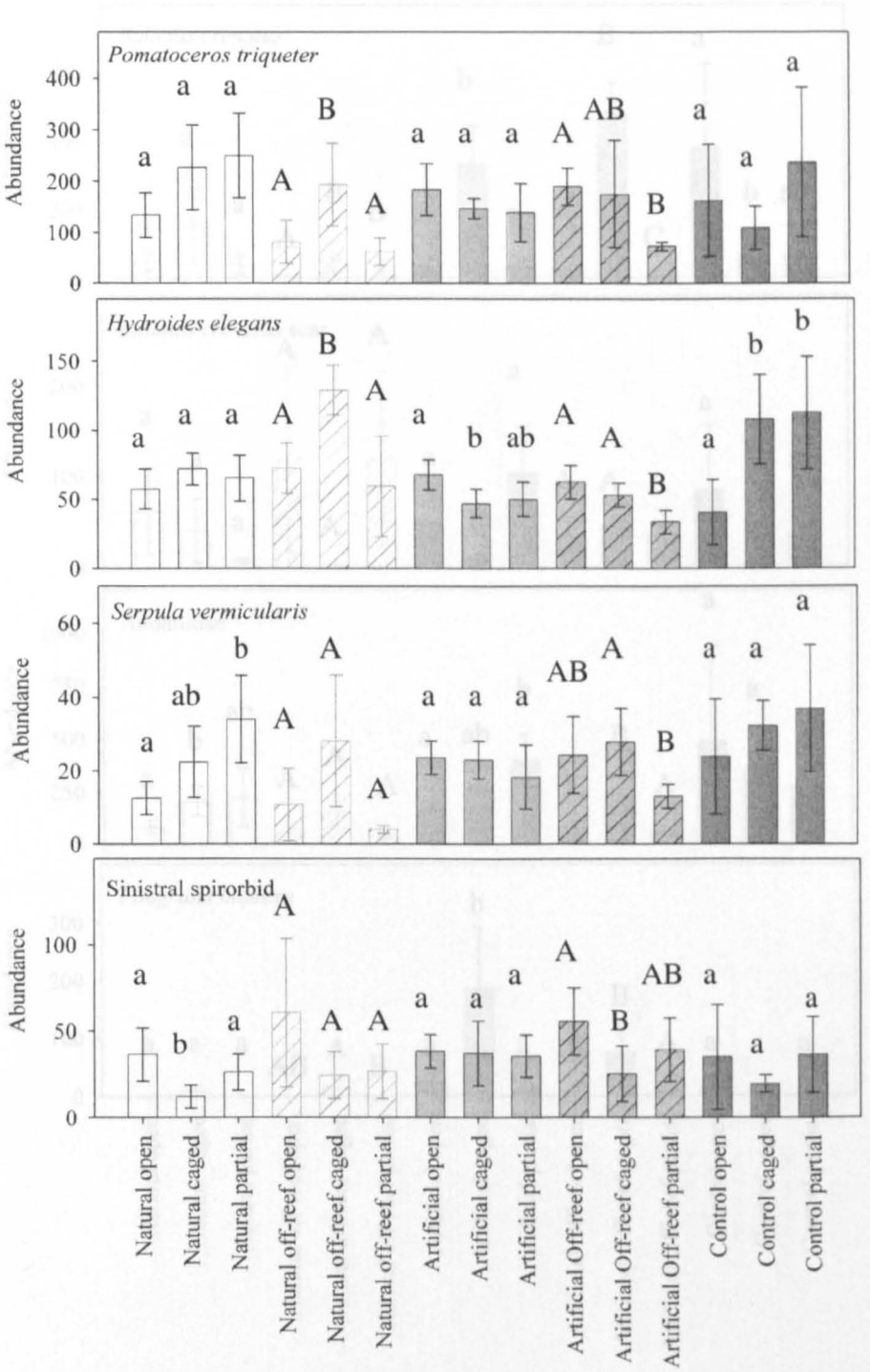

Figure 3.15 Mean abundance of *P. triqueter*, *H. elegans*, *S. vermicularis*, and sinistral spirorbids on PVC panels on different treatments at different reef types after 15 months of fouling with 95% confidence intervals (n = 4). Different letters indicate significant differences between treatments within reef types (Kruskall Wallis pairwise tests, $p < 0.05$; Appendix II). Comparisons were only made between treatments within reef type and not between reef types.

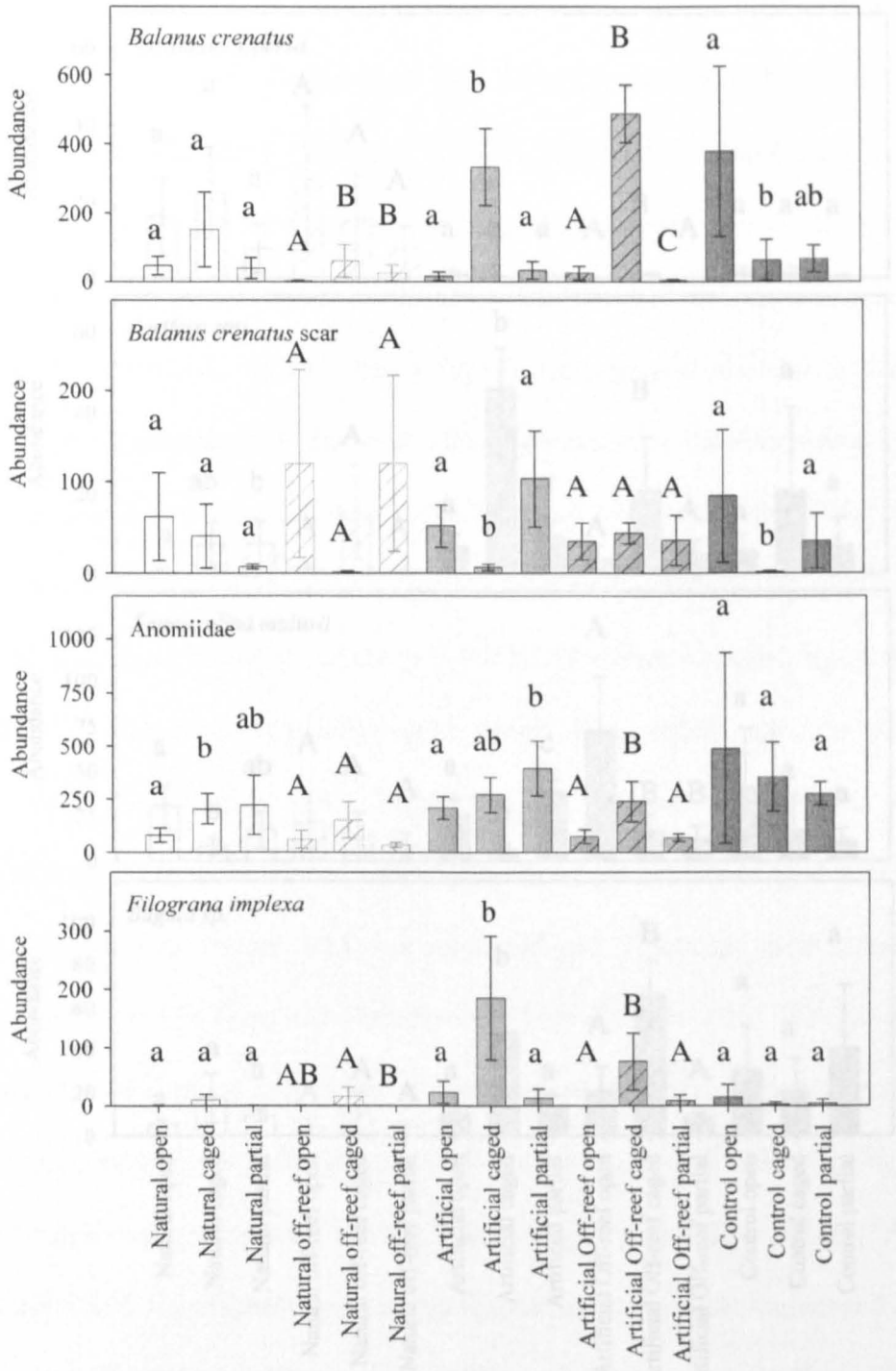

Figure 3.16 Mean abundance of *B. crenatus*, *B. crenatus* scar, Anomiidae and *F. implexa* on PVC panels on different treatments at different reef types after 15 months of fouling with 95% confidence intervals (n = 4). Different letters indicate significant differences between treatments within reef types (Kruskall Wallis pairwise tests, $p < 0.05$; Appendix II). Comparisons were only made between treatments within reef type and not between reef types.

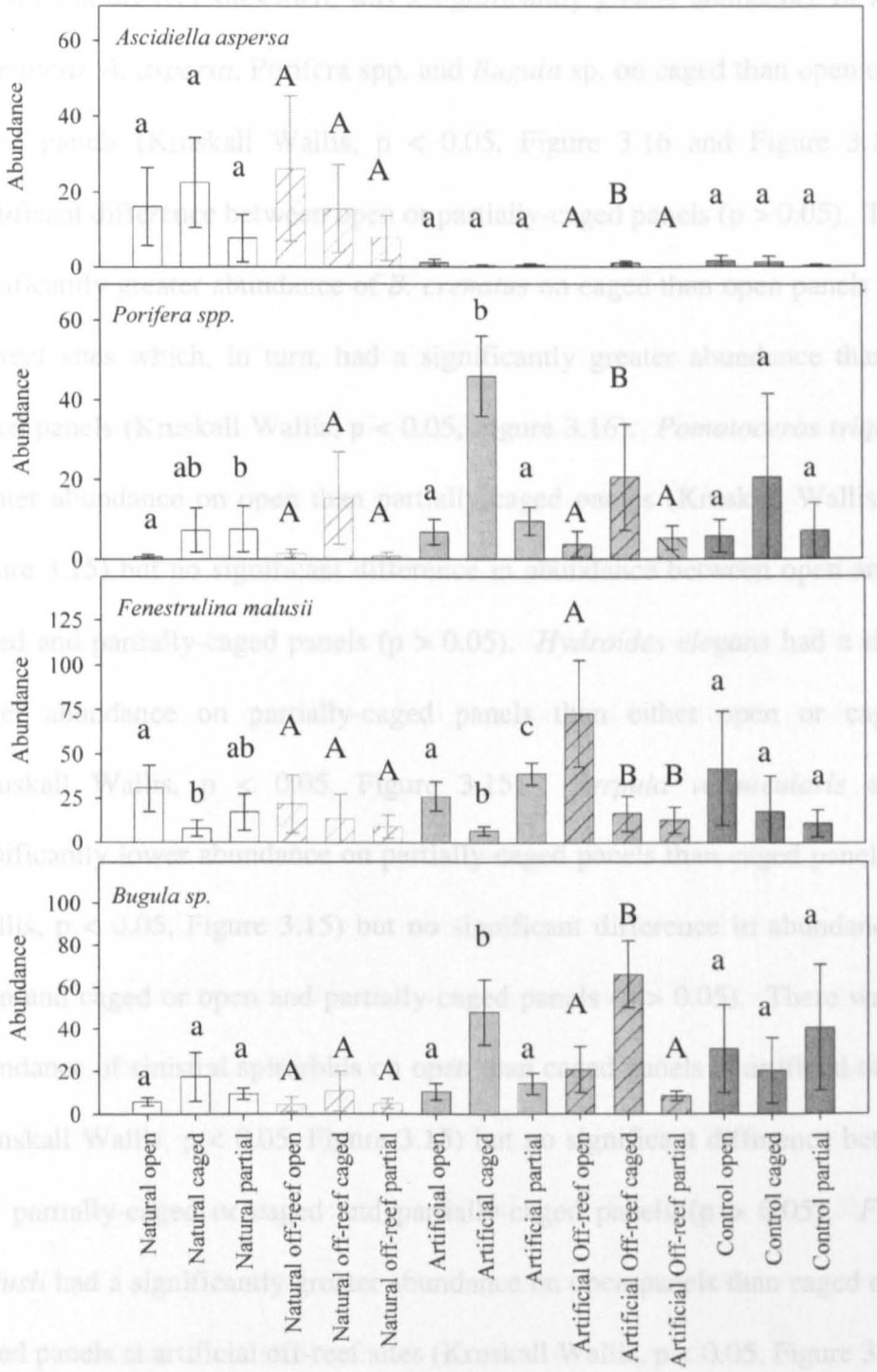

Figure 3.17 Mean abundance of *A. aspersa*, Porifera sp., *F. malusii* and *Bugula* sp. on PVC panels on different treatments at different reef types after 15 months of fouling with 95% confidence intervals (n = 4). Different letters indicate significant differences between treatments within reef types (Kruskall Wallis pairwise tests, $p < 0.05$; Appendix II). Comparisons were only made between treatments within reef type and not between reef types.

At artificial off-reef sites there was a significantly greater abundance of Anomiidae, *F. implexa*, *A. aspersa*, Porifera spp. and *Bugula* sp. on caged than open or partially-caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.16 and Figure 3.17) but no significant difference between open or partially-caged panels ($p > 0.05$). There was a significantly greater abundance of *B. crenatus* on caged than open panels at artificial off-reef sites which, in turn, had a significantly greater abundance than partially-caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.16). *Pomatoceros triqueter* had a greater abundance on open than partially-caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference in abundance between open and caged or caged and partially-caged panels ($p > 0.05$). *Hydroides elegans* had a significantly lower abundance on partially-caged panels than either open or caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.15). *Serpula vermicularis* also had a significantly lower abundance on partially-caged panels than caged panels (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference in abundance between open and caged or open and partially-caged panels ($p > 0.05$). There was a greater abundance of sinistral spirorbids on open than caged panels at artificial off-reef sites (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference between open and partially-caged or caged and partially-caged panels ($p > 0.05$). *Fenestrulina malusii* had a significantly greater abundance on open panels than caged or partially-caged panels at artificial off-reef sites (Kruskall Wallis, $p < 0.05$, Figure 3.17) and no significant difference between caged and partially-caged panels ($p > 0.05$).

At control sites there were no significant differences in abundance between treatments for *P. triqueter*, *S. vermicularis*, sinistral sprirorbid, Anomiidae, *F. implexa*, *A. aspersa*, Porifera spp., *F. malusii* or *Bugula* sp. (Kruskall Wallis, $p <$

0.05, Figure 3.15, Figure 3.16 and Figure 3.17). *Hydroides elegans* had a significantly lower abundance on open panels than caged or partially-caged panels at control sites (Kruskall Wallis, $p < 0.05$, Figure 3.15) but no significant difference between abundances on caged or partially-caged panels ($p > 0.05$). There was a significantly greater abundance of *B. crenatus* on open panels than caged panels at control sites (Kruskall Wallis, $p < 0.05$, Figure 3.16) but no significant differences between abundances on open and partially-caged or caged and partially-caged panels ($p > 0.05$). There was, however, a significantly lower abundance of *B. crenatus* scars on caged than either open or partially-caged panels at control sites (Kruskall Wallis, $p < 0.05$, Figure 3.16) but no significant difference in abundance between open or partially-caged panels ($p > 0.05$). Full Kruskall Wallis tables are given in Appendix II.

As predators had access to both open and partially-caged panels but not caged panels, and cage artefacts with respect to water flow have been shown to be similar between caged and partially-caged treatments, similarities and differences between open, caged and partially-caged treatments can be used to investigate the effects of predation at different reef types. A significant difference in assemblage structure (multivariate analysis), epifaunal biomass or taxonomic abundance between caged panels and open or partially-caged panels suggests predation had influenced the epifaunal assemblage, especially if there are no significant differences between open and partially-caged panels. Conversely, if there are significant differences between open and caged or partially-caged panels but no significant differences between caged and partially-caged panels this suggests that cage artefacts had influenced the epifaunal assemblage. The relative influence of cage artefacts and predation can,

therefore, be inferred from the results presented in section 3.3. These are summarised in Table 3.6 where it can be seen that predation had a greater influence on epifaunal assemblage structures at artificial and artificial off-reef sites than it did at natural, natural-off or control sites.

Table 3.6 Summary table of Figure 3.12, Figure 3.13, Figure 3.14, Table 3.5, Figure 3.15, Figure 3.16 and Figure 3.17 showing which sites had epifaunal biomasses, assemblages structures or taxonomic abundances influenced by predation and/or cage artefacts. P = predation, C = cage artefacts, P/C = both predation and cage artefacts. No entry shows no evidence of either predation or cage artefacts.

	Natural	Natural Off-reef	Artificial	Artificial Off-reef	Control
Epifaunal Biomass					
Dry weight			P	P	
Ash free dry weight			P	P	
Multivariate Assemblage Structure			C/P	C/P	C
Univariate, Taxonomic					
Pomatoceros triqueter		P			
Hydroides elegans		P	P/C		C
Serpula vermicularis					
Sinistral spirorbid	Inverse P			Inverse P/C	
Balanus crenatus		C	P	P	P/C
Balanus crenatus scar			P		P
Anomiidae	P/C			P	
Filograna implexa			P	P	
Ascidiella aspersa				P	
Porifera spp.			P	P	
Fenestrulina malusii	Inverse P/C		Inverse P	C	
Bugula sp.			P	P	

3.4 Discussion

This study has shown that predation has an important influence on the development of some epifaunal assemblage structures. In addition, differences were found in either the effect of predation or in the scale of predation pressures between the natural and artificial reef sites assessed in Loch Linnhe.

3.4.1 Site characteristics

Local hydrodynamics are known to influence the supply of propagules to an area (Underwood & Keough 2001, Gilg & Hilbish 2003). Although the meso-scale flow field and currents, which deliver propagules to the study sites, were not investigated in detail in the current study (but see chapter 4), particle size analysis (PSA) of sediments showed current velocities were similar across study sites. This is important as significant differences in factors such as current velocity could potentially contribute to differences found between treatments at different reef types. Factors such as temperature, depth and salinity can also influence the recruitment and growth of sessile marine invertebrates (e.g. Nellis & Bourget 1996, Dethier & Schoch 2005) and all sites in this study were selected to be as similar with respect to environmental characteristics as possible. Temperature was recorded over a one month period (*unpubl.*) at each of the six on-reef sites used in this study and no apparent differences were seen between sites or reef type. However, current velocity is the main factor that could likely influence the relationship between epifaunal assemblage development under different cage treatments.

All sites had either bimodal or poorly-sorted sediments which suggests they were all low energy sites (Tucker 1991). The best current-related parameters with respect to particle size analysis of sediments are the modal or mean size of the 10-63 micron fraction (Ambrose & Anderson 1990). This "sortable silt fraction" (Hass 2002) is liable to winnowing by currents and so the proportion of this fraction within a sample can be used to assess the relative current velocities at different sites. Although traditionally used for palaeoceanographic studies in the deep sea, this technique has recently been shown to be a useful technique for use in inshore fjordic environments

(Howe *pers. coms.*). This method was used in the present study in preference to the deployment of current meters as it both avoided the potential problems of current meters getting tangled up in drifting macroalgae, which can be a significant problem in Loch Linnhe, and also because it gives a longer-term indication of the prevalent current regimes at a site.

Two of the artificial reefs used in this study were constructed of simple reef blocks and the third of complex blocks. Ideally only one type of reef module would have been used, but at the start of this study the Loch Linnhe artificial reef complex was still under construction and the choice of reef modules of appropriate age and depth was very limited. Although not ideal, both the simple and complex reef modules had a significantly greater habitat complexity than the natural rocky reefs in Loch Linnhe (Rose 2005) and so the use of both types of reef module was not thought to have compromised the conclusions drawn from this study.

As discussed previously there were difficulties in selecting suitable natural sites and natural-off reef sites. This meant that there were some differences between the natural sites and also between the natural sites and the artificial sites used in this study. For example, the artificial reef sites were clustered in a small area within the Loch Linnhe artificial reef complex whereas the natural reef sites were more spread out along the loch. However, all sites were within Loch Linnhe and, as such, should have been subjected to a similar water mass with similar temperature and salinity conditions. Results from the particle size analysis suggested that natural reef site N3 may have had a quite different current regime than any of the other sites used in this study. While this was not ideal, data in chapter 4 shows that of the natural sites it

was site N2 that was the most distinct of the natural reef sites, and not N3, so this is not thought to have influenced the conclusions made in this study.

3.4.2 Predation pressures at artificial and natural reefs

Biomass data, multivariate analysis on assemblage structure and univariate analysis on characterising taxa have all shown that epifaunal assemblages on PVC panels at artificial reef sites are influenced by the effects of predation to a greater extent than those at natural reef sites in Loch Linnhe. This trend was especially evident in the epifaunal biomass data where there was a much greater dry weight and ash free dry weight on caged panels than either open or partially-caged panels, which suggests heavy predation at these sites.

Multivariate analysis of assemblage structure showed no significant differences between treatments at natural or natural off-reef sites and clear evidence of cage artefacts at control sites. Significant differences between all treatments at artificial sites suggested both cage artefacts and predation may have influenced epifaunal assemblage structure at artificial and artificial off-reef reef sites. It is interesting to note that the percentage dissimilarity at both artificial and artificial off-reef sites was much lower between open and partially-caged treatments than either open and caged or caged and partially-caged treatments (Table 3.5) suggesting that, of the two factors assessed, it was predation that had exerted the stronger influence. This supports the conclusions drawn from the biomass analysis.

None of the characteristic taxa showed consistent cage artefacts or predation between reef types with the exception of *S. vermicularis* which showed no evidence of either

at any reef type. This implies that predation pressures and cage artefacts are dependent on both the taxa and the site being studied. The univariate analysis of taxonomic data showed that *B. crenatus, B. crenatus* scar, *F. implexa,* Porifera sp. and *Bugula* sp. exhibited similar trends to the biomass data in that they appeared to be more influenced by predation at artificial and artificial off-reef sites compared with natural reef sites.

There are various explanations as to why there might be a greater influence of predation on the epifaunal assemblage structures on PVC panels at artificial reef sites than natural reef sites. One explanation is that when new hard substrata, such as artificial reefs, are placed on the seabed away from areas of natural hard substratum predators have been observed to congregate around the new reefs in search of prey items (Arntz 1977). Arntz (1977) suggested that even the presence of his predator exclusion cages on the Baltic sea floor attracted great numbers of predators such as *A. rubens*, the shore crab *Carcinus maenas (L.)* and the whelk *Buccinum undatum* (L.) as a result of the introduced secondary hard substratum.

Another explanation for the increased effects of predation at artificial reef sites is the difference in the topography of the artificial and natural reefs in this study. As discussed in chapter 1, the complexity of a habitat can influence its associated biological community (Bohnsack & Sutherland 1985, Barkai & Branch 1988, Sebens 1991, Potts & Hulbert 1994, Guichard & Bourget 1998, Waide et al. 1999, Guichard et al. 2001, Svane & Peterson 2001, Bradshaw et al. 2003). The artificial reef modules of the Loch Linnhe artificial reef have a greater habitat complexity than the local natural rocky reefs (Rose 2005). This high habitat complexity provides a large

surface area, on many different orientations including vertical, horizontal upper and horizontal under surfaces, suitable for epifaunal colonisation and, in turn, providing a food supply for epifaunal predators. The high complexity of the artificial reef modules, with a large number of crevices, could also enhance populations of mobile predators through the provision of shelter and habitat (Bulleri 2005b).

These conclusions are in contrast to work by Turner and Todd (1991) who showed *A. rubens* and the whelk, *Nucella lapillus* (L.), to have minimal deleterious effects on developing epifaunal assemblages through predator exclusion and predator inclusion experiments. However, their work was carried out in the intertidal zone unlike the present study which was subtidal. Nevertheless, it would be interesting to investigate which predators were important in structuring the developing epifaunal assemblages on experimental surfaces in the present study.

3.4.3 Proximity to reefs

All analysis carried out in this study showed epifaunal assemblages on PVC panels at off-reef sites to have the same trends as their respective on-reef sites (Table 3.6). For example, there was little evidence for the effects of predation on the epifaunal assemblages at natural or natural off-reef sites but clear evidence of predation at both artificial and artificial off-reef sites. There was no evidence at the control sites of the increased influence of predation on epifaunal assemblage structure that was seen at the artificial and artificial-off reef sites. This suggests that the increase in epifaunal predation at artificial and artificial off-reef sites was a result of the presence of the artificial reef and not an effect of increased distance from natural reefs.

Results from the current study complement previous studies that have investigated the impacts of artificial reefs on the surrounding environment. Frazer and Lindberg (1994) showed the abundance of infaunal prey items to increase significantly with distance from artificial reef units in the Gulf of Mexico, suggesting that predators move off the reef to feed on infauna. Davis et al. (1982) recorded diminished sea pen colony densities in excess of 100m from their artificial reef in Southern California within just six months of reef deployment. The presence of healthy, intact colonies within predator exclusion cages and stripped colonies outside cages within the diminished area lead them to conclude that this effect was caused by reef-associated fish. The current study has shown epifaunal predators to be exerting an increased predation pressure on epifaunal fouling assemblages at distances of 100m from the artificial reef modules in Loch Linnhe. This suggests that 100m may not have been far enough away from the reef sites to constitute a true off-reef site.

3.4.4 Effects of predation on different taxa

The majority of species showing evidence of the effects of predation on their abundance had a greater abundance on PVC panels within cages than on open or partially-caged panels. Examples of this include taxa such as the barnacle *B. crenatus*; the saddle oyster Anomiidae; calcareous tube worms *F. implexa*, *P. triqueter*, *H. elegans*; the sponges Porifera spp. and the erect bryozoan *Bugula* sp. It can be assumed that a reduced abundance on open and partially-caged panels, exposed to predators, when compared to abundances on caged panels, reflects mortality as a direct result of predation. However, both the sinistral spirorbids and the encrusting bryozoan *F. malusii* had increased abundances on open and partially-caged panels. One explanation for this is that these taxa have "r-selected" life-

histories (MacArthur and Wilson (1967) in Begon et al. 1986). "r-selected" animals are good colonisers with high reproductive potential but poor competitive abilities (Begon et al. 1986).

The Intermediate Disturbance Hypothesis (IDH) (Connell 1978) states that species richness is highest at an intermediate level of disturbance with respect to both disturbance frequency and intensity. Too intense a disturbance excludes all but the most resistant species while too weak or rare a disturbance fails to impair dominant competitors. In order for the IDH to occur the dominant competitor must be affected by the disturbance applied and competitive exclusion must take place. Intermediate levels of disturbance such as predation, therefore, allows taxa with r-selected life histories to re-establish and co-exist alongside competitively dominant taxa while the latter are suppressed in their abundances (Lenz et al. 2004). Able to take advantage of areas cleared by epifaunal predators, but less able to compete interspecifically on areas protected from predation, these taxa would have elevated abundances inside cage treatments. Whilst many of the taxa on the recruitment panels after 15 months of fouling in this study could be expected to be r-selected taxa, the IDH, as a result of predation, may have allowed the weaker of these taxa to move onto panels and out-compete stronger r-selected taxa. This highlights the role of competition in structuring epifaunal communities on PVC recruitment panels in this study.

The effects of cage artefacts were not consistent between species. The abundances of *H. elegans* and *B. crenatus* showed evidence of cage artefacts, at control sites and natural off-reef sites respectively, with a lower abundance on open panels than on caged or partially-caged panels. These taxa, therefore, showed a preference for

settlement inside cages at these sites. Conversely, the encrusting bryozoan *F. malusii* had a significantly higher abundance on open panels than on caged or partially-caged panels at artificial off-reef sites suggesting that this taxon preferentially selected settlement sites outside cage treatments at these sites. These findings indicate that settlement preferences are species specific, in agreement with previous studies (e.g. Todd & Turner 1986).

3.4.5 Recruitment panel orientation

Many studies have investigated the effects of substratum orientation on epifaunal recruitment (e.g. Todd & Turner 1986, Glasby 2000, Glasby & Connell 2001, Maughan 2001) and, as a result, it is well known that the underside of horizontal surfaces support the most diverse assemblages, possibly as a result of low siltation rates (Todd & Turner 1986, Turner & Todd 1993). There is little natural horizontal underside surface in Loch Linnhe and so a study investigating the effects of predation on epifaunal recruitment at different reef types using horizontal undersides of panels would have had little relevance to actual processes occurring on the reefs themselves. Topside horizontal surfaces, on the other hand, are prone to heavy siltation thereby reducing the availability of primary substratum for larval attachment and reducing epifaunal recruitment (Todd & Turner 1986, Maughan 2001). The majority of both natural and artificial reef surfaces at 15-18m on the study reefs in Loch Linnhe are on vertical or near vertical plane and so vertically orientated recruitment panels were used in this study.

The use of vertically orientated panels introduced a directional factor into the experiment as the orientation of vertical panels will determine the extent to which

experimental surfaces are subjected to tidal currents. Glasby (2001) investigated the effects of water movement on recruitment through the use of rotating and fixed panels and found a 2 to 3-fold greater biomass on the rotating panels which always lie parallel to the prevailing current. He concluded that differential water movement over recruitment panels greatly affects the resulting cover of barnacles, sponges and ascidia. Therefore, every effort was made to align panels, at all sites, parallel to the prevailing tidal flow, as assessed on pre-deployment dives, to expose the experimental surface of the panels to the full tidal current. Nevertheless, some differences in communities between sites could have been caused by different current exposure.

3.4.6 Predator exclusion cages

Galvanised wire mesh was chosen for construction of the predator exclusion cages because of its physical properties minimising the potential for cage artefacts, by allowing maximum light penetration and water movement through the mesh, whilst still providing a robust and easily workable material. The mesh size was small enough to keep out the majority of important/large predators, particularly the starfish, *A. rubens*, and the edible urchin, *E. esculentus*. However, small and/or flexible predators and grazers would still have had access to the panels at all reef types. These include small starfish, nudibranchs, small crabs, newly settled urchins and small gastropods. It has been suggested that these small, non-target, predators can have a significant influence on the development of epifaunal assemblages (Bulleri et al. 2000, Osman & Whitlatch 2004). However, the use of a smaller mesh that would have excluded all but newly settling predators would have exerted greater cage artefacts on the epifaunal assemblages. There was evidence of the effects of

predation at many reef sites in this study, suggesting that the majority of important predators were successfully excluded by the cages.

Cage artefacts in the form of reduced water flow were assessed in this study using plaster clods. Jokiel and Morrissey (1993) showed weight loss of clods to be linear until the clod had dissolved to approximately 30 percent of its original weight. Clods in the present study lost a maximum of 50 percent of their original weight and so it can be assumed that dissolution of clods was linear. No calibration was carried out to determine the actual current velocities the clods were exposed to *in situ*. However, this experiment showed a reduction of 23-25 percent in water flow between open and caged and open and partially-caged treatments, with similar water movement across clods in cages and partial cages. It was, therefore, possible to use the similarities or differences seen between taxonomic abundances or epifaunal biomass on open, caged and partially-caged treatments to assess cage artefacts and predation pressures at different reef types.

The use of partial cages to distinguish between the effects of cage artefacts and predation has been shown to have a weakness in that predators have been found to either avoid or aggregate under the partial cages (Arntz 1977, Steele 1996, Moksnes 2002). Olafsson et al. (1994) suggested that the effects of reduced water velocity could be balanced by the effects of density-dependent or cage-attracted predation. They concluded that "this problem of confounded and possibly compensatory artefacts inside partial cages affects the interpretation even of those studies that employ cage controls" (Olafsson et al. 1994). Taxa found inside partial cages in this study included the brown crab *Cancer pagurus* (L.), the velvet swimming crab

Necora puber (L.) and the squat lobster *Munida rugosa* (Fabricius) (*pers. obs.*). However, as these taxa were only ever seen on the sediment below the panels or occasionally on cages, but not on panels, it is assumed that these taxa did not have a significant impact on the epifaunal assemblages on partially-caged panels. The abundance of *A. rubens* and *E. esculentus* on panels inside partial cages was not noted to be greater than that on open panels in this study (*pers. obs.*).

The effectiveness of the panel and cage design in this study could be questioned as all four replicate panels for each treatment were on the same PVC frame. Where predator exclusion cages were used, it was one single cage that was used to exclude predators from all four panels. The four replicates were, therefore, not independent. In the case of a full cage, as long as the integrity of the cage was not compromised by falling over, or by the presence of a large predator inside the cage, then all panels were protected from predation by the same amount at each site. However, in the case of partial predator exclusion cages if a large predator, such as *E. esculentus*, was to enter the cage and crawl up the PVC frame onto the experimental surface, this predator would then have had access to all four replicates without leaving the frame. Had the partially-caged panels had individual partial cages over each panel then a predator would have had to enter each cage individually to predate the experimental surfaces. Individually framed panels and cages would, therefore, have been a better experimental design.

This problem with the design of the predator exclusion cages, however, was unavoidable as it was not logistically possible to deploy the required number of replicate panels using individual cages and frames. Although the experimental

design could have been improved with greater time and resources, the clear trends in predation pressures seen in this study, both between artificial and natural reef types and between these reef types and sites 100m away from these reefs, demonstrates that the experimental design was sufficient to investigate predation pressures at these sites.

3.4.7 Conclusions

Predation had a greater influence on developing epifaunal assemblages on PVC panels at artificial and artificial off-reef sites than at natural, natural off-reef or control sites in Loch Linnhe. Null hypothesis 1 H_o, that there are no effects of reef type on the effects of predation on epifaunal recruitment, can, therefore, be rejected. Null hypothesis 2 H_0, that there are no effects of distance from reef on the effects of predation on epifaunal recruitment can be accepted with respect to the 100m off-reef sites used in this study. However, it would appear that null hypothesis 2 H_0 can be rejected with respect to the control sites which were greater than 100m distant from any natural or artificial reefs. This study would have been improved by replicating the entire 15 month exposure panels in time (Reimers & Branden 1994); however, this was not possible because of time and logistical constraints. Nevertheless, there is strong evidence for increased predation at the artificial reef site compared with that at the natural reef sites.

Higher predation on epifaunal assemblages on recruitment panels at artificial sites compared with natural sites implies that there is a greater abundance of epifaunal predators per unit area of seabed at the artificial reefs than natural rocky reefs in Loch Linnhe. Assuming predation is density-dependent (e.g. Connell & Anderson

1999) artificial reefs in this study would have had a greater density of epifaunal prey than the natural reef sites. Alternatively, there could have been a greater density of epifaunal predators at artificial reefs as a result of the greater habitat complexity offered by the artificial reefs than the natural rocky reefs. Productivity can be defined as the rate of conversion of resources to biomass per unit area per unit time (Waide et al. 1999). It could, therefore, be concluded that the artificial reefs may be more productive than the natural rocky reefs in Loch Linnhe; providing a habitat and/or food source to support a greater number of epifaunal predators per unit area which, in turn, could support a greater population of higher predators. This study has also demonstrated the need to assess or control for the effects of predation when comparing epifaunal recruitment or colonisation at different reef types/sites.

Chapter 4 Epifaunal recruitment at artificial and natural reefs in Loch Linnhe

4.1 Introduction

The recruitment of propagules has been shown to be an important determinant of the distribution and abundance of adults of a species, and even community structure (Connell 1985, Davis 1988b). It is, therefore, important to know how quickly artificial reefs are colonized and what factors influence rates of colonization, and to understand large-scale recruitment processes in order to make predictions on the development of artificial reefs (Carr & Hixon 1997, Svane & Peterson 2001). Despite this, large-scale studies of spatial and temporal recruitment patterns of epibenthos on reefs are rare, and according to Svane and Peterson (2001) no such data are available for artificial reefs.

4.1.1 Supply-side ecology

Epibiotic settlement, as discussed in chapter 1, is a highly complex process with many controlling and influencing factors. The supply of larvae to an area has been suggested to be the critical first step in determining the structure of epibiotic assemblages (Underwood & Anderson 1994, Underwood & Keough 2001, Brown 2005); a process termed "supply-side ecology" (Lewin 1986, Underwood & Keough 2001). Supply-side ecology is determined by processes which include the transport of larvae by water currents, the period during which they disperse, and the mortality that they suffer during dispersal (Underwood & Keough 2001).

The distance that planktonic larvae can travel to a suitable substratum is dependent

on both water currents and the competence period of the larvae; the time period that the larvae can survive for before settling. Larvae of different species have variable competence periods (Kennelly 1991). The major phyla, such as Annelida, Mollusca, Echinodermata and Crustacea, mostly have species which produce pelagic larvae with the ability to feed during the planktonic phase (Barnes et al. 2001). These planktotrophic larvae have a longer competence period than lecithotrophic larvae; larvae which are released with a yolk sac but which are unable to feed from the plankton. The majority of sessile invertebrate community species produce lecithotrophic larvae that live for only a few minutes to a day. Ascidia, for example, are known to have large planktonic larvae with short competence periods (Osman & Whitlatch 2004). Larvae with short competence periods are likely to be retained in local populations (Underwood & Keough 2001) but as the competence period increases dispersal can be extensive. The rate of fouling of an artificial reef, and the type of assemblage that develops, could, therefore, be expected to be determined by the distance from established epifaunal populations.

The supply of larvae to a particular location is dependent on the production of planktonic larvae from an established population and the transport of larvae by water currents (Richmond & Seed 1991, Underwood & Keough 2001). In this way a habitat supporting established communities that produce planktonic larvae can act a source for recruitment into other areas where populations produce few larvae and primarily act as larval sinks (Underwood & Keough 2001). Artificial reefs are initially colonised through the arrival of planktonic propagules derived from existing, sessile, epifaunal populations on nearby natural rocky reefs. In this context, natural rocky reefs could be regarded as larval sources and newly deployed artificial reefs,

with no established epifauna, as larval sinks. However, developing epifaunal populations on artificial reefs will become established and could, in time, be expected to emit their own planktonic larvae. In this way artificial reefs may begin life as larval sinks but could be expected to become larval sources with time. Underwood and Keough (2001) have suggested that identifying source and sink populations is an important step to understanding metapopulation dynamics which, in turn, leads to an understanding of how competitive interactions and predation are spatially structured.

4.1.2 Epifaunal assemblages on natural and artificial reefs

The extent to which the dynamics of developing epifaunal assemblages are similar to those occurring at natural habitats is an important aspect of artificial reef ecology (Svane & Peterson 2001). Although epibiotic colonisation of hard substrata has been studied extensively and there are many examples of short-term monitoring of colonisation on artificial reefs (e.g. Cummings 1994, Jensen et al. 1994, Nelson et al. 1994, Palmer-Zwahlen & Aseltine 1994, Pamintuan et al. 1994, Relini et al. 1994, Relini et al. 1998, Perkol-Finkel & Benayahu 2005) fewer studies have made comparisons between the epibiotic assemblages developing on artificial structures and those on natural rocky reefs.

Butler and Connolly (1996), Connell and Glasby (1999), Glasby (1999a), Connell (2001) and Bulleri (2005a, b) all found significantly different epifaunal assemblages on natural rocky reefs and artificial structures (such as pier pilings, pontoons and sandstone walls). Knott et al. (2004) found differences in assemblages on natural reefs and concrete breakwalls on horizontal surfaces but not on vertical surfaces. All

these studies were located in or around Sydney harbour, Australia. Bulleri (2005a, b) investigated the processes causing differences in assemblage structure on artificial and natural structures in Sydney harbour and concluded that these differences were apparent from the very early stages of succession and that they were not caused by differences in substrata; differences were found in epifaunal assemblages on uniform recruitment panels placed at the different reef types. This suggests that there may have been differences in the supply of larvae to the artificial and natural reefs in the Sydney harbour study.

4.1.3 Epibiotic communities on artificial and natural reefs in Loch Linnhe

The natural rocky reefs in Loch Linnhe mostly consist of low relief bedrock with relatively low structural complexity. Although results in chapter 3 have shown predation pressures on epifaunal recruitment to be greater at artificial reef sites than natural reef sites, the surfaces of the natural rocky reefs in Loch Linnhe are relatively barren with respect to epifaunal assemblages (Figure 4.1) with apparently high levels of grazing by species such as the common starfish *Asterias rubens* (L.) and the edible urchin *Echinus esculentus* (L.) *(pers. obs.)*. The sparse epifaunal and epifloral assemblages on these surfaces are comprised of calcareous tube worms such as *Pomatoceros triqueter* (L.), the occasional barnacle (*Balanus crenatus* (Bruguière)) coralline algae, and patches of encrusting coralline algae (Lithothamnia). There are, however, small crevices and overhangs on the reefs which provide habitat for diverse epifaunal assemblages (Figure 4.2), including the barnacle *B. crenatus*; calcareous tube worms such as *Serpula vermicularis* (L.), *Hydroides elegans* (Haswell), and *P. triqueter*; encrusting and erect bryozoa, Porifera spp., solitary ascidia, Anomiidae and patches of Lithothamnia. Large fronds of *Laminaria* spp. also support

communities comprising encrusting and erect bryozoa, spirorbidae and solitary ascidia (Figure 4.3). The majority of surfaces of artificial reefs, on the other hand, support diverse epifaunal assemblages (Figure 4.4).

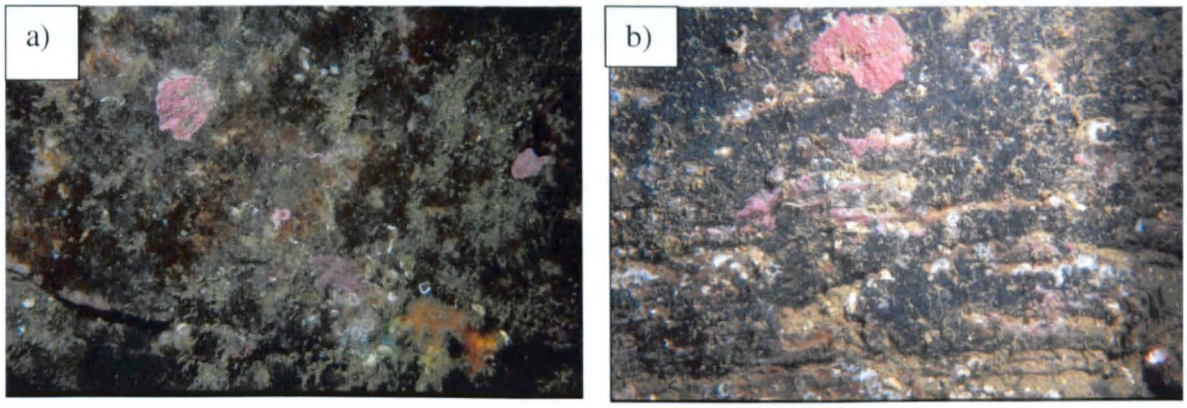

Figure 4.1 Pictures taken of typical epifaunal assemblages on vertical rocky reef surfaces at a) N1 and b) N2 in October 2004. Size of photograph = 18.5 x 13.2 cm. Taxa include coralline algae, *Pomatoceros* spp. and *B. crenatus*

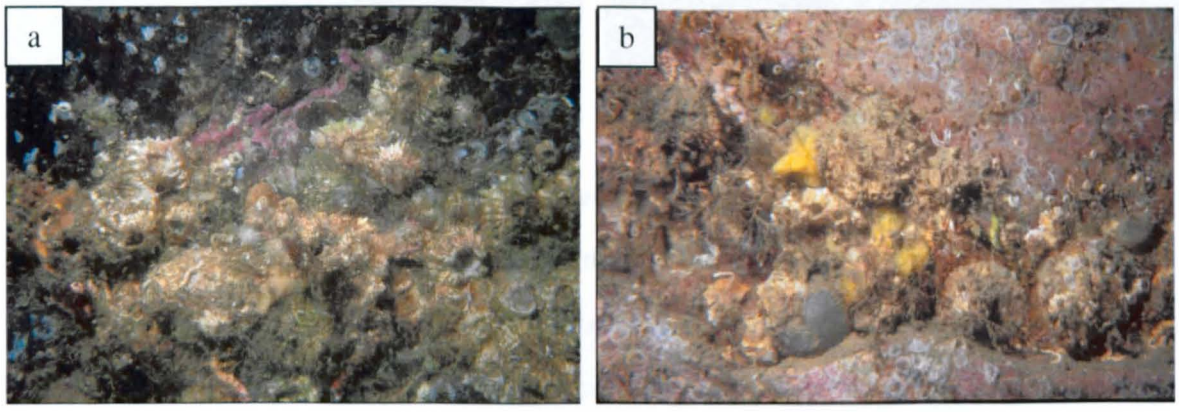

Figure 4.2 Pictures taken of crevices at a) N1 and b) N2 in October 2004. Size of photograph = 18.5cm x 13.2cm. Taxa include *B. crenatus*, Calcareous tube worms such as *S. vermicularis*, *H. elegans*, and *Pomatoceros* spp.; encrusting and erect bryozoa, Anomiidae, Calcareous algae, Porifera spp. and solitary ascidia such as *Ascidiella aspersa* (Müller).

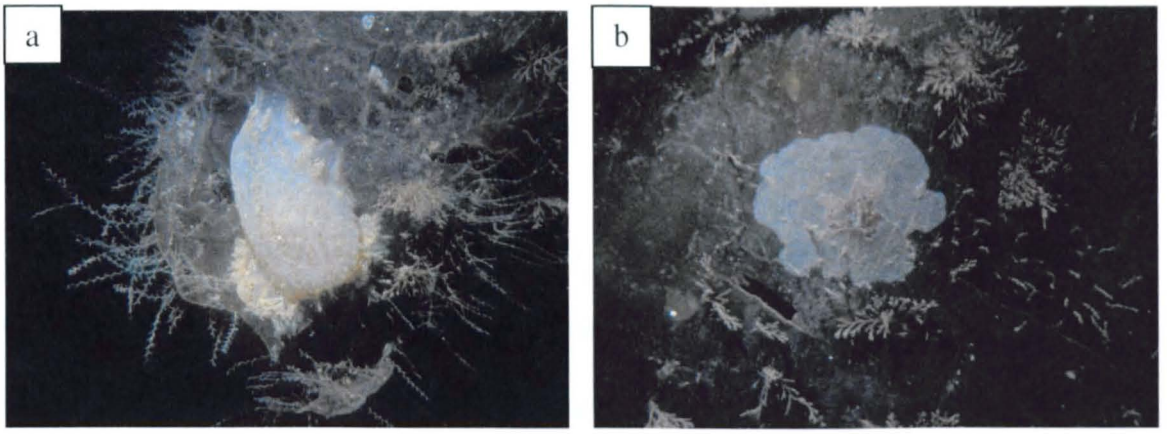

Figure 4.3 Laminarian fronds on natural reefs supporting communities of encrusting (e.g. *Haplopoma sciapilum* (Silén and Harmelin) and erect bryozoa (e.g. *Bugula* sp.), hydroids and solitary ascidia (e.g. *A. aspersa*). Photographs taken at natural reef site N3 in October 2004. Size of photograph = 18.5 x 13.2cm.

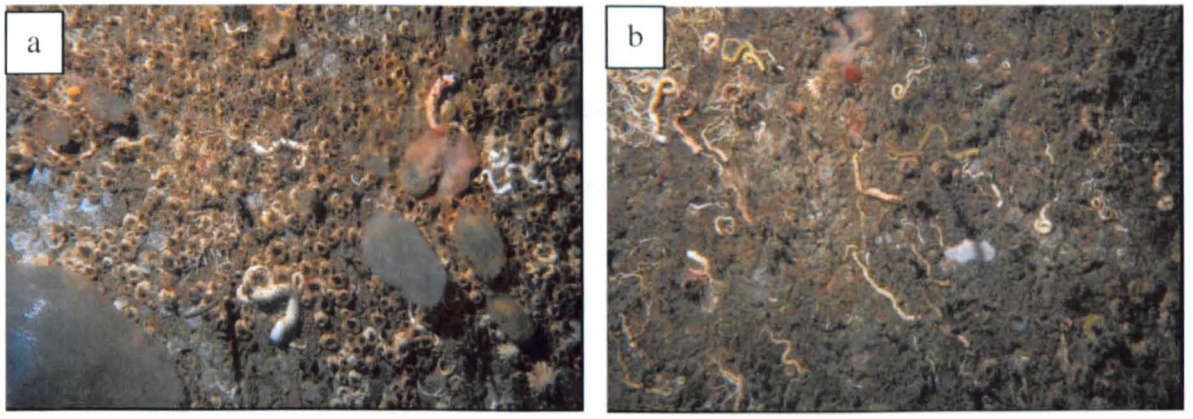

Figure 4.4 Photographs of epifaunal assemblages on surfaces of reef modules A2. Size of photograph = 18.5 x 13.2cm. Typical taxa include the barnacle *B. crenatus*; calcareous tube worms such as *Pomatoceros* spp., *H. elegans, S. vermicularis* and *Filograna implexa* (Berkeley); ascidia such as Didemnidae, *Dendrodoa* sp. and *Asicidella* spp.; and encrusting bryozoa such as *Smittoidea reticulata* (MacGillivray).

Although there appear to be differences in the assemblage structure on natural and artificial reefs in Loch Linnhe, the patchiness of the epifaunal assemblages on natural reefs make it difficult to quantify any similarities or differences there might be

between reef types.

4.1.4 This study

The aims of this study were three-fold: 1) to assess seasonal trends in predation pressures at selected artificial and natural reef sites in Loch Linnhe, 2) to identify differences in seasonal early epifaunal recruitment at artificial and natural reef sites in Loch Linnhe and 3) to identify differences in epifaunal recruitment at artificial and natural sites in Loch Linnhe.

Null hypotheses tested:

1. H_0: There are no effects of reef type on the effects of epifaunal predation on seasonal recruitment
2. H_0: There are no effects of reef type on seasonal early epifaunal recruitment
3. H_0: There are no effects of reef type on longer term epifaunal recruitment

4.2 Materials and methods

4.2.1 Seasonal predation study

PVC recruitment panels, as described in chapter 3, were deployed at each of the 6 on-reef sites (3 artificial and 3 natural) used in chapter 3 (see Table 3.1, Figure 3.3). Every 3 months one set of four replicate caged, partially caged, and open panels was recovered from each site and replaced with a fresh set of panels. This study ran from August 2003 to August 2004. Seasons were autumn (fouled from August 2003 to October 2003), winter (October 2003 to January 2004), spring (January 2004 to April 2004) and summer (April 2004 to August 2004).

All panels were labelled as per previous chapters. Panels were recovered and analysed using the same method as described in chapter 3. All recruitment panels were initially deployed within the same two week period as the recruitment panels used in chapter 3. In subsequent sampling periods, recruitment panels at all sites were recovered and new panels deployed within a one-week period.

4.2.2 Seasonal early epifaunal recruitment study

Although there was no consistent evidence of differences in the effects of predation or cage artefacts on the seasonal epifaunal recruitment at artificial and natural sites in Loch Linnhe (see sections 4.2.1 and 4.3.1), there was a stronger influence of epifaunal predation on longer-term epifaunal recruitment at artificial than natural reef sites in Loch Linnhe (chapter 3). Therefore, seasonal data from caged recruitment panels (section 4.2.1) were used to assess differences in early epifaunal recruitment in the absence of large-scale epifaunal predation. This study was only carried out at on-reef (3 artificial and 3 natural sites) sites. The seasonal sampling periods were the same as those in the seasonal predation study (section 4.2.1).

4.2.3 Epifaunal recruitment study

In light of the findings from the seasonal recruitment study (sections 4.2.2 and 4.3.2), which showed the early epibiotic recruitment and, therefore, maybe the seasonal supply of larvae to be similar between artificial and natural reefs, data from the epifaunal assemblages colonising the open (uncaged) PVC recruitment panels used in chapter 3 were used to assess differences in epifaunal recruitment between reef types after 15 months of fouling. The use of open recruitment panels meant the epifaunal assemblages that developed on the panels had been subjected to post-

settlement processes such as predation. This will allow a comparison of how predation pressure differences between artificial and natural reefs (as found in chapter 3) affects community development.

4.2.4 Data analysis

Seasonal predation study

Community structures on recruitment panels from different treatments were assessed using multivariate statistical methods within the PRIMER software package (Clarke & Warwick 2001). Non-parametric Multi-Dimensional Scaling (nMDS) ordinations and analysis of similarity (ANOSIM, Clarke 1993) were used to assess differences between treatments at artificial and natural reefs. Data were log (x+1) transformed prior to multivariate analysis to minimise bias caused by very abundant taxa.

Biomass data were tested for equal variances using Levene's test (Dytham 2003) and the effect of treatment at the different reef types was tested using one-way ANOVAs with Fisher's pairwise comparisons.

Epifaunal recruitment studies

Biomass and diversity data on caged panels at artificial and natural reef sites were tested for equal variances using Levene's test (Dytham 2003) and the effect of reef type was tested using two-way nested ANOVAs.

Community structures on recruitment panels from different treatments were assessed using multivariate statistical methods within the PRIMER software package (Clarke & Warwick 2001). Non-parametric Multi-Dimensional Scaling (nMDS) ordinations

and two-way nested analysis of similarity (ANOSIM, Clarke 1993) were used to assess differences between reef types. Data were log (x+1) transformed prior to multivariate analysis to minimise bias caused by very abundant taxa.

Characterising taxa were identified using the SIMPER procedure (PRIMER, Clarke 1993). The abundances of characterising taxa were assessed for differences between reef types using two-way nested ANOVAs (site nested within reef type). The ANOVA model used was: 'reef type' 'site (reef type)'. Site was a random factor; reef type was fixed (Underwood 1997).

4.3 Results

4.3.1 Effects of predation and cage artefacts on seasonal recruitment

Autumn

Epifaunal recruitment in the autumn (from August to October 2003) was relatively heavy (Figure 4.5) and consisted of many calcareous tube worms, bryozoa and ascidia. Multivariate analysis showed there to be a clear separation between all treatments at all sites with the exception of site N2 where caged was distinct from open and partially-caged data points (Figure 4.6). Significant differences were found between the epifaunal assemblage structures on panels from all treatments at all sites with the exception of N2 open versus partially-caged data where there was no significant difference (Figure 4.6, Table 4.1).

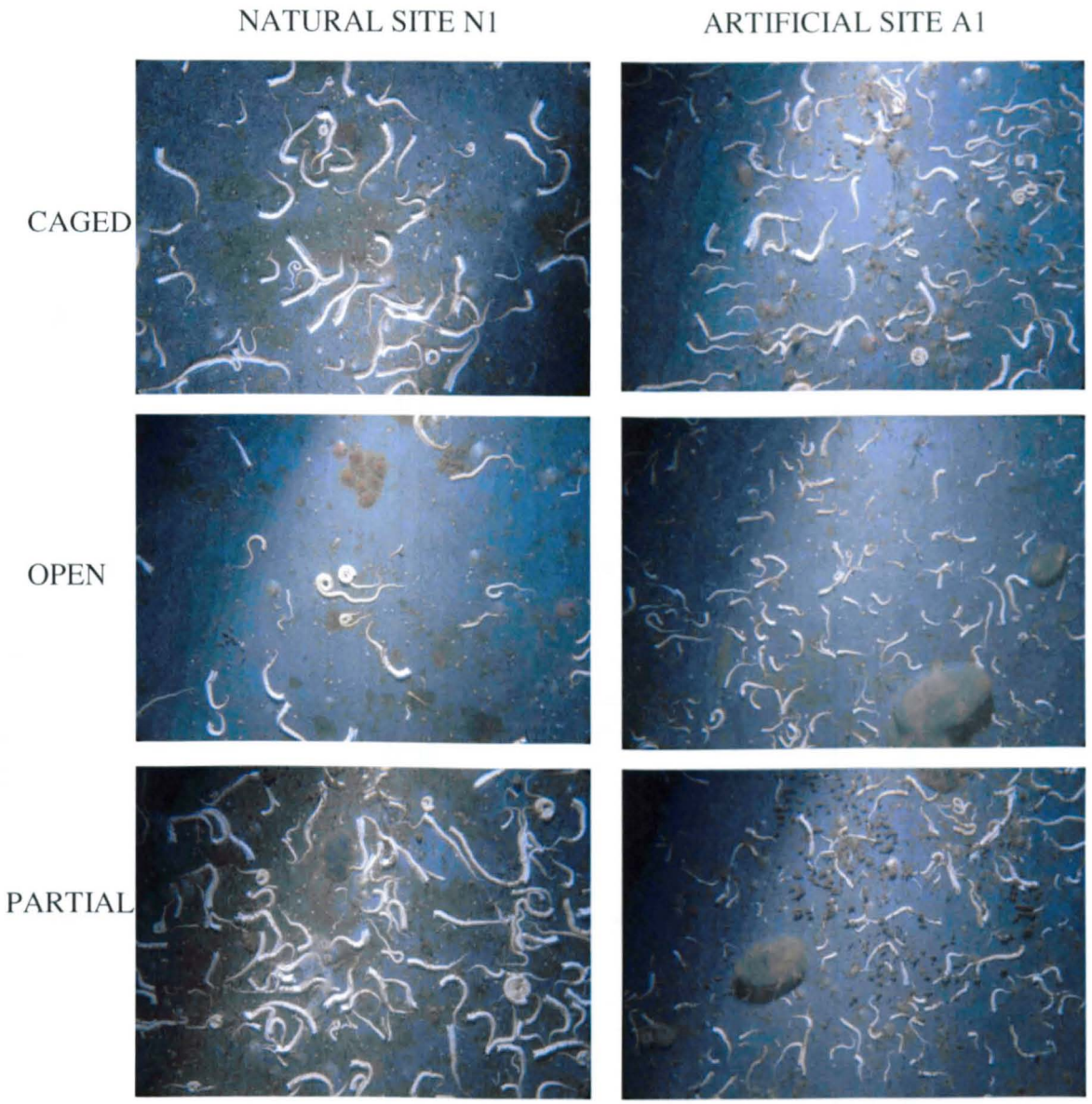

Figure 4.5 Examples of epifaunal assemblages on PVC recruitment panels at different treatments at an artificial and natural reef following the autumn sampling period (August to October 2003).

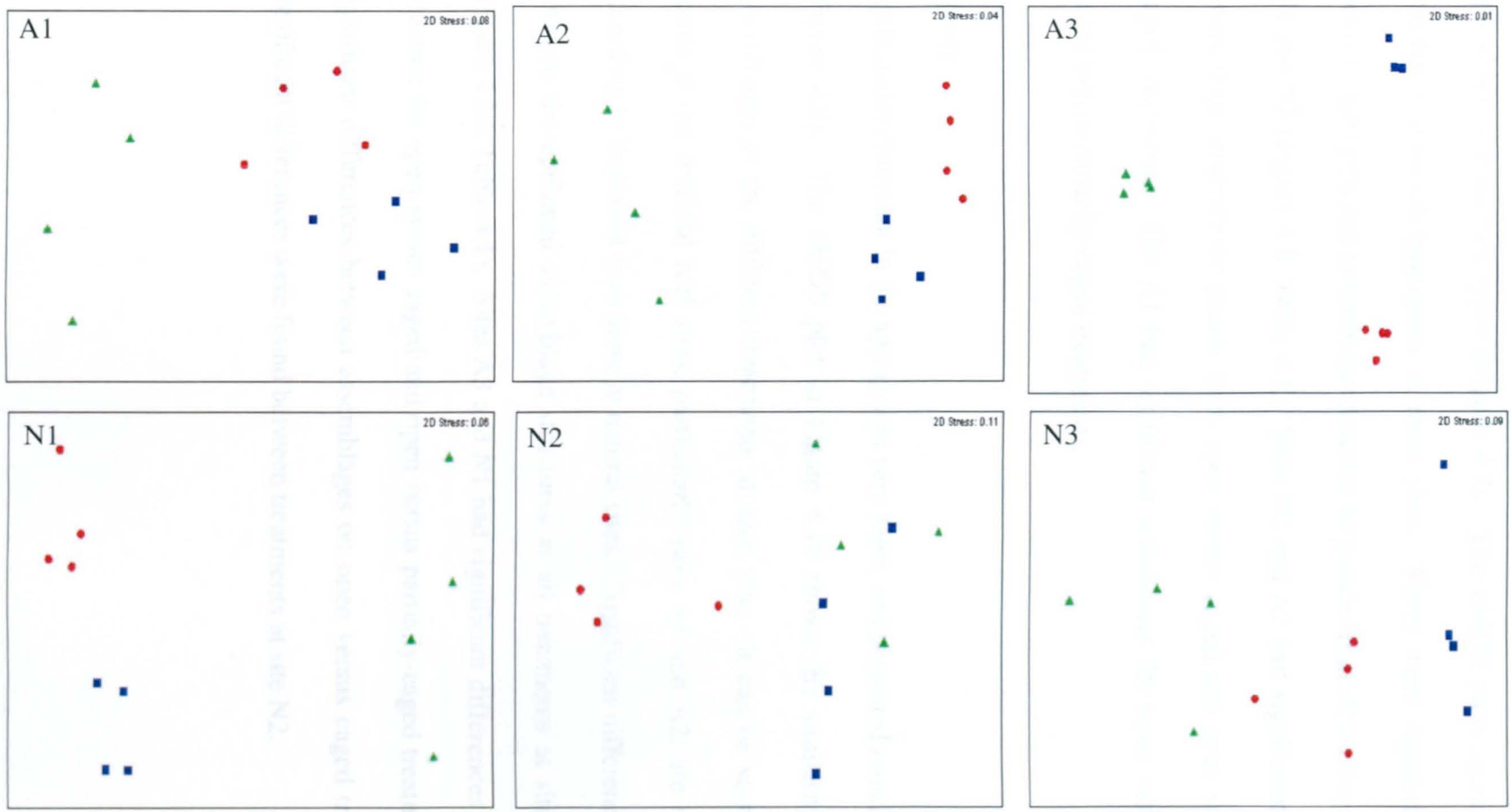

Figure 4.6 nMDS plot of abundance data of epifaunal assemblages on PVC recruitment panels fouled in the autumn sampling period. Factor = treatment; ▲ open, ● caged, ■ partial.

Winter

There was little epifaunal fouling at either artificial or natural reef sites in winter. These epifaunal assemblages were dominated by calcareous tube worms and spirorbids at both reef types (Figure 4.7). The nMDS plots again showed clear separation between treatments at most sites. There were significant differences between the epifaunal assemblage structure on panels from all treatments at sites A3, N1 and N3 (Figure 4.8, Table 4.1). Sites N2 and A2 had significant differences in assemblage structure on panels from open versus caged and open versus partially-caged treatments. Site A1 had significant differences for open versus caged and caged versus partially-caged treatments.

Spring

Epifaunal recruitment in the spring was very light, and consisted mostly of spirorbids (Figure 4.9). The nMDS plot in Figure 4.10 shows the similarity of epifaunal assemblages at the different treatments at each site. It can be seen that the data points at the artificial reef sites, particularly sites A1 and A2, are more clustered according to treatment than those at natural sites. Significant differences were found between the epifaunal assemblage structures at all treatments at sites A1 and A2 (Figure 4.10, Table 4.1). Sites A3 and N1 had significant differences in assemblage structure for open versus caged and open versus partially-caged treatments. N3 had significant differences between assemblages on open versus caged treatments. No significant differences were found between treatments at site N2.

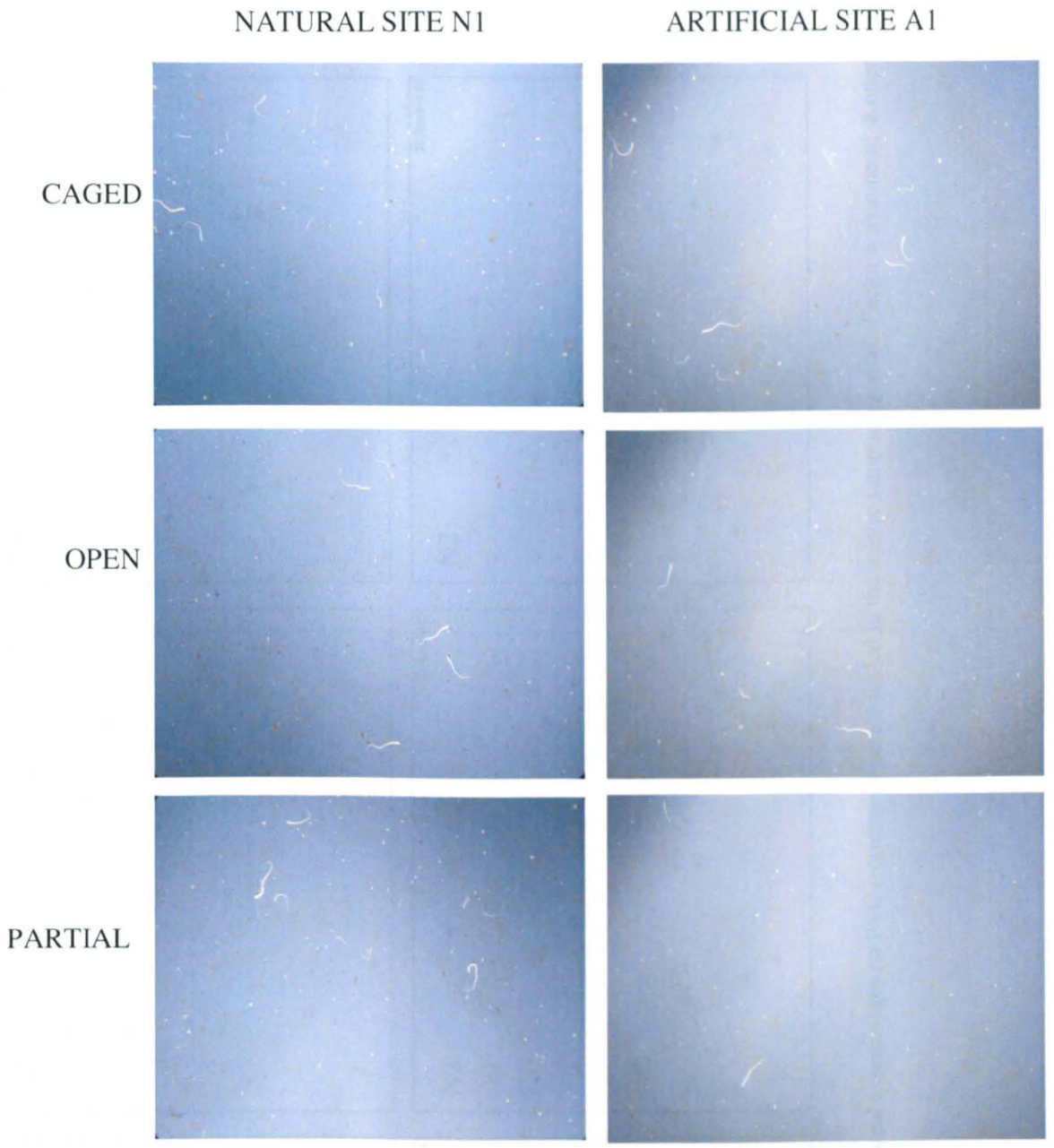

Figure 4.7 Examples of epifaunal assemblages on PVC recruitment panels at different treatments at an artificial and natural reef following the winter sampling period (October 2003 to January 2004)

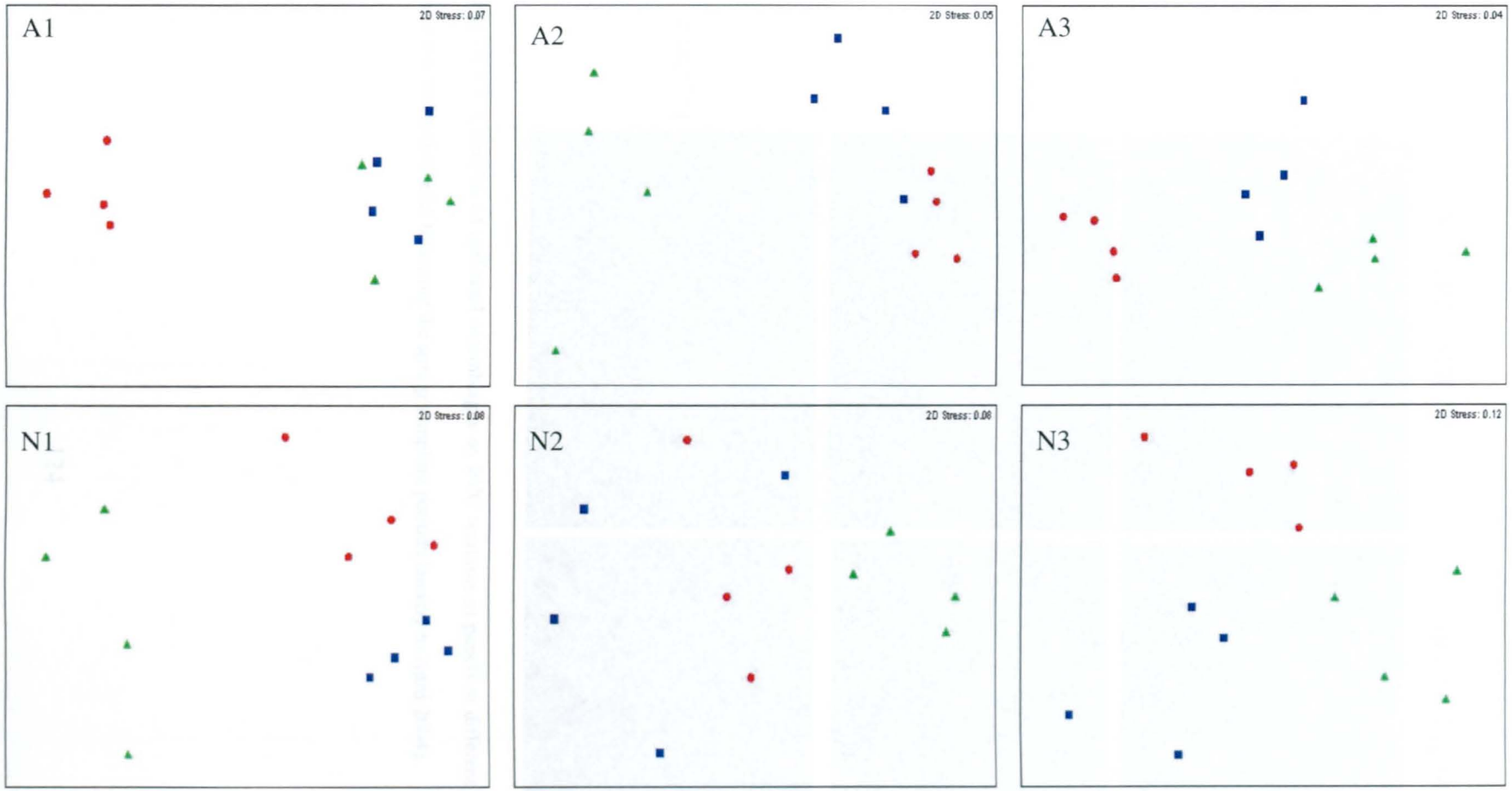

Figure 4.8 nMDS plot of abundance data of epifaunal assemblages on PVC recruitment panels fouled in the winter sampling period. Factor = treatment; ▲ open, ● caged, ■ partial.

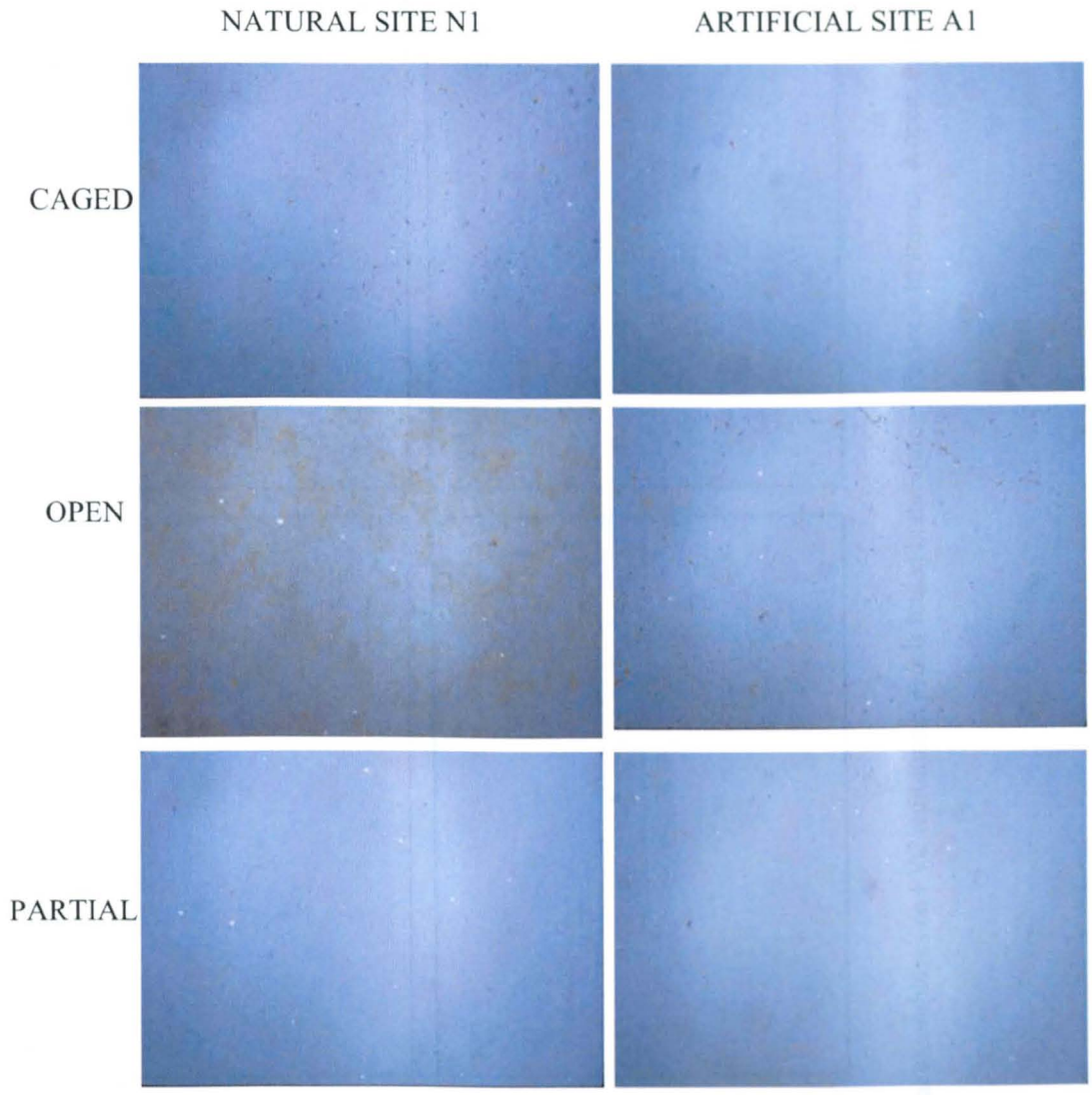

Figure 4.9 Examples of epifaunal assemblages on PVC recruitment panels at different treatments at an artificial and natural reef following the spring sampling period (January to April 2004).

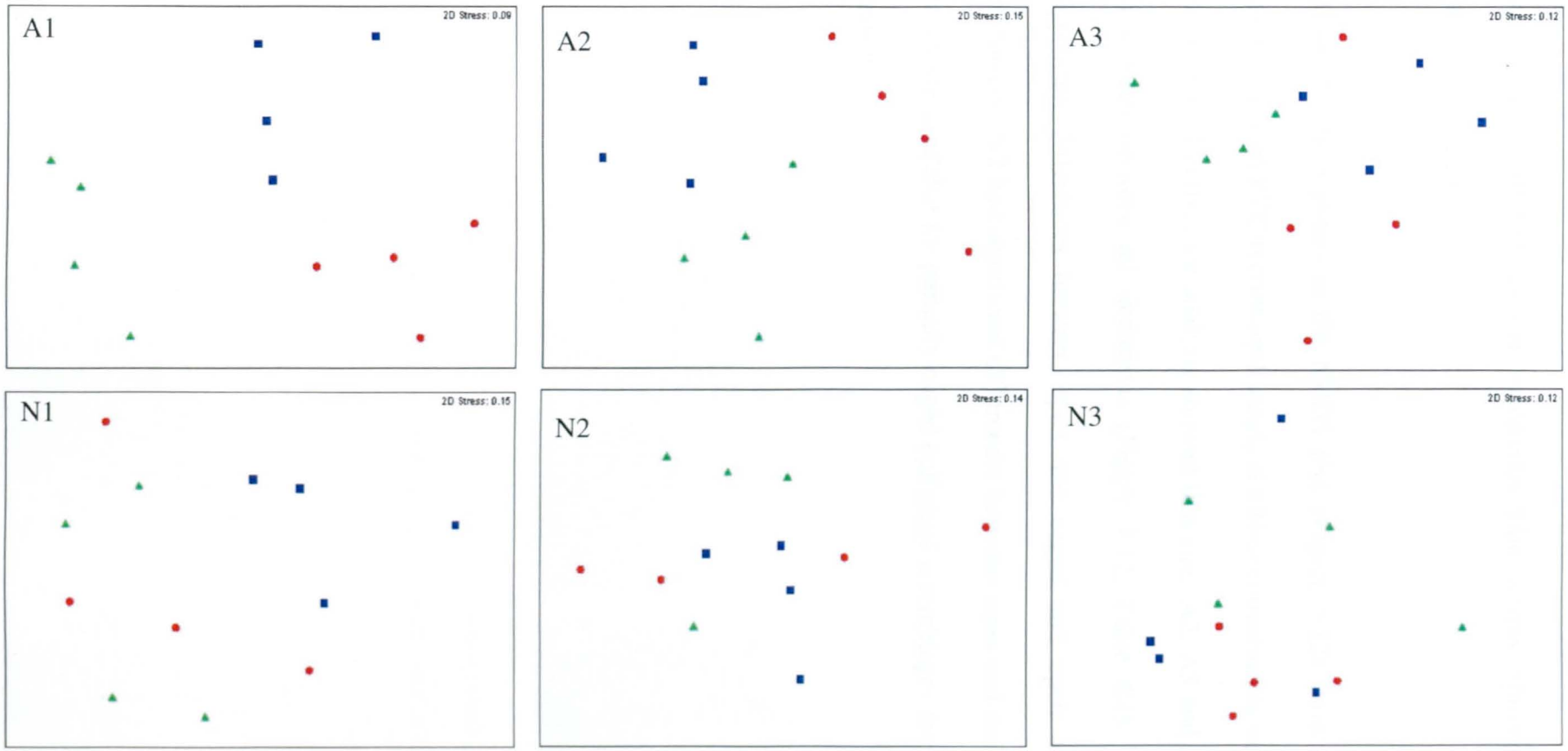

Figure 4.10 nMDS plot of abundance data of epifaunal assemblages on PVC recruitment panels fouled in the spring. Factor = treatment; ▲open, ● caged, ■ partial.

Summer

Epifaunal recruitment was heavy at all sites in the summer. Assemblages were dominated by solitary ascidia, calcareous tube worms, spirorbid and encrusting bryozoa (Figure 4.11).

Again, the data points in the nMDS plot (Figure 4.12) show that the epifaunal assemblages on PVC recruitment panels at different treatments were quite distinct at most sites. Multivariate analysis showed that sites A2, A3 and N1 had significant differences between all treatments (Figure 4.12, Table 4.1). A1 and N3 had significant differences between open and caged and open and partially-caged treatments. N2 had significant differences between open and caged treatments. No data were available for partially-caged epifaunal assemblages for N2 in the summer season.

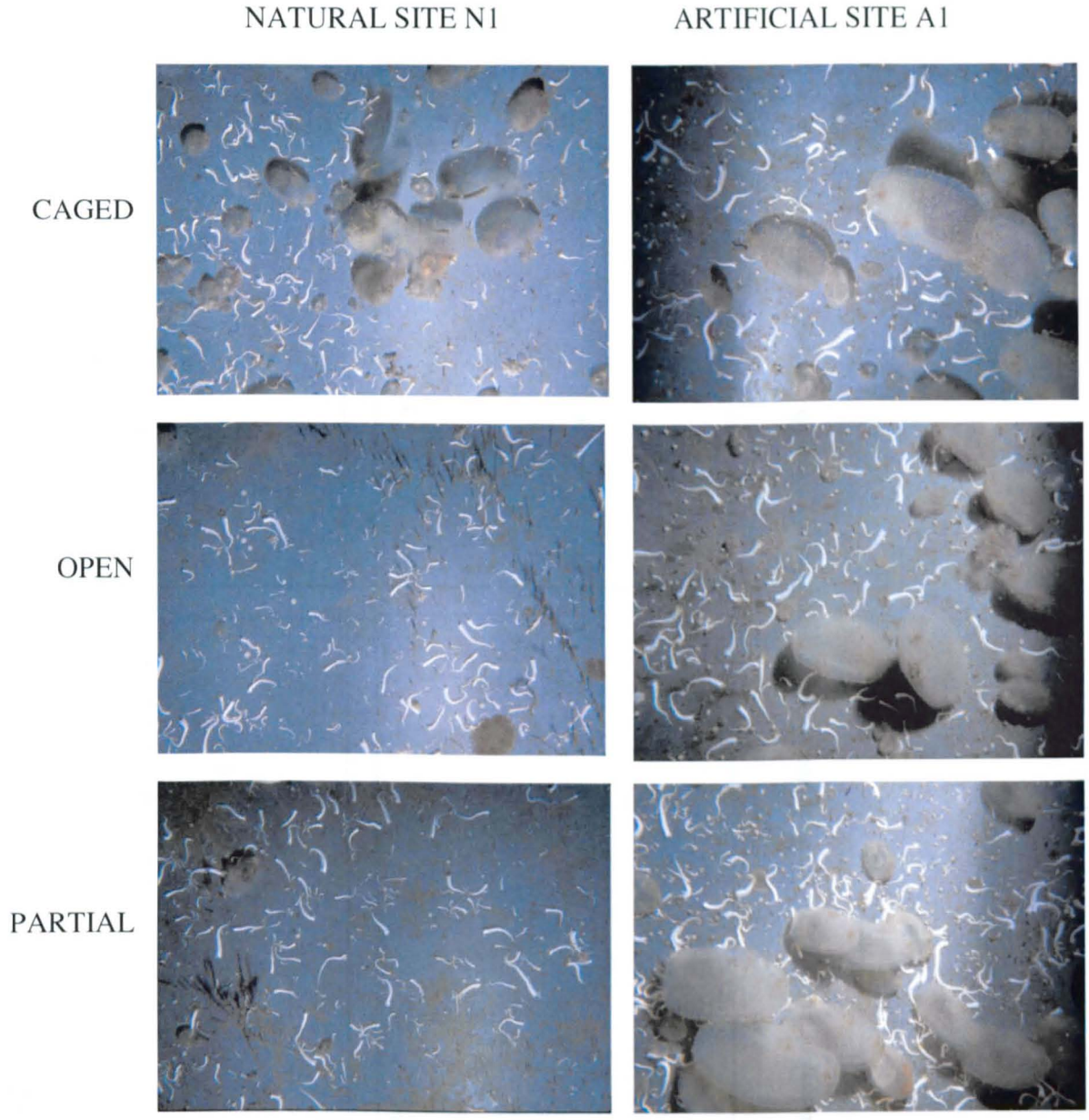

Figure 4.11 Examples of epifaunal assemblages on PVC recruitment panels at different treatments at an artificial and natural reef following the summer sampling period (April to August 2004).

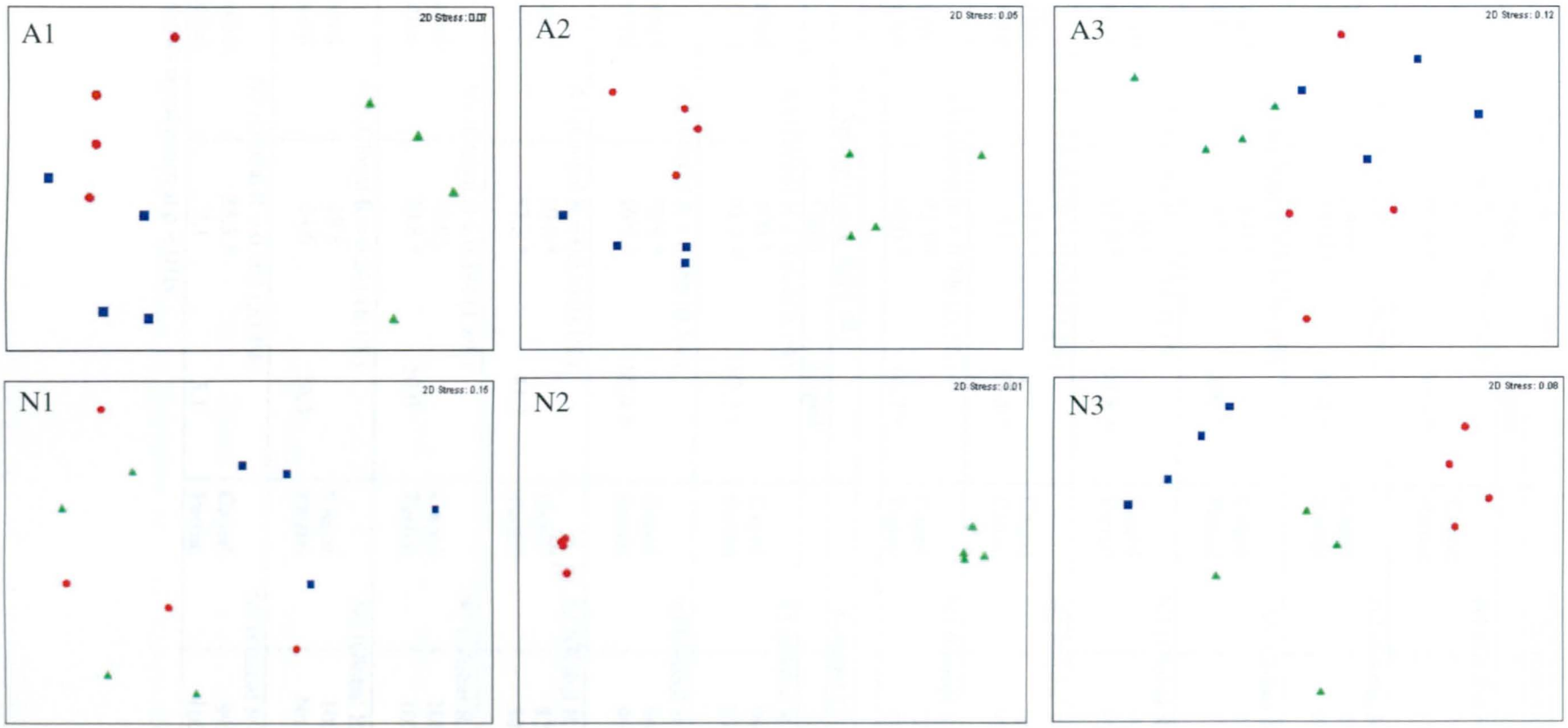

Figure 4.12 nMDS plot of abundance data of epifaunal assemblages on PVC panels fouled in the summer. Factor = treatment; ▲ open, ● caged, ■ partial.

Table 4.1 ANOSIM results (% dissimilarity) for seasonal data for the assessment of the effects of predation.

Autumn (Aug to Oct 03)			Winter (Oct 03 – Jan 04)		
	Open	Caged		Open	Caged
A1 (Global R = 0.796 (0.1%)			A1 (Global R = 0.773 (0.3%)		
Caged	91.7 *		Caged	100 *	
Partial	97.9 *	63.5 *	Partial	14.6	100 *
A2 (Global R = 1.00 (0.2%)			A2 (Global R = 0.757 (0.1%)		
Caged	100.0 *		Caged	100 *	
Partial	100.0 *	97.9 *	Partial	97.9 *	49.0
A3 (Global R = 1.00 (0.2%)			A3 (Global R = 0.94 (0.2%)		
Caged	100 *		Caged	100 *	
Partial	100 *	100 *	Partial	77.1 *	100 *
N1 (Global R = 0.919 (0.1%)			N1 (Global R = 0.794 (0.1%)		
Caged	100 *		Caged	99.0 *	
Partial	95.8 *	94.8 *	Partial	99.0 *	44.8 *
N2 (Global R = 0.639 (0.2%)			N2 (Global R = 0.440 (0.3%)		
Caged	89.6 *		Caged	53.1 *	
Partial	3.1	87.5 *	Partial	92.9 *	4.2
N3 (Global R = 0.796 (0.1%)			N3 (Global R = 0.699 (0.1%)		
Caged	82.3 *		Caged	72.9 *	
Partial	99.0 *	66.7 *	Partial	82.3 *	53.1 *

Spring (Jan to April 04)			Summer (April to Aug 04)		
	Open	Caged		Open	Caged
A1 (Global R = 0.914 (0.1%)			A1 (Global R = 0.755 (0.1%)		
Caged	100 *		Caged	99.0 *	
Partial	91.7 *	82.3 *	Partial	100.0 *	37.5
A2 (Global R = 0.685 (0.1%)			A2 (Global R = 0.859 (0.1%)		
Caged	72.9 *		Caged	96.9 *	
Partial	46.9 *	85.4 *	Partial	99.0 *	82.3 *
A3 (Global R = 0.516 (0.1%)			A3 (Global R = 0.852 (0.1%)		
Caged	50.0 *		Caged	82.3 *	
Partial	57.3 *	41.7	Partial	59.4 *	100.0 *
N1 (Global R = 0.384 (1.8%)			N1 (Global R = 0.986 (0.2%)		
Caged	-0.01		Caged	100.0 *	
Partial	70.8 *	50.0 *	Partial	100.0 *	95.8 *
N2 (Global R = 0.241 (6.1%)			N2 (Global R = 1.00 (2.9%)		
Caged	19.8		Caged	100.0 *	
Partial	14.6	36.5	Partial	No data	No data
N3 (Global R = 0.102 (20.4%)			N3 (Global R = 0.745 (0.1%)		
Caged	33.3 *		Caged	99.0 *	
Partial	2.1	3.1	Partial	100.0 *	31.3

* shows significance at $p < 0.05$

The relationships between open, caged and partially-caged treatments were interpreted to assess the effects of cage artefacts and predation on epifaunal assemblages on PVC recruitment panels. There were five instances where cage artefacts appeared to be more important than predation in structuring seasonal epibiotic assemblage structure and one instance where predation was the key factor (Table 4.2). However, results from most sites and seasons showed evidence of both cage artefacts and predation.

Table 4.2 Interpretation of ANOSIM results (Table 4.1), with respect to the influence of predation and cage artefacts, for epifaunal assemblage structures on recruitment panels at all six study sites in each of the four seasons. P = predation, C = cage artefacts, C/P = both cage artefacts and predation evident. No entry indicates no cage artefacts or predation were apparent.

	AUTUMN	WINTER	SPRING	WINTER
A1	C/P		C/P	C
A2	C/P	C	C/P	C/P
A3	C/P	C/P	C	C/P
N1	C/P	C/P		C/P
N2	P	C		No data
N3	C/P	C/P		C

A clearer picture emerged when data for all sites were combined. Figure 4.13 shows the nMDS plots for each reef type for each season. It can be seen that data points clustered according to site at the natural reefs but according to treatment at artificial reef sites. ANOSIM results are given in Table 4.3. With the exception of open versus caged data in the summer there were no significant differences between treatments at natural reef sites. There were, however, significant differences in epifaunal assemblage structure at all treatments in all seasons at artificial reef sites.

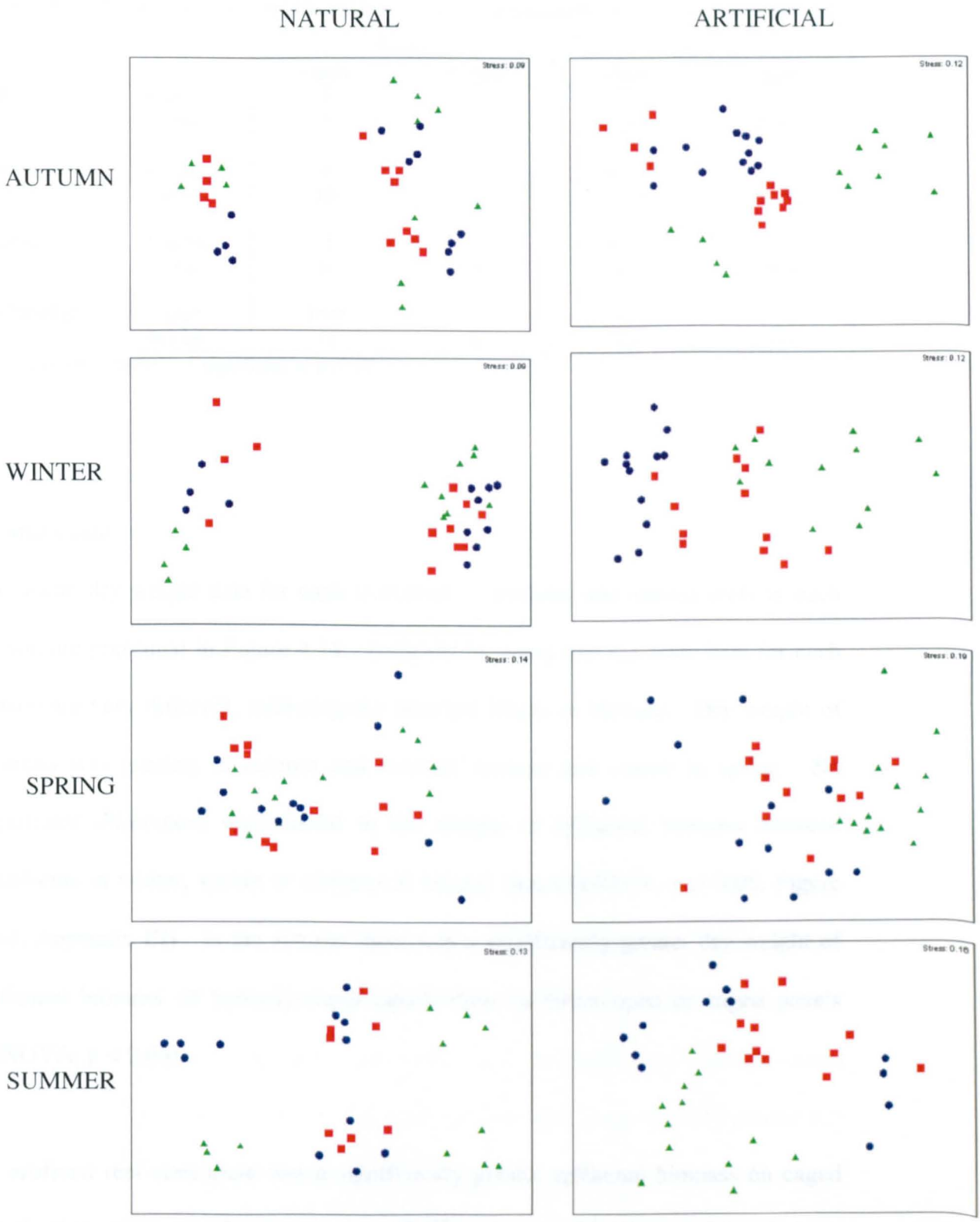

Figure 4.13 nMDS plots for each seasonal sampling period. Factor = treatment; ▲ Open, ● Caged, ■ Partial.

Table 4.3 ANOSIM results showing dissimilarity (%) between treatments at reef types. Seasonal data

		Natural		Artificial	
		Open	Caged	Open	Caged
AUTUMN	Caged	8		57**	
	Partial	5	1	32**	24**
WINTER	Caged	4		83**	
	Partial	10	-2	27**	45**
SPRING	Caged	-1		47**	
	Partial	0	-6	36**	18**
SUMMER	Caged	21**		34*	
	Partial	14	8	56*	15**

** significant at $p<0.01$, * significant at $p<0.05$

Biomass data

The mean dry weight data for each treatment at artificial and natural reefs in each season are presented in Figure 4.14. It should be noted that the scale bars for each season are very different, reflecting the seasonal trends in biomass. Dry weight of biomass was greatest in autumn and summer seasons and lowest in spring. No significant differences were found in dry weight of epifaunal biomass between treatments in winter, spring or summer at natural sites (ANOVA, $p > 0.05$, Figure 4.14, Appendix III). In the autumn there was a significantly greater dry weight of epifaunal biomass on partially-caged panels than on either open or caged panels (ANOVA, $p < 0.05$).

At artificial reef sites there was a significantly greater epifaunal biomass on caged panels than open panels in autumn (ANOVA, $p < 0.05$, Figure 4.14) but no significant difference between the dry weight of biomass on open and partially-caged or caged and partially-caged panels. In winter there was a significantly lower dry weight of epifaunal biomass on open than either partially-caged or caged panels

(ANOVA, $p < 0.05$). There were no significant differences between any treatments in spring at artificial reef sites ($p > 0.05$). In the summer there were significant differences in the dry weight of biomass between caged and partially-caged panels ($p < 0.05$) but no significant differences between open and caged or open and partially-caged panels ($p > 0.05$).

Ash free dry weight of biomass at both artificial and natural reefs was also greatest in autumn and summer and lowest in spring (Figure 4.15). No significant differences were found at natural sites in the ash free dry weight of epifaunal biomass on panels in winter, spring or summer. However, there was a significantly greater ash free dry weight of epifaunal biomass on partially-caged panels than on either open or caged panels in autumn (ANOVA, $p < 0.05$, Figure 4.15). No significant differences were found between open and caged panels in autumn ($p > 0.05$).

At artificial sites, there were no significant differences in the ash free dry weight of epifaunal biomass on panels from any treatment in autumn and winter (ANOVA, $p > 0.05$). There was a significantly greater biomass on open panels than partially-caged panels at artificial sites in spring (ANOVA, $p < 0.05$, Figure 4.15). No significant differences were found between open and caged or caged and partially-caged treatments in spring ($p > 0.05$). In the summer there was a significantly greater ash free dry weight of epifaunal biomass on caged panels than on open or partially-caged panels (ANOVA, $p < 0.05$). There were no significant differences between open and partially-caged panels in the summer ($p > 0.05$).

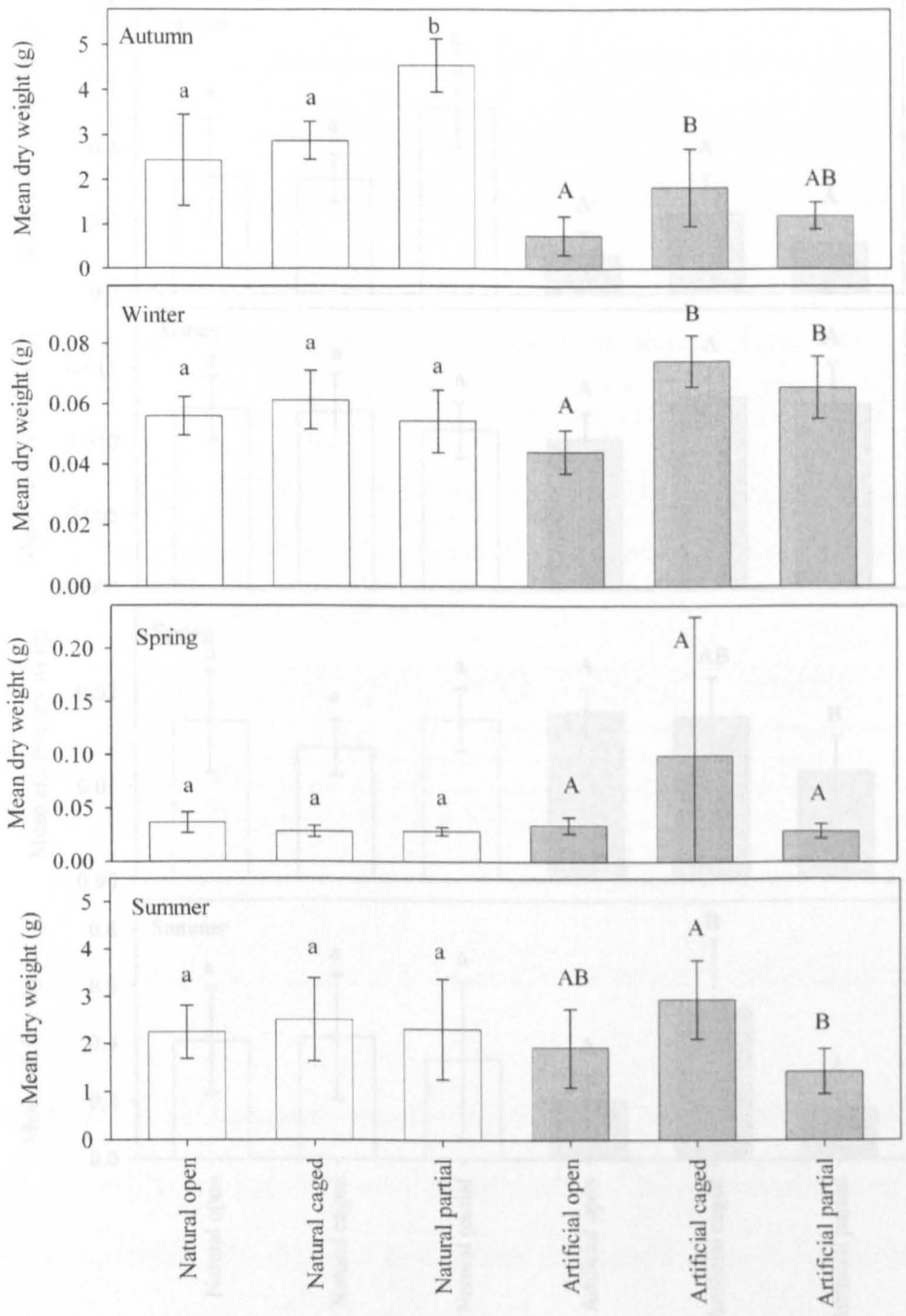

Figure 4.14 Seasonal mean dry weights of epifaunal biomass on PVC panels with 95% confidence intervals (n = 12). Different letters indicate significant differences between treatments within reef type (ANOVA, $p < 0.05$, Appendix III). Comparisons were only made between treatments within reef type and not between reef types. Note the differences in scale between seasons.

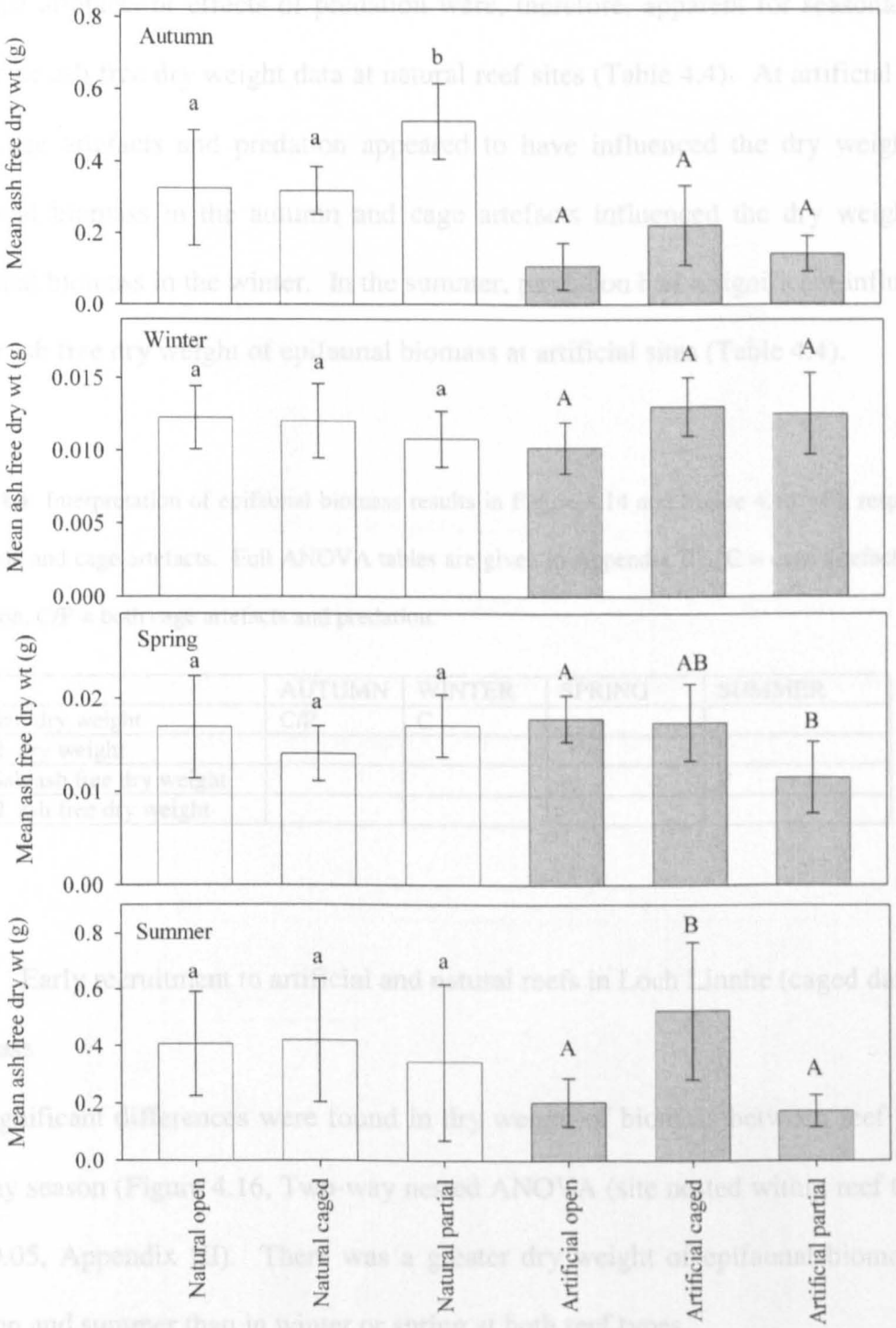

Figure 4.15 Seasonal mean ash free dry weights of epifaunal biomass on PVC panels with 95% confidence intervals (n = 12). Different letters indicate significant differences between treatments within reef type (ANOVA, $p < 0.05$, Appendix III). Comparisons were only made between treatments within reef type and not between reef types. Note the difference in scale between seasons.

No cage artefacts or effects of predation were, therefore, apparent for seasonal dry weight or ash free dry weight data at natural reef sites (Table 4.4). At artificial sites both cage artefacts and predation appeared to have influenced the dry weight of epifaunal biomass in the autumn and cage artefacts influenced the dry weight of epifaunal biomass in the winter. In the summer, predation had a significant influence on the ash free dry weight of epifaunal biomass at artificial sites (Table 4.4).

Table 4.4 Interpretation of epifaunal biomass results in Figure 4.14 and Figure 4.15 with respect to predation and cage artefacts. Full ANOVA tables are given in Appendix III. C = cage artefacts, P = predation, C/P = both cage artefacts and predation.

	AUTUMN	WINTER	SPRING	SUMMER
Artificial: dry weight	C/P	C		
Natural: dry weight				
Artificial: ash free dry weight				P
Natural: ash free dry weight				

4.3.2 Early recruitment to artificial and natural reefs in Loch Linnhe (caged data).

Biomass

No significant differences were found in dry weight of biomass between reef types for any season (Figure 4.16, Two-way nested ANOVA (site nested within reef type), $p > 0.05$, Appendix III). There was a greater dry weight of epifaunal biomass in autumn and summer than in winter or spring at both reef types.

No significant differences were found for ash free dry weight of biomass between reef types for any season (Figure 4.17, Two-way nested ANOVA (site nested within reef type), $p > 0.05$, Appendix III). Again there was a greater ash free dry weight of epifaunal biomass in autumn and summer than there was in winter or spring at both

reef types.

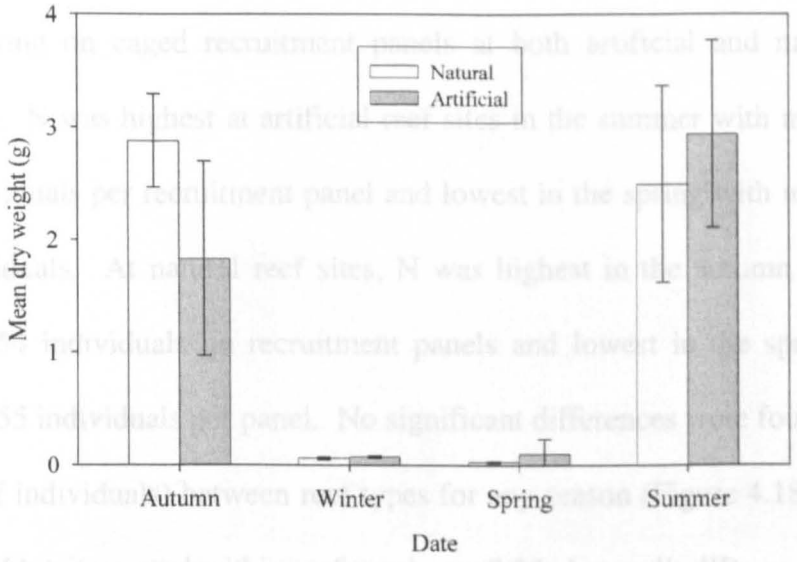

Figure 4.16 Mean dry weight of epifaunal biomass on caged PVC recruitment panels at artificial and natural reef types in all seasonal sampling periods. Error bars show 95% confidence intervals (n = 12).

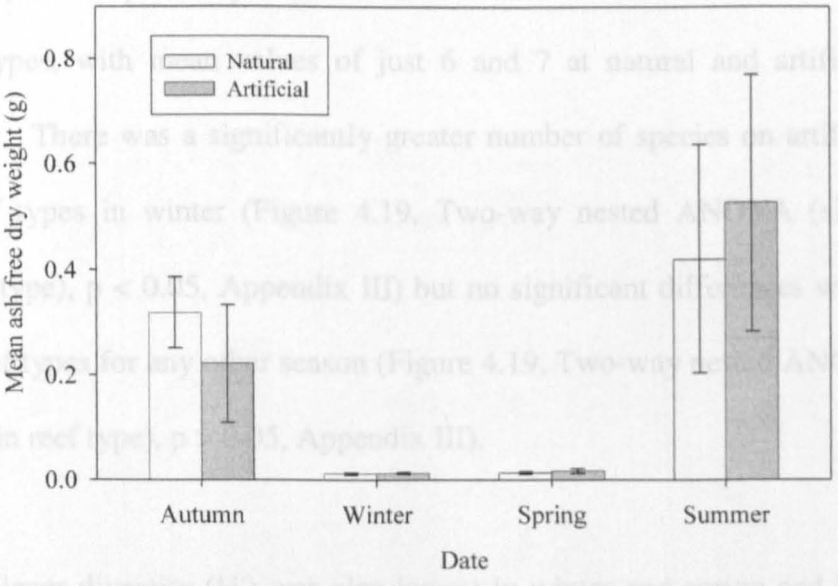

Figure 4.17 Mean ash free dry weight of epifaunal biomass on caged PVC recruitment panels at artificial and natural reef types in all seasonal sampling periods. Error bars show 95% confidence intervals (n = 12).

Diversity

The number of individuals (N) was greatest in autumn and summer seasons and lowest in spring on caged recruitment panels at both artificial and natural reefs (Figure 4.18). N was highest at artificial reef sites in the summer with mean values of 1507 individuals per recruitment panel and lowest in the spring with mean values of 121 individuals. At natural reef sites, N was highest in the autumn with mean values of 1454 individuals on recruitment panels and lowest in the spring with a mean of just 55 individuals per panel. No significant differences were found in mean N (number of individuals) between reef types for any season (Figure 4.18, Two-way nested ANOVA (site nested within reef type), $p > 0.05$, Appendix III).

A similar trend was seen for the number of species (S). S was highest at both artificial and natural reef sites in the summer with mean values of 20 and 23 taxa per recruitment panel respectively. The lowest S values were recorded in the spring at both reef types, with mean values of just 6 and 7 at natural and artificial reefs respectively. There was a significantly greater number of species on artificial than natural reef types in winter (Figure 4.19, Two-way nested ANOVA (site nested within reef type), $p < 0.05$, Appendix III) but no significant differences were found between reef types for any other season (Figure 4.19, Two-way nested ANOVA (site nested within reef type), $p > 0.05$, Appendix III).

Shannon-Wiener diversity (H') was also lowest in winter and spring and highest in summer at both reef types. Mean values ranged from 0.9 and 1.0 at natural and artificial reefs in winter to 2.8 and 2.9 at natural and artificial reefs respectively in the summer. No significant differences were found in mean Shannon-Wiener diversity

(H′) between reef types for any season (Figure 4.20, Two-way nested ANOVA (site nested within reef type), $p > 0.05$, Appendix III).

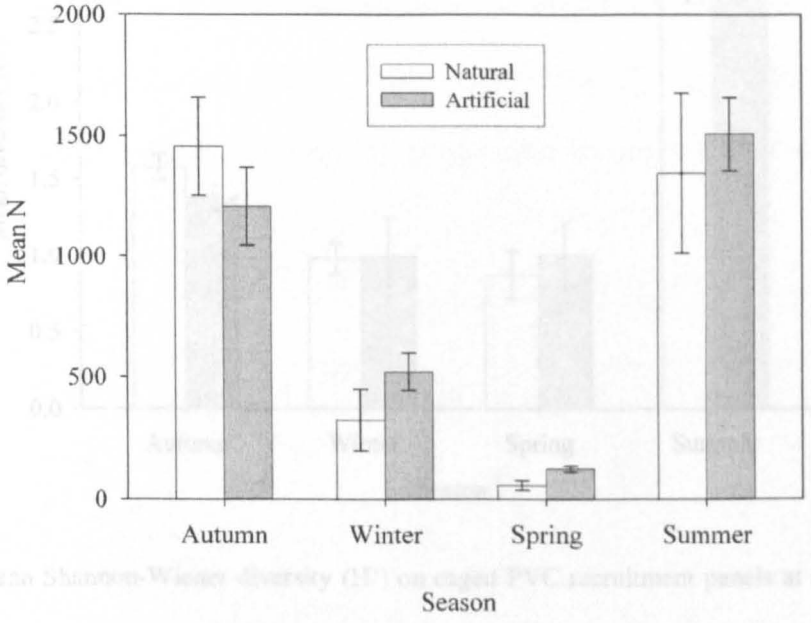

Figure 4.18 Mean N (number of individuals) on caged PVC recruitment panels at artificial and natural reef types in all seasonal sampling periods. Error bars show 95% confidence intervals (n = 12).

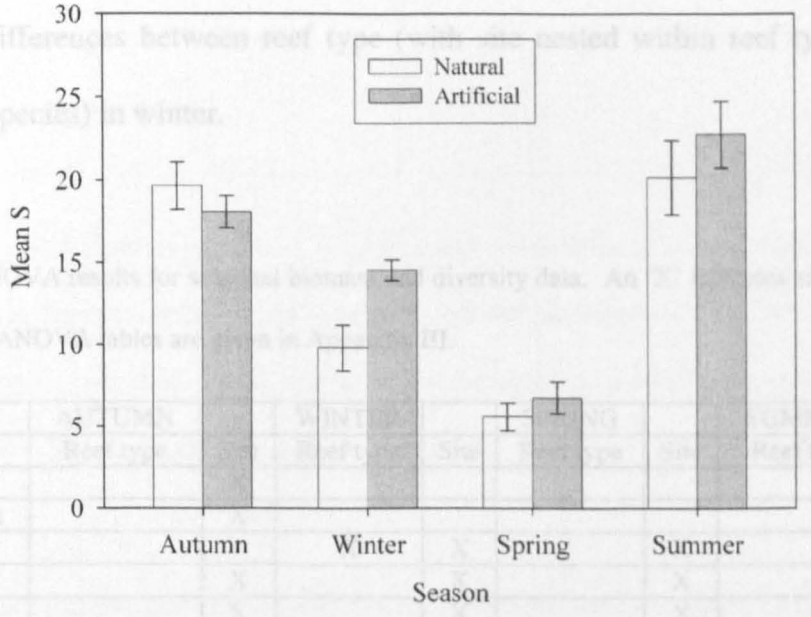

Figure 4.19 Mean S (number of species) on caged PVC recruitment panels at artificial and natural reef types in all seasonal sampling periods. Error bars show 95% confidence intervals (n = 12).

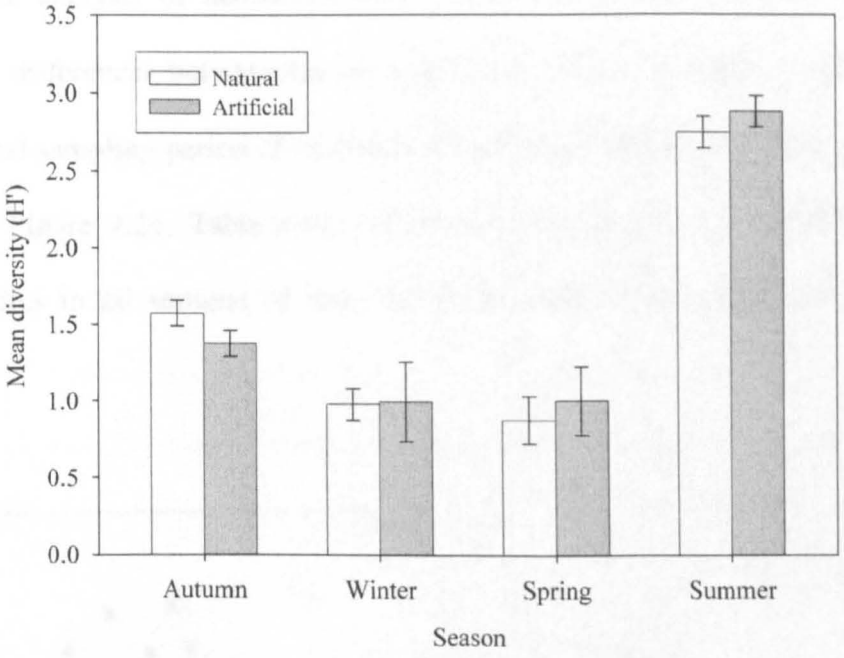

Figure 4.20 Mean Shannon-Wiener diversity (H') on caged PVC recruitment panels at artificial and natural reef types in all seasonal sampling periods. Error bars show 95% confidence intervals (n = 12).

Table 4.5 summarises the significant and non-significant results for caged data between artificial and natural reef types in Loch Linnhe. The only factor to show significant differences between reef type (with site nested within reef type) was S (number of species) in winter.

Table 4.5. ANOVA results for seasonal biomass and diversity data. An 'X' indicates significance at $p < 0.05$. Full ANOVA tables are given in Appendix III.

	AUTUMN		WINTER		SPRING		SUMMER	
	Reef type	Site	Reef type	Site	Reef type	Site	Reef type	Site
Dry weight		X						X
Ash free dry wt		X						X
S			X	X		X		X
N		X		X		X		X
H'		X		X		X		X

Multivariate analysis of taxonomic data from PVC recruitment panels found no significant differences between the assemblage structures at different reef types in any seasonal sampling period (2–way nested ANOSIM (site nested within reef type), $p > 0.05$, Figure 4.21, Table 4.6). There were, however, significant differences between sites in all seasons (2 way ANOSIM, site nested within reef type, $p < 0.001$).

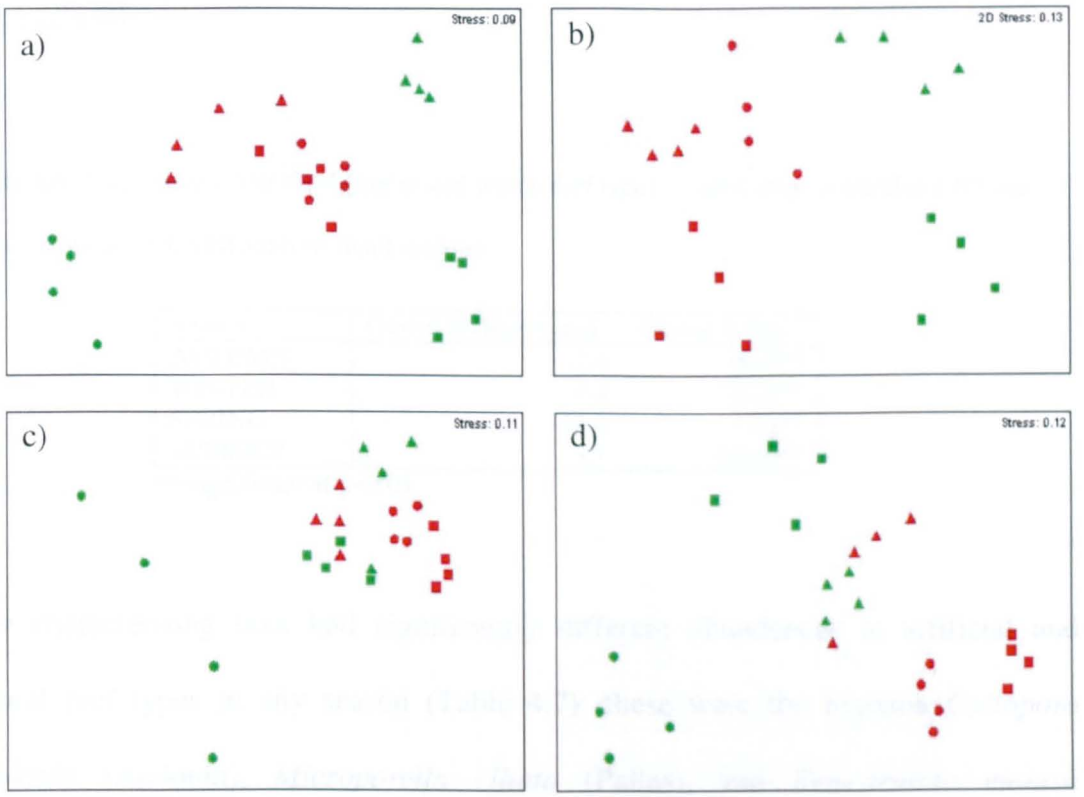

Figure 4.21 nMDS plots for caged data from each seasonal sampling period; a) Autumn, b) Winter; c) Spring and d) Summer. Factor = reef type; red = artificial, green = natural; ▲ A1, ● A2, ■ A3, ▲ N1, ● N2, ■ N3. Data from natural site N2 was removed from the nMDS for winter to make the nMDS clearer as N2 was very distant from the other sites.

Seasonal recruitment patterns at natural and artificial study sites in Loch Linnhe for characteristic taxa are shown in Figure 4.22. Epifaunal assemblages on PVC panels

in the autumn were dominated by large abundances of sinistral spirorbids and anomiidae at both artificial and natural sites. There were also moderate abundances of *Pomatoceros* sp., *H.elegans* and *Bugula* sp. In both winter and spring the epifaunal assemblages were dominated by the sinistral spirorbid at both artificial and natural sites. In the summer the epifaunal assemblage was dominated by high abundances of *Pomatoceros* sp. and sinistral spirorbid, with moderate abundances of *H. elegans* and Anomiidae. Full SIMPER tables for each season are given in Appendix III.

Table 4.6 2 way nested ANOSIM (site nested within reef type). Caged data Natural site N2 was included in the ANOSIM analysis in all seasons.

Season	Global R (Reef type)	Global R Site
AUTUMN	-7.4	90.5**
WINTER	-7.4	92.8**
SPRING	-14.8	77.0**
SUMMER	3.7	100.0**

** significant at $p<0.01$

Few characterising taxa had significantly different abundances at artificial and natural reef types in any season (Table 4.7); these were the bryozoa *Callopora dumerilii* (Audouin), *Microporella ciliata* (Pallas), and *Fenestrulina malusii* (Audouin) in winter, Tubulipora in spring and Tubulipora, *Escharoides coccinea* (Abildgaard) and *Electra pilosa* (L.) in summer. All had significantly higher abundances at artificial than natural reef sites (nested ANOVA, $p < 0.05$ in all cases, Figure 4.22).

All characterising taxa on the PVC recruitment panels in this study showed seasonal patterns in recruitment, although *H. elegans*, the sinistral spirorbid, the dextral

spirorbid, the small solitary ascidia, Tubulipora, *H. sciaphilum*, and *M. ciliata* all had some recruitment in all seasons. The fewest number of taxa recruited to PVC recruitment panels in the spring. Recruitment was also fairly low in winter. Autumn and summer seasons had the highest recruitment across all taxa.

Table 4.7 ANOVA results for characteristic taxa. ANOVA model: 'Reef type' 'site (reef type)' Site = random. Full ANOVA tables are given in Appendix III.

Taxa	AUTUMN		WINTER		SPRING		SUMMER	
	Reef type	Site	Reef type	Site	Reef type	Site	Reef type	Site
Pomatoceros sp.		X		X	-	-		X
Hydroides elegans		X		X		X		X
Sinistral spirorbid		X		X		X		X
Dextral spirorbid				X		X		X
Anomiidae		X		X	-	-		X
Small porifera		X		X	-	-		X
Balanus crenatus	-	-	-	-	-	-		X
Ascidiella aspersa			-	-	-	-		X
Corella parallelogramma			-	-	-	-		X
Small solitary ascidian		X		X		X		X
Bugula sp.		X			-	-		
Tubulipora		X		X	X*	X*	X	X
Lichenopora		X	-	-	-	-		X
Callopora craticula		X	-	-	-	-		X
Callopora dumerilii		X	X		-	-		X
Haplopoma sciaphilum		X	*	X*				X
Microporella ciliata		X	X	X			*	X*
Fenestrulina malusii		X	X*	X*	-	-		X
Escharoides coccinea		X		X			X	
Electra pilosa		X				X	X	
Modiolarca tumida			-	-	-	-	-	-

X shows significance at $p<0.05$. * shows taxa with heterogeneous variances which may be susceptible to false positives (type II errors). '-' shows not tested as abundances were too low.

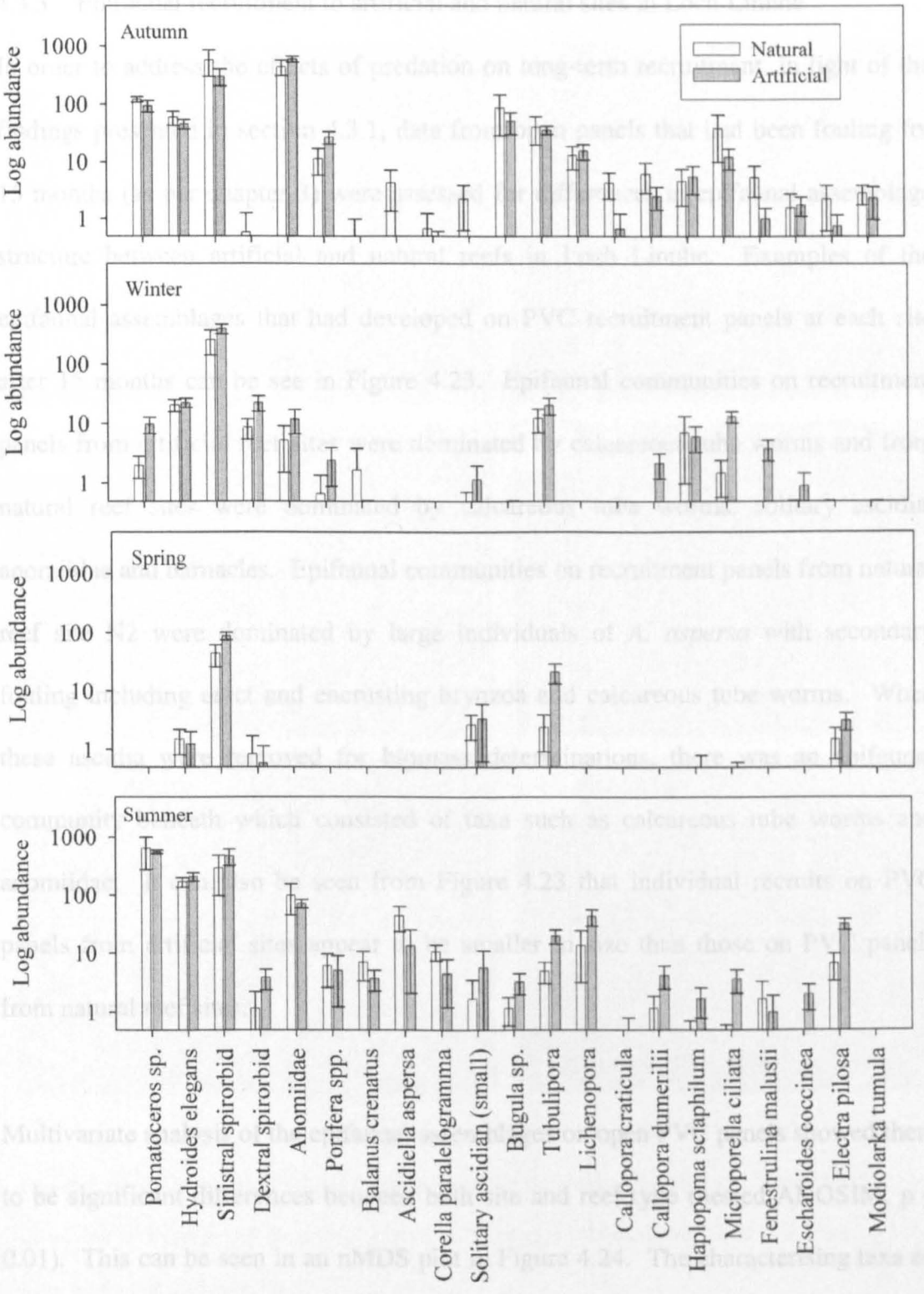

Figure 4.22 Seasonal mean abundance (log scale) of characterising taxa on caged panels at artificial and natural sites in Loch Linnhe. Error bars show 95% confidence intervals (n = 12)

4.3.3 Epifaunal recruitment to artificial and natural sites in Loch Linnhe

In order to address the effects of predation on long-term recruitment, in light of the findings presented in section 4.3.1, data from open panels that had been fouling for 15 months (as per chapter 3) were assessed for differences in epifaunal assemblage structure between artificial and natural reefs in Loch Linnhe. Examples of the epifaunal assemblages that had developed on PVC recruitment panels at each site after 15 months can be see in Figure 4.23. Epifaunal communities on recruitment panels from artificial reef sites were dominated by calcareous tube worms and from natural reef sites were dominated by calcareous tube worms, solitary ascidia, anomiidae and barnacles. Epifaunal communities on recruitment panels from natural reef site N2 were dominated by large individuals of *A. aspersa* with secondary fouling including erect and encrusting bryozoa and calcareous tube worms. When these ascidia were removed for biomass determinations, there was an epifaunal community beneath which consisted of taxa such as calcareous tube worms and anomiidae. It can also be seen from Figure 4.23 that individual recruits on PVC panels from artificial sites appear to be smaller in size than those on PVC panels from natural reef sites.

Multivariate analysis of the epifaunal assemblages on open PVC panels showed there to be significant differences between both site and reef type (nested ANOSIM, $p < 0.01$). This can be seen in an nMDS plot in Figure 4.24. The characterising taxa on PVC recruitment panels at artificial and natural sites were identified using the SIMPER routine (PRIMER, Clarke & Warwick 2001) and are shown in Table 4.8. It can be seen that the community composition was similar between artificial and natural reef sites. Taxa causing dissimilarity between sites are given in Appendix III.

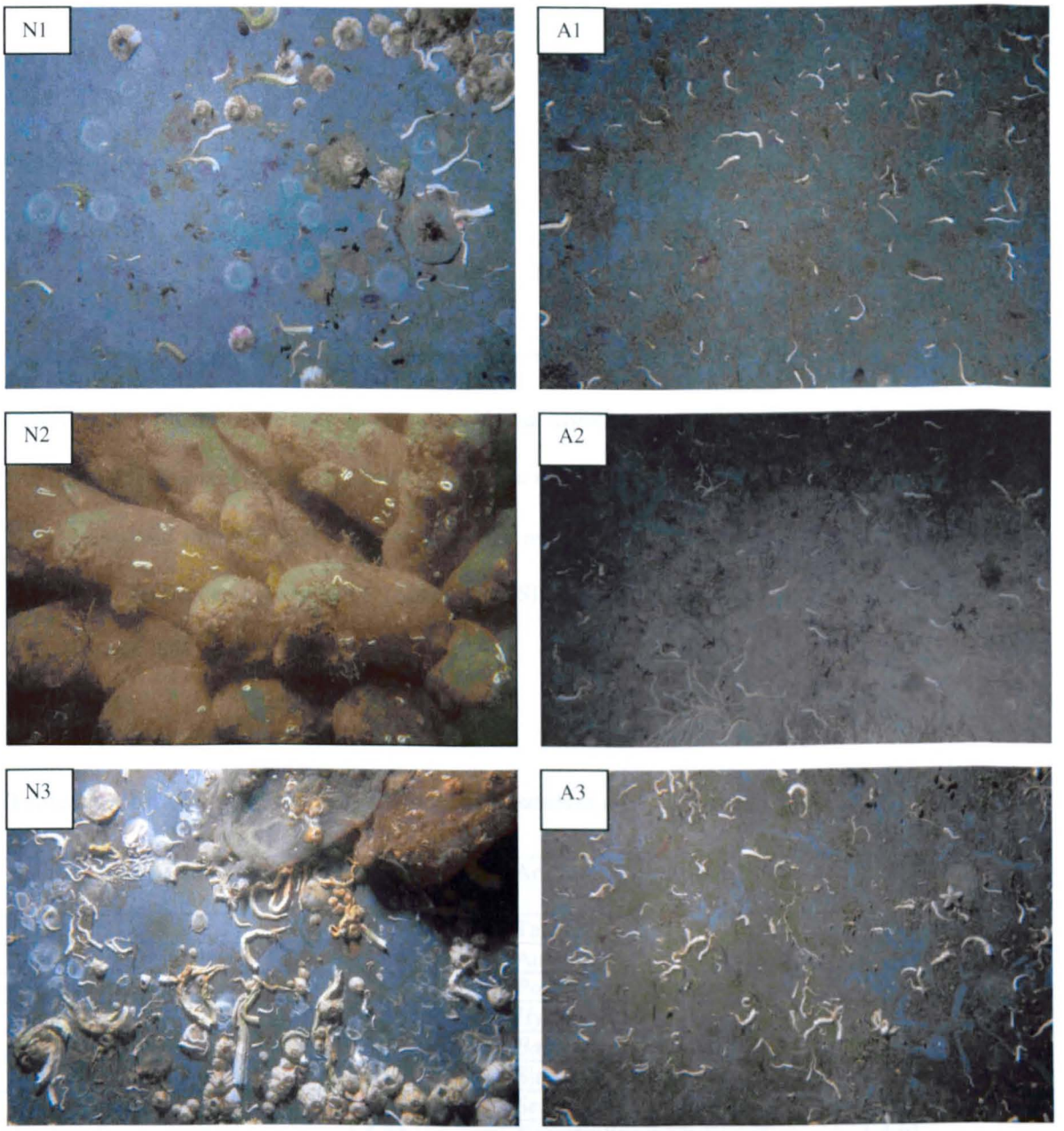

Figure 4.23 Epifaunal assemblages on open recruitment panels at artificial and natural reef sites after 15 months of fouling. All photographs were taken using a Nikonos 35mm lens with close-up kit and show an area of 19.5cm x 14cm.

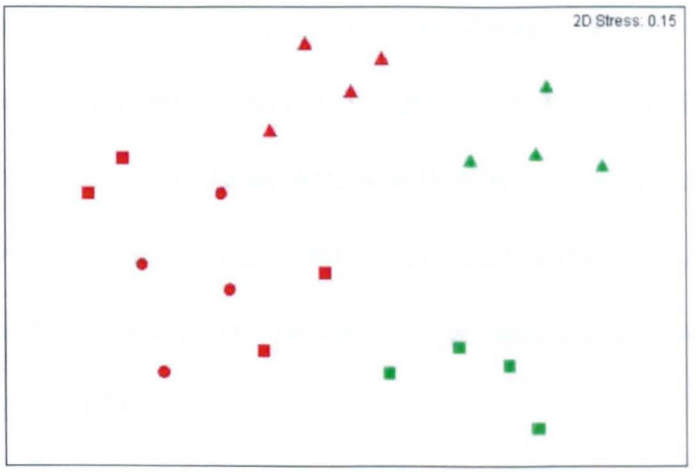

Figure 4.24 nMDS plot of open (uncaged) epifaunal assemblage structures at artificial and natural reef sites. Factor = reef type; red = artificial, green = natural; ▲ A1, ● A2, ■ A3, ▲ N1, ■ N3. Site N2 was removed from the nMDS plot to show the remaining data points more clearly. Significant differences were found between sites (nested ANOSIM, $p < 0.001$) and between reef types (nested ANOSIM, $p < 0.01$).

Table 4.8 Characterising taxa on PVC recruitment panels at artificial and natural reef types.

Natural (average similarity 64.95%)		Artificial (average similarity 77.96%)	
Taxon	% contr.	Taxon	% contr.
Pomatoceros triqueter	15.85	Anomiidae	10.96
Hydroides elegans	13.34	*Pomatoceros triqueter*	10.76
Anomiidae	12.92	*Hydroides elegans*	8.93
Sinistral spirorbid	7.59	*Balanus crenatus* scar	7.17
Serpula vermicularis	7.18	Sinistral spirorbid	6.97
Balanus crenatus	6.99	*Serpula vermicularis*	6.57
Fenestrulina malusii	5.33	*Fenestrulina malusii*	4.61
Bugula sp.	4.66	*Microporella ciliata*	4.40
Balanus crenatus scar	4.33	*Tubulipora*	4.28
Ascidiella aspersa	4.14	*Bugula* sp.	4.08
Microporella ciliata	3.51	Bryozoan ancestrulae	3.78
Modiolarca tumida	3.21	*Callopora dumerilii*	3.75
Callopora dumerilii	2.53	*Porifera* spp.	3.30
		Balanus crenatus	2.92
		Electra pilosa	2.65
		Escharoides coccinea	1.85
		Filograna implexa	1.72

The abundances of the main characterising taxa are shown in Figure 4.25 and Figure 4.26. Few taxa had significantly different abundances on PVC recruitment panels at artificial and natural reef sites (Table 4.9; ANOVA results in Appendix III). The saddle oyster Anomiidae, the sponges Porifera spp., and the bryozoa *E. pilosa* and *E. coccinea* all had significantly greater abundances at artificial than natural reef sites (nested ANOVA, $p < 0.05$).

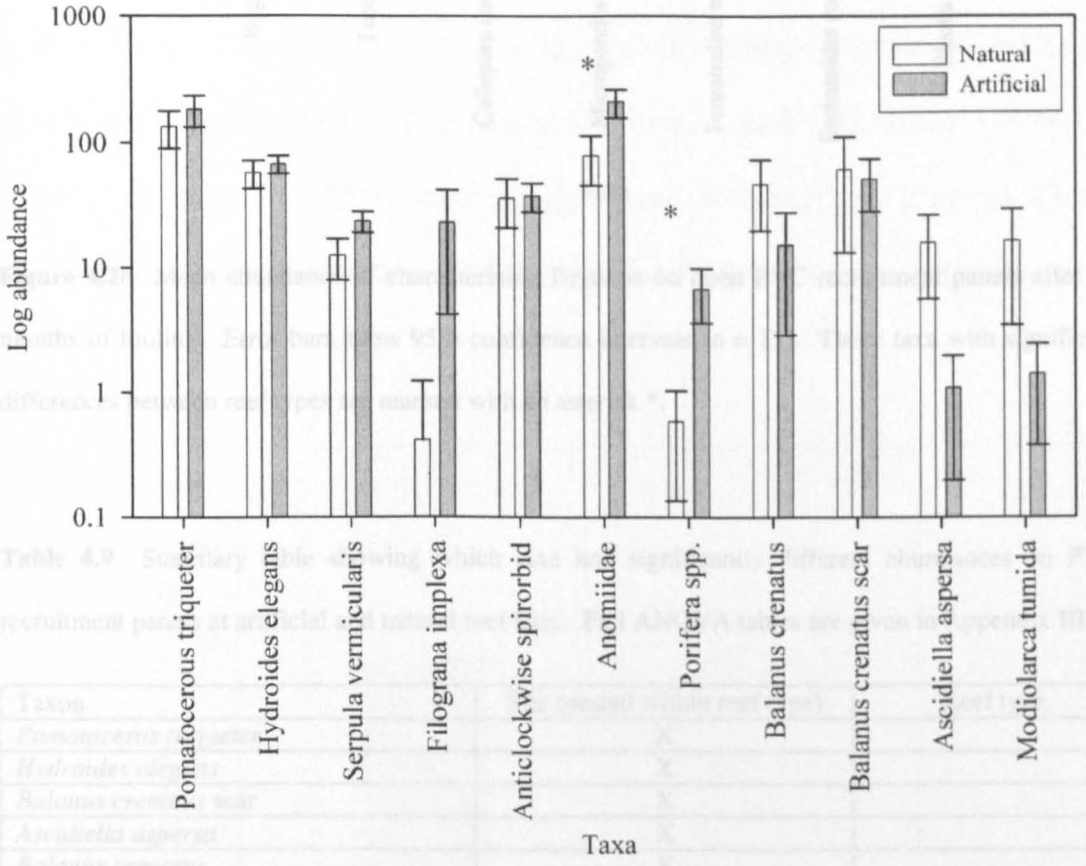

Figure 4.25 Mean abundance of characterising taxa on open PVC recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12). Those taxa with significant differences between reef types are marked with an asterisk *.

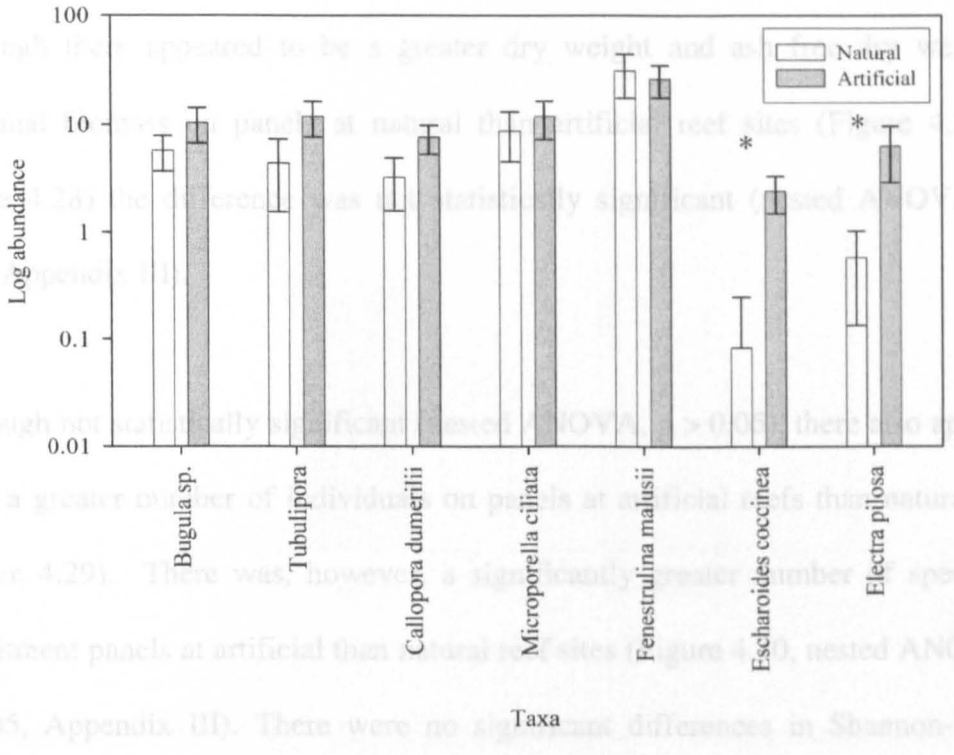

Figure 4.26 Mean abundance of characterising Bryozoa on open PVC recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12). Those taxa with significant differences between reef types are marked with an asterisk *.

Table 4.9 Summary table showing which taxa had significantly different abundances on PVC recruitment panels at artificial and natural reef sites. Full ANOVA tables are given in Appendix III.

Taxon	Site (nested within reef type)	Reef type
Pomatoceros triqueter	X	
Hydroides elegans	X	
Balanus crenatus scar	X	
Ascidiella aspersa	X	
Balanus crenatus	X	
Filograna implexa	X	
Modiolarca tumida	X	
Fenestrulina malusii	X	
Porifera spp.	X	X
Electra pilosa		X
Tubulipora	X	
Anomiidae		X
Sinistral spirorbid	X	
Microporella ciliata	X	
Escharoides coccinea		X
Callopora dumerilii	X	
Serpula vermicularis		
Bugula sp.	X	

Biomass

Although there appeared to be a greater dry weight and ash free dry weight of epifaunal biomass on panels at natural than artificial reef sites (Figure 4.27 and Figure 4.28) the difference was not statistically significant (nested ANOVA, $p > 0.05$, Appendix III).

Although not statistically significant (nested ANOVA, $p > 0.05$), there also appeared to be a greater number of individuals on panels at artificial reefs than natural reefs (Figure 4.29). There was, however, a significantly greater number of species on recruitment panels at artificial than natural reef sites (Figure 4.30, nested ANOVA, $p < 0.05$, Appendix III). There were no significant differences in Shannon-Wiener diversity on panels at different reef types (nested ANOVA, $p > 0.05$, Appendix III).

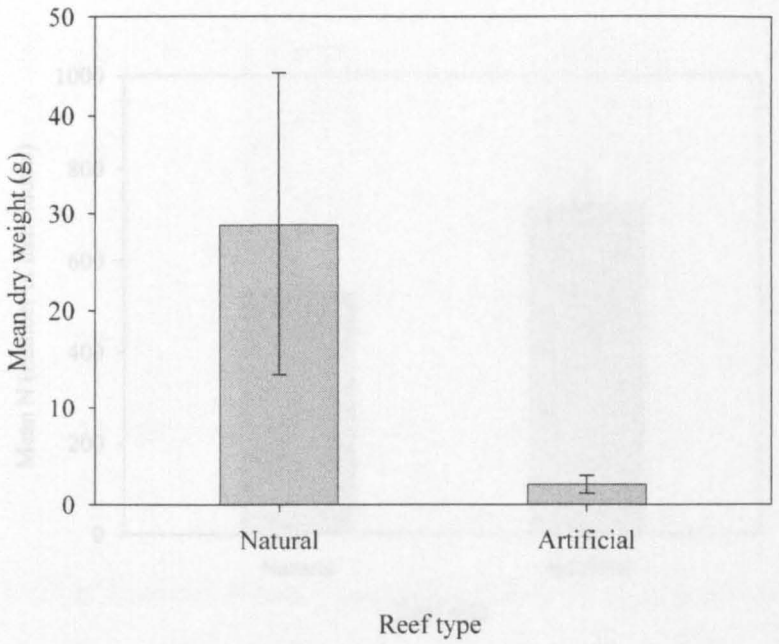

Figure 4.27 Mean dry weight of epifaunal biomass on open recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12).

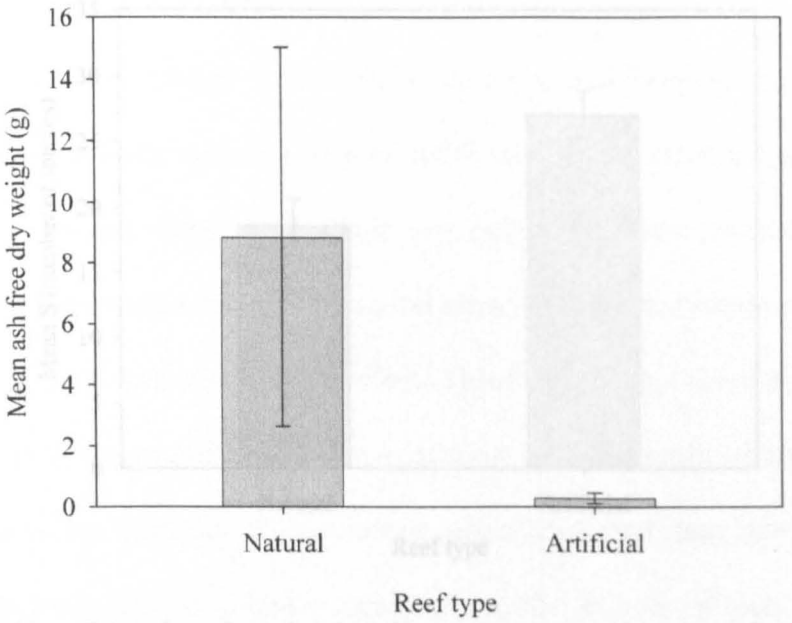

Figure 4.28 Mean ash free dry weight of epifaunal biomass on open recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12).

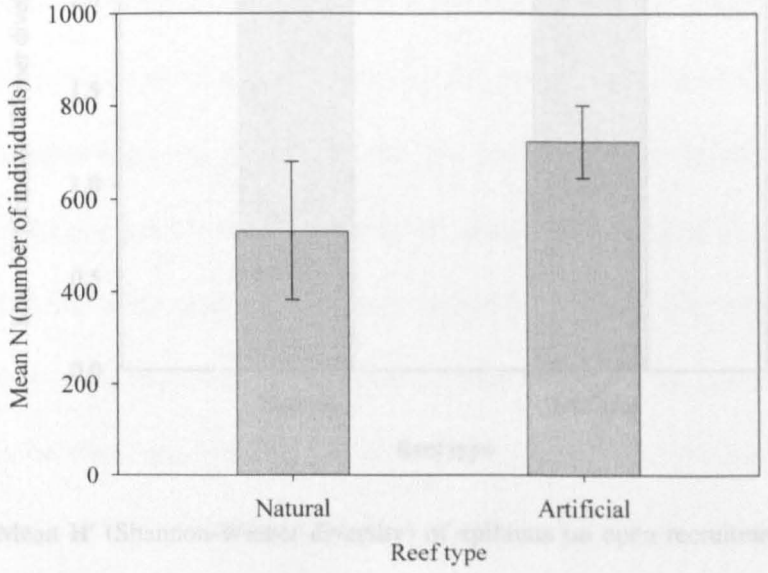

Figure 4.29 Mean N (number of individuals) of epifauna on open recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12).

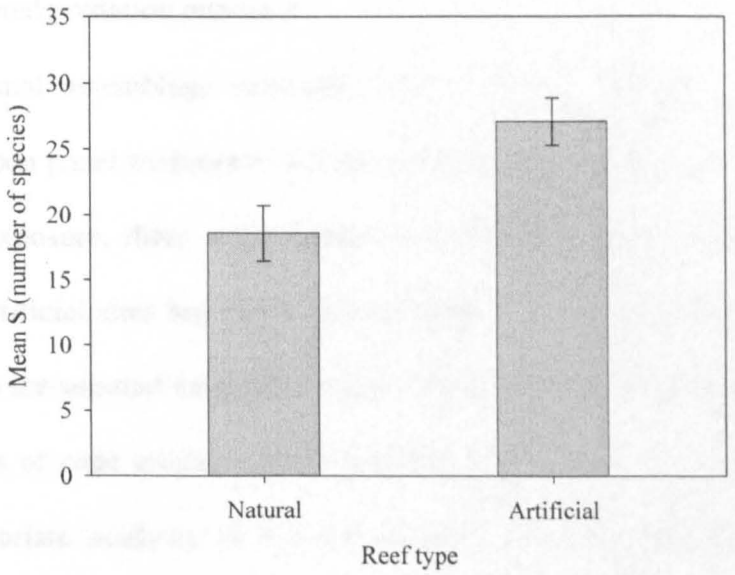

Figure 4.30 Mean S (number of species) in epifauna on open recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12).

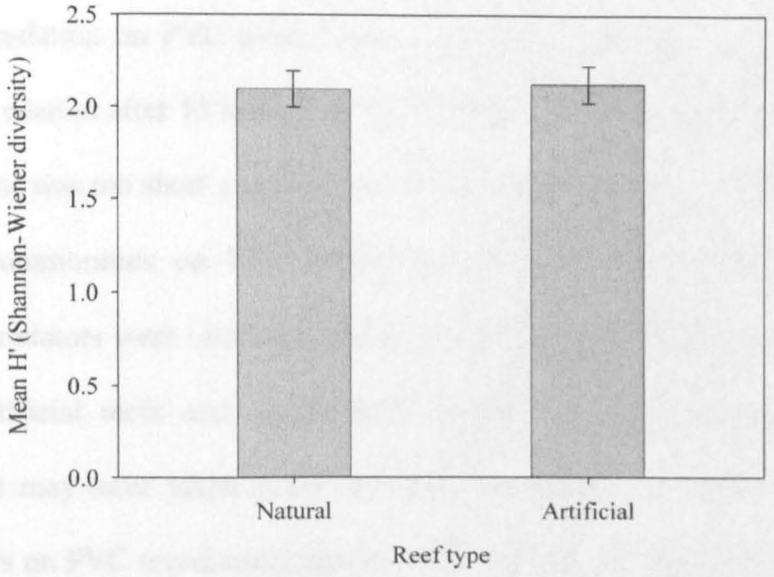

Figure 4.31 Mean H' (Shannon-Wiener diversity) of epifauna on open recruitment panels after 15 months of fouling. Error bars show 95% confidence intervals (n = 12).

4.4 Discussion

4.4.1 Seasonal predation pressures

When epifaunal assemblage structures were compared between caged, partially-caged and open panel treatments at both artificial and natural reef types, after three months of exposure, there were significant differences between treatments in all seasons at artificial sites but not at natural sites, with the exception of open versus caged data in the summer sampling period. This indicates that there were differences in the effects of cage artefacts and/or predation between artificial and natural reef sites. Univariate analysis of taxonomic abundance and measures of epifaunal biomass showed little conclusive evidence of the effects of predation or cage artefacts on seasonal epifauna recruitment.

There are various possible explanations for the lack of evidence for the effects of epifaunal predation on PVC panels after 3 months despite the strong influence of epifaunal predation after 15 months at artificial reefs shown in chapter 3. It may be that 3 months was too short a time period for the predators to exert their influence on epifaunal communities on PVC panels, particularly those inside partial cages. Epifaunal predators were observed during all seasons on natural rocky reefs, on the concrete artificial reefs and on the soft sediment around the reefs (*pers. obs.*). However, it may have taken some time for the predators to locate the epifaunal communities on PVC recruitment panels. Although partial cages had holes to allow predators access to the recruitment panels, it may be that the predators took longer to locate the PVC recruitment panels inside the cages than those panels that were uncaged. As predation and cage artefacts in this study were assessed using the relationship between the epifaunal communities on panels from different treatments,

any difference in the accessibility of recruitment panels to predators may have obscured any trends between the treatments in a study run over a short time scale.

The Optimal Foraging Theory (Stephens & Krebs 1986), whereby on perceiving a prey item a predator makes a choice to either pursue the item it comes across or to continue to search for a better item, may provide a second explanation. According to the Prey Model (Stephens & Krebs 1986) a predator makes this decision taking into account the net energy gain, the handling time and the encounter rate of prey types and sizes. Prey value has been defined as the ratio of energy yield to handling time (Hughes 1980). As a result, there will be a minimum size of prey below which the energy cost of locating and handling the prey item exceeds the energy return. It can, therefore, be expected that foraging predators use size selection of prey in order to maximise their net rate of energy intake (Hughes 1980). The epifaunal communities that had developed on the PVC recruitment panels in the current study after 3 months may have had a lower prey value than the epifaunal communities that had developed over a 15 month fouling period. This may explain the lack of evidence for epifaunal predation after 3 months and the strong evidence of predation after 15 months at the same sites.

4.4.2 Seasonal early epifaunal recruitment to artificial and natural reefs.

Although there was no consistent evidence of the effects of predation or cage artefacts on seasonal epifaunal recruitment, predation was shown to have a stronger influence on epifaunal assemblages on recruitment panels at artificial than natural reef sites in Loch Linnhe after 15 months of immersion (see chapter 3) with no consistent effects of cage artefacts at any site. Caged data were, therefore, used in

this study in order to compare seasonal epibiotic recruitment to PVC recruitment panels at artificial and natural sites in Loch Linnhe. As the use of cages reduced the effects of post-settlement mortality through predation, seasonal early epifaunal recruitment data from caged panels can, perhaps, be used to infer seasonal epifaunal larval supply at the study sites.

There was no difference in the overall epifaunal assemblage structure on caged PVC panels at artificial and natural reef sites in any season suggesting that the early epifaunal recruitment and, therefore, the larval supply may have been similar between reef types in this study. When the abundances of characterising taxa were compared there were few significant differences between artificial and natural reef types in any season. Only the bryozoa *C. dumerilii*, *M. ciliata*, and *F. malusii* in winter, Tubulipora in spring and Tubulipora, *E.coccinea* and *E. pilosa* in the summer had significantly different abundances at the two reef types. All these taxa had significantly higher abundances on PVC panels at artificial reef sites compared with natural reef sites. It can, therefore, be hypothesised that the artificial reefs themselves may be a greater source of bryozoan larvae than the local natural rocky reefs in Loch Linnhe. This is not altogether surprising as many encrusting bryozoan species are known to have opportunistic life history strategies (McKinney & Jackson 1991) and so would be expected to be present in high abundances on recently deployed artificial structures or habitats with high disturbance rates. The artificial reefs in Loch Linnhe fall into both of these categories being approximately two years old and subject to high predation pressures (chapter 3).

Although it was not possible to determine the actual source of the epifaunal larvae in

this study, the majority of bryozoans release larvae with very short competence periods that are ready to settle within a few seconds to a few hours of parental release (McKinney & Jackson 1991). The exception to this is the bryozoan *E. pilosa* which is known to release larvae with a long competence period (McKinney & Jackson 1991). Elevated abundances of bryozoa such as *E. coccinea* on recruitment panels at artificial reef sites, therefore, suggests that the artificial reefs are acting as a "source" for some bryozoa larvae (see discussion about sources and sinks in section 4.1.1).

Data presented in this chapter showed that the early recruitment to artificial and natural reef study sites in Loch Linnhe was equal, with the exception of a few bryozoa species. This is in contrast to the findings of Bulleri (2005a) who showed epifaunal recruitment onto panels to differ between sites despite the fact that he had also controlled for predation differences by removing the most common herbivores. However, in contrast to the present study which was carried out in Scottish subtidal environment, Bulleri (2005a) carried out the study in the intertidal zone in Sydney, Australia. This is one possible explanation for the differences between findings in these studies. Results from the present study, therefore, suggest that there was a fairly uniform supply of propagules, both in terms of species composition and abundance, throughout the study area in Loch Linnhe.

4.4.3 Epifaunal recruitment to artificial and natural reefs

Although the present study has shown early epibiotic recruitment and, therefore, seasonal larval supply to the artificial and natural study sites to be similar, there were significant differences in assemblage structure on open (uncaged) recruitment panels at artificial and natural reef sites after 15 months of fouling. There also appeared to

be a greater epifaunal biomass on PVC panels at natural sites than at artificial reef sites although this was not significant; perhaps a result of the large variability in data from the natural sites. There was, however, a significantly greater number of species on PVC panels at artificial than at natural reef sites. No significant differences in N (number of individuals) or H' (Shannon-Wiener diversity) were found between reef types although there did appear to be a generally higher N at artificial sites.

It was, therefore, surprising that few significant differences in abundance of characterising taxa were found between artificial and natural reef sites in Loch Linnhe after 15 months. The bryozoa *E. pilosa* and *E. coccinea* had significantly greater abundances on PVC panels at artificial sites than at natural sites. This is perhaps not surprising because these two species also had elevated abundances at artificial sites in the summer sampling period of the seasonal recruitment/larval supply study. The only other characterising taxa with significantly different abundances at artificial and natural reef sites were the Porifera spp. and Anomiidae, both of which also had higher abundances on PVC panels at artificial compared with natural reef sites. It is interesting to note, however, that individuals on PVC panels after 15 months at artificial reef sites appeared to be smaller than those on PVC panels at natural reef sites. Although this could not be examined in detail in this study because no information was available on the biomass for each individual taxon, this is supported by the greater biomass at natural compared with artificial reef sites despite the lack of significant differences in taxon abundance. This suggests that although there were few differences in taxon abundance between reef types, there were differences in the community development at artificial and natural reefs in Loch Linnhe.

Predation has been shown to exert a greater influence on epifaunal assemblages on PVC recruitment panels at artificial than natural reef sites in Loch Linnhe (chapter 3) and this can be used to explain many of the differences seen in the longer-term (15 months) epifaunal recruitment to open panels at artificial and natural reef sites in this chapter. A disturbance such as predation on epifaunal communities clears areas on the substratum thereby providing free space for the arrival of new recruits (e.g. Paine 1966, Menge 1976). Through the removal of dominant competitors, predation can lead to epifaunal communities with greater species diversity (Paine 1966, Peterson 1979). This could explain the higher abundance of the bryozoa, Porifera spp. and Anomiidae on PVC panels at artificial reef sites compared to natural reef sites; these are known to be pioneering taxa with poor competitive abilities but good dispersive capabilities (e.g. McKinney & Jackson 1991). An exception to this are the sponges (Porifera spp.) which are generally regarded as later colonisers rather than pioneering taxa (e.g. Bell et al. 2006). However, although Sebens (1986) found that sponges were slow to recolonise cleared areas, the sponges were ranked lower than Bryozoa in the competitive hierarchy of epifaunal community assemblages in New England, USA. The low competitive ability of the sponges as shown by Sebens (1986) could explain the higher abundance of Porifera spp. in relatively highly disturbed areas such as the recruitment panels at artificial reef sites in the present study.

The difference in size of individuals within the epifaunal communities on PVC panels at artificial and natural reef types can also be explained by disturbance caused by predation. Subjected to a high rate of disturbance, it is likely that individuals in the epifaunal communities on PVC recruitment panels at artificial reef sites were unable to grow to a large size before being predated or bulldozed off the substratum

by grazing invertebrates. The epifaunal communities that had recruited to open PVC panels at the artificial sites after 15 months of fouling were, therefore, composed mostly of relatively newly settled recruits. Many studies have shown that vulnerability to disturbance by epifaunal predators may decrease with size or age of an individual (e.g. Davis 1988a, Hunt & Scheibling 1997, Osman & Whitlatch 2004). This means that not only were epifaunal assemblages exposed to higher predation rates at artificial sites than natural sites, but that individuals at artificial sites would have been more vulnerable to disturbance by predation as a result of their smaller size.

It also seems likely that species richness was higher on recruitment panels at artificial than natural reef sites as a result of disturbance by predation. Paine (1966) hypothesised that "local species diversity is directly related to the efficiency with which predators prevent the monopolisation of the major environmental requisites by one species". Not only does predation clear space on recruitment panels thereby allowing the settlement of new recruits, including taxa with high dispersive and colonising potential and low competitive abilities, but high disturbance rates prevent the growth and maturity of individuals thereby reducing post-settlement mortality caused by interspecific competition. According to the Intermediate Disturbance Hypothesis (Connell 1978) species richness is highest at an intermediate level of disturbance; in this case predation.

Russ (1980) investigated the effects of fish predation on epifaunal community development in Australia and found no significant differences in dry weight of biomass on caged and partially-caged panels after four months but a significant

difference after seven months of immersion. The present study (chapters 3 and 4) showed a similar trend with respect to both dry weight and ash free dry weight of epifaunal biomass whereby there were no consistent differences between open, caged and partially-caged panels after three months of immersion but clear differences after 15 months of immersion; with caged panels supporting a greater epifaunal biomass than open or partially-caged panels (chapter 3). This again indicates that three or four months may not be a sufficient length of time for predators to exert their influence on epifaunal communities on open or partially-caged recruitment panels, either as a result of lack of time or because of the low prey value of the recruits (see section 4.4.1).

Epifaunal communities on PVC panels used in this study do not necessarily reflect the epifaunal communities found on the artificial and natural reefs themselves (McGuinness 1989, Glasby & Connell 2001). However, this study suggests that different epifaunal communities may develop on the reefs as a result of predation pressures regardless of the differences in substrata between the PVC recruitment panels used in this experiment, natural rock and concrete reef blocks. Perkol-Finkel et al. (2005) found differences between artificial and natural reefs and questioned whether epifaunal communities on artificial reefs will eventually mimic those on natural reefs as a result of structural and environmental differences between reef types. The present study has shown that differences in epifaunal assemblage structures may persist between reef types in Loch Linnhe as a result of biotic interactions such as predation.

4.4.4 Conclusion

Epifaunal assemblages on open PVC recruitment panels after 15 months of fouling at artificial reef sites in Loch Linnhe were significantly different to those on PVC panels at natural reef sites despite the fact that seasonal epifaunal recruitment to these sites was shown not to be significantly different.

There was inconclusive evidence of seasonal epifaunal predation on three month old communities at either natural or artificial reef sites in this study. Null hypothesis 1 H_0, that there are no effects of reef type on seasonal epifaunal predation, should, therefore, be neither accepted nor rejected. Data presented in chapter 3, however, had shown that the longer-term effects of predation do have a significant influence on epifaunal assemblage structures at different reef types. The short time scale of the 3 month study and the Optimal Foraging Theory and Prey Model (Stephens & Krebs 1986) are likely explanations for the lack of evidence for epifaunal predation after 3 months despite the strong evidence of predation effects after 15 months of fouling at the same sites.

Seasonal early epibiotic recruitment to the different reef types was shown to be similar, suggesting there may have been a fairly uniform supply of propagules across the study area. Null hypothesis 2 H_0, that there are no effects of reef type on seasonal early epifaunal recruitment, could, therefore, be accepted with the exception of a few bryozoa species. Conversely, null hypothesis H_2, that there are no effects of reef type on epifaunal recruitment should be rejected as differences were found in epifaunal assemblage structure between reef types after 15 months of fouling. Although there were few differences in the abundances of characterising taxa on

panels from artificial and natural reef sites, there was a seemingly greater epifaunal biomass at natural reef sites compared with artificial sites, and a greater species richness at artificial compared with natural reef sites. In light of the findings in chapter 3, it seems likely that the influence of increased epifaunal predation at the artificial reef sites caused these differences.

It is widely acknowledged that spatial distribution patterns of epifaunal communities are controlled by a combination of environmental variation and biotic interactions (Turner & Todd 1993, Yakovis et al. 2004, Perkol-Finkel et al. 2005). However, this study has shown that biotic interactions in the form of predation were responsible for many of the differences in epifaunal community assemblages on recruitment panels at artificial and natural reef sites in Loch Linnhe.

Chapter 5 Changes in productivity associated with artificial reef construction

5.1 Introduction

Epifaunal colonisation on the surfaces of artificial reefs has been well documented (e.g. Cummings 1994, Falace & Bressan 1994, Foster et al. 1994, Nelson et al. 1994, Palmer-Zwahlen & Aseltine 1994, Pamintuan et al. 1994, Reimers & Branden 1994, Relini et al. 1994, Falace & Bressan 2002) and it has been suggested that the rate of epifaunal fouling of an artificial reef can be correlated with reef productivity (Relini & Relini 1997). Productivity is the rate of conversion of resources to biomass per unit area per unit time; the rate at which organic matter is made available to higher trophic levels (Taylor 1998, Waide et al. 1999). A key question associated with artificial reef use is whether the deployment of a reef increases the biological production in the local area, yet estimates of production for reef or hard-surface epifauna are scarce (Steimle et al. 2002).

As discussed in chapters 1 and 3, the complexity of a habitat is known to be an important factor in structuring benthic communities (e.g. Bohnsack & Sutherland 1985, Barkai & Branch 1988, Sebens 1991, Potts & Hulbert 1994, Guichard & Bourget 1998, Waide et al. 1999, Guichard et al. 2001, Svane & Peterson 2001, Charbonnel et al. 2002, Bradshaw et al. 2003, Almany 2004). Increased habitat complexity, especially with respect to the provision and size of refuge holes, has been shown to increase the species richness, abundance and biomass of fish assemblages on artificial reefs (e.g. Hixon & Beets 1993, Gratwicke & Speight 2005). Although Steimle et al. (2002) showed the epifauna on their artificial reef to

be more productive than the infauna in natural soft sediments no studies have investigated the effects of varying habitat complexity or reef design on the epifaunal productivity of artificial reefs.

The presence of an artificial reef has been shown to affect infaunal communities in close proximity to the reef edge as a result of predation, changes in sediment composition and reduction in oxygenation (Davis et al. 1982, Ambrose & Anderson 1990, Barros et al. 2001, Danovaro et al. 2002, Fabi et al. 2002, Wilding 2006). The placement of an artificial reef, such as the Loch Linnhe artificial reef, on the seabed results in an area of sediment being covered by hard substrata. It is likely that the infauna in the sediments underneath an artificial reef will be negatively affected by the reef placement; perhaps as a result of the compacting of sediments and/or decreased oxygenation. Information on the impacts of artificial reef placement on infauna would be helpful in order to assess the net increase in productivity of artificial reefs to allow true comparisons between the functioning of artificial and natural reefs. No studies to date have investigated the effects of reef block placement on the infauna in underlying sediments.

The Loch Linnhe artificial reef complex comprises many different reef modules of which half are composed of simple, solid reef blocks, and half of complex reef blocks (see chapter 1 for more information). The complex blocks, with two large holes (see Figure 1.3), are designed to increase habitat complexity and provide a greater surface area to volume ratio resulting in a greater surface area for epifaunal colonisation than the simple reef blocks.

This chapter will assess the differences in epifaunal biomass on the two types of reef block used in the Loch Linnhe artificial reef complex, estimate the different epifaunal biomass potential of a typical complex and simple reef module, and investigate biomass differences, per unit area of seabed, on artificial reef blocks and their underlying sediments. In this way comparisons can be made of the biomass of a unit area of seabed to assess whether the Loch Linnhe artificial reef has increased the productivity of the local area though the introduction of hard substrata.

Null hypothesis tested:

H_0: there are no effects of artificial reef block type on epifaunal productivity

5.2 Materials and methods

5.2.1 Experimental design

Six simple and six complex reef blocks were placed in a randomised grid, incorporating six control (without-block) areas, approximately 50m to the north of artificial reef module M1s (grid reference 56° 32.185N 05° 27.091W; see figures 1.1 and 1.2 in chapter 1 for location). There was a distance of 2m between each block and/or control area. Blocks were sited in a depth of 15m, standing in an upright orientation, on silty sand overlain by cobbles and stones. Prior to deployment all blocks were marked with a plastic label and a unique number. Blocks were deployed in September 2002.

5.2.2 Block recovery and sediment coring

After 21 months of fouling on the sea bed the complex and simple blocks were recovered, using SCUBA, and sediment cores were taken from underneath the reef

blocks and from the control sites. Figure 5.1 shows a representation of the experiment showing the reef blocks stood upright on the sediment and the location from where the sediment cores were taken once the blocks had been removed. One block at a time was gently tipped over to reveal the underlying sediment. A 100mm diameter clear Perspex core tube (Figure 5.2) was driven into the centre of the uncovered area of sediment, by hand, as far as possible. Rubber bungs were used to retain the sediment in the cores until processing. One core was also taken from each of the six control areas within the grid.

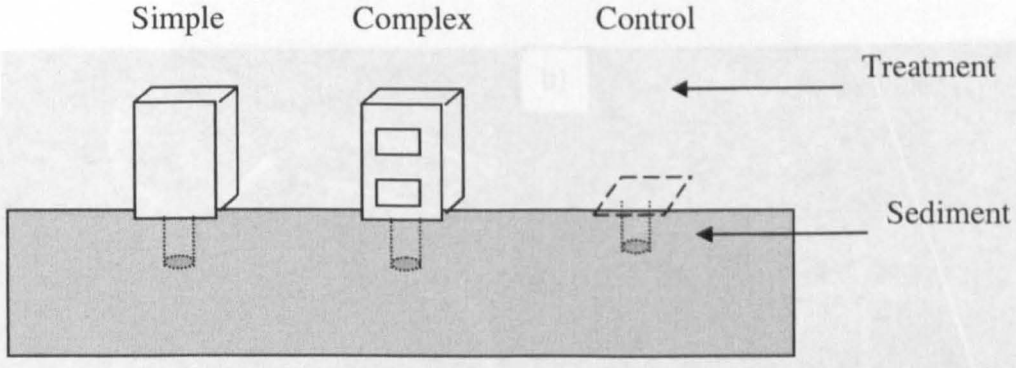

Figure 5.1 Diagram of the experimental set-up showing the reef blocks *in situ* in an upright position and the locations from which sediment cores were collected beneath the reef blocks and in control areas.

Block recovery

Once the sediment had been sampled, each block was gently lifted, secured into a plastic crate using bungee cord and winched from the seabed to a surface support vessel (Figure 5.3). Plastic crates were used to recover the blocks, rather than netting or sacks, to minimise damage to epifouling communities on the surfaces of the blocks. In every case, the westerly facing reef block surface was laid face-down in the crate.

Figure 5.2 100mm diameter perspex sediment core with sediment sample prior to sieving.

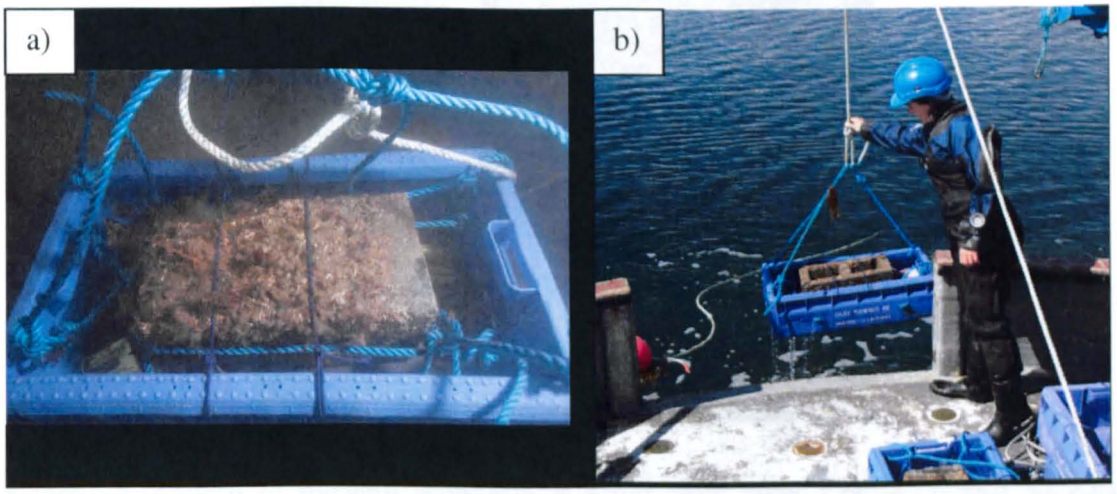

Figure 5.3. a) Simple reef block, *in situ*, secured into a plastic crate for recovery and b) complex reef block being winched from the seabed onto the dive support vessel.

5.2.3 Abundance

The north faces of all reef blocks were photographed before being analysed for taxon abundance using a boom-mounted binocular microscope and wooden grid with 100 counting squares (as used in previous chapters, Figure 5.4). The north faces of all blocks (complex and simple) were solid faces with no voids in them. Taxa were identified using authoritative texts to species level where possible.

5.2.4 Biomass

After the epifauna had been counted all surfaces, including interior surfaces of complex blocks, were scraped clean of biological material with a metal scraper. Firmly attached material was removed with forceps and a scalpel. A wire brush was used to remove loose biological debris. Care was taken to remove any concrete fragments attached to organisms prior to biomass measurements. All biological matter was placed in pre-weighed foil trays and dried to constant weight at 50°C before being ashed in a muffle furnace for 12 hours at 450°C.

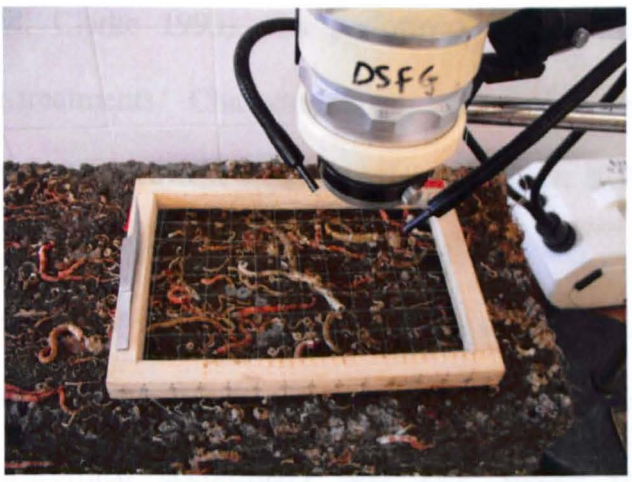

Figure 5.4. Analysis of epifaunal abundance of a reef block using a boom-mounted binocular microscope and a wooden grid with 100 counting squares.

5.2.5 Cores

Sediment cores were sieved though a 1mm geological mesh on return to the laboratory. All material greater than 1mm was preserved in four percent buffered ($CaCO_3$) formalin. Material was later washed in fresh water, sorted into Phyla and preserved in 70 percent ethanol. All infaunal taxa were identified using authoritative keys and texts to species level where possible (polychaetes were only identified to family). Infauna was then dried to constant weight at 50°C before being ashed in a

muffle furnace at 450°C for 12 hours.

5.2.6 Data analysis

Multivariate statistical methods within the PRIMER software package (Clarke & Warwick 2001) were used to assess both the differences in community structure of epibiota on complex and simple reef blocks and differences in infaunal community structure in sediments from different treatments (complex, simple and control). Log (x+1) transformed data were analysed using non-parametric Multi-Dimensional Scaling (nMDS) ordination with the Bray Curtis similarity measure. Analysis of similarity (ANOSIM, Clarke 1993) was performed to test the significance of differences between treatments. Characterising species were determined using the SIMPER routine within the PRIMER software package (Clarke & Warwick 2001).

Biomass and diversity data were tested for equal variances using Levene's test (Dytham 2003) prior to univariate statistical analysis. Data with heterogeneous variances were transformed accordingly (log x+1, square root or 4^{th} root) (Underwood 1997) before being tested using one- and two-way ANOVA within the MINITAB statistical package.

5.2.7 Biomass estimates of reef modules

a) Surface area estimates of reef modules

The area of vertical, horizontal upper and horizontal under-sides within each of four randomly placed replicate $1m^2$ quadrat areas (Figure 5.5) was estimated using a 30cm ruler. This was carried out on both a complex and simple reef module and repeated four times using SCUBA.

b) Biomass estimates for different surface orientations

Twelve concrete experimental units were suspended on a frame above the seabed in horizontal up, horizontal down and vertical orientations (four replicates of each) in Dunstaffnage Bay (56°27.10N 5°26.16W); an area close to the Loch Linnhe artificial reef complex. The units were made by slicing up a number of simple artificial reef blocks as used in the construction of the Loch Linnhe artificial reef complex. Each unit measured 10cm x 20cm x 10cm, and the designated experimental surface area of each concrete unit was 200cm^2 (10cm x 20cm). In August 2003, following 12 months of fouling, the experimental units were recovered using SCUBA and taken back to the laboratory where biomass estimates were determined. Again, care was taken to remove any concrete attached to epifaunal taxa such as barnacles. The epifauna on each surface was scraped into pre-weighed foil trays and dried to constant weight at 50°C. Samples were then ashed at 450°C for 12 hours.

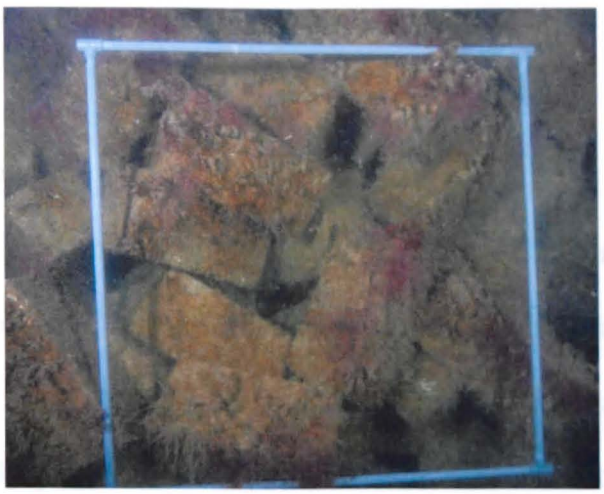

Figure 5.5 Photograph of a 1m^2 quadrat on a simple reef module at the Loch Linnhe artificial reef complex. Vertical, horizontal upper and horizontal underside surfaces were measured *in situ* using a 30cm ruler.

Experimental concrete units were used to estimate epifaunal biomass because they could be made to a standard size and orientated as required. It was not possible to use the reef blocks used in section 5.2.4 for these measurements as only vertical and horizontal upper surfaces were available.

c) Biomass estimates of reef modules

As part of a mapping survey of the Loch Linnhe artificial reef site a high-resolution multibeam survey was carried out in August 2004 using a Reson SeaBat 8125 Multibeam Echo Sounder. The system was operated at 455KHz and was combined with a motion reference sensor and gyro for accurate bathymetric measurement. A digital bathymetric model (DBM) was created using a triangular irregular network to represent the seafloor surface and imported into GIS (Brown & Harper 2006). The height and footprint of seven typical complex and simple reef modules were measured from the resulting multibeam image of the Loch Linnhe artificial reef site using ArcMap within ArcGIS 9 software. The surface area of each reef module was calculated assuming a circular footprint and a conical shape.

d) Biomass calculations

The sediment cores used in this study had a diameter of 100mm and sampled a 78.5cm^2 area of sediment. The artificial reef blocks used in this study had dimensions of 21 x 21 x 42cm. The surface area of sediment covered by one concrete block stood upright on the sediment, therefore, covered an area 441cm^2. Infaunal biomass estimates taken from sediment cores were scaled up to represent the infaunal biomass in a unit area of seabed under an upright reef block (441cm^2).

Mean values of epifaunal and infaunal biomass and surface area were used to estimate and compare the biomass per unit area of seabed with and without the presence of artificial reef blocks and modules.

5.3 Results

5.3.1 Assemblage structure of epibiota on complex and simple reef blocks

No significant differences were found between the assemblage structures on the north face of complex or simple reef blocks after 21 months of fouling (ANOSIM, $p > 0.05$, Figure 5.6).

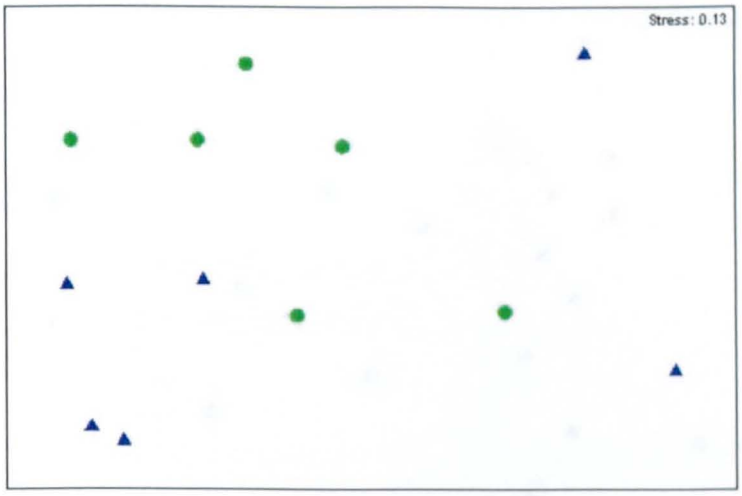

Figure 5.6 nMDS plot showing the similarity between epibiotic assemblages on north facing surfaces of complex and simple reef blocks after 21 months of fouling. Factors: ● = simple, ▲ = complex.

No significant difference were found between the assemblage structure of complex or simple reef blocks (ANOSIM, Global R = 0.057, significance level 26.4%). Note that the internal surfaces of complex blocks were not included in this analysis.

5.3.2 Infaunal assemblages in sediments

There were significant differences in the >1mm infaunal assemblage structure in sediments under different block treatments; control, under complex and under simple reef blocks (ANOSIM, $p < 0.01$, Table 5.1 , Figure 5.7). The characterising taxa, determined using the SIMPER routine (PRIMER, Clarke & Warwick 2001) in sediments from each treatment are shown in Table 5.2. The abundances of the main characterising taxa are shown for each treatment in Figure 5.8. Most taxa had higher abundance in control sediments than in the sediments under reef blocks. Abundances of taxa were also often higher under complex than simple blocks.

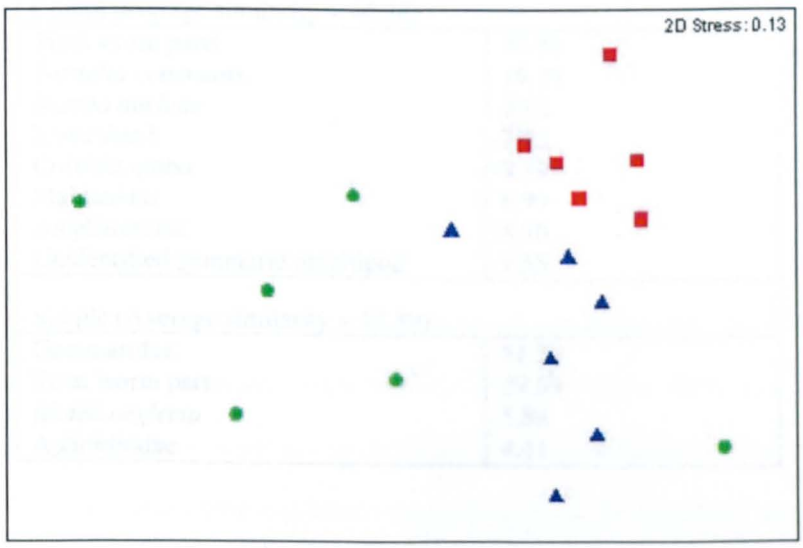

Figure 5.7 nMDS plot showing the similarity between epibiotic assemblages in sediments in control areas (■), in sediments under complex reef blocks (▲) and in sediments under simple reef blocks (●).

Table 5.1 ANOSIM results showing percent dissimilarity between infaunal samples.

	Complex	Control
Control	53.9**	
Simple	47.7**	70.2**

** shows significance at $p < 0.01$

Table 5.2 SIMPER results showing characterising taxa in sediments in each treatment

Taxon	% contribution
Complex (Average similiarity = 38.06)	
Total worm parts	32.03
Nucula nucleus	23.63
Abra alba	15.35
Hiatella arctica/Gari ferensis	9.71
Turitella communis	4.18
Corbula gibba	3.11
Sabellidae	1.45
Terebellidae	1.45
Contol (average similarity = 44.48)	
Total worm parts	32.83
Turitella communis	19.79
Nucula nucleus	9.83
Eunicidae I	7.75
Corbula gibba	7.59
Maldanidae	6.99
Ampharetidae	5.20
Unidentified gammarid amphipod	1.55
Simple (Average similarity = 17.89)	
Gammaridae	51.26
Total worm parts	29.59
Idotea neglecta	5.88
Aphroditidae	4.41

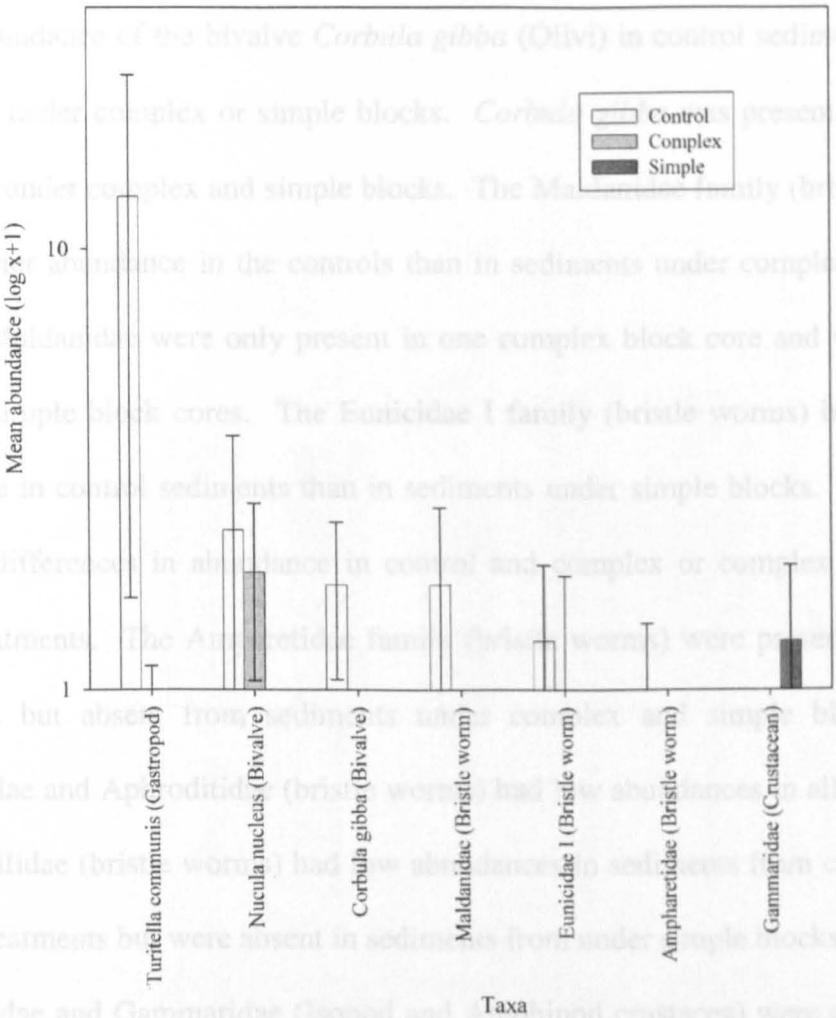

Figure 5.8. Mean infaunal abundance of characterising taxa in sediments from different treatments (control, under complex blocks and under simple blocks). The Terebellidae, Sabellidae, Aphroditidae and Idotidae families had abundances too low to be visible in the bar graph and so have been removed from the figure. Error bars show 95% confidence intervals (n = 6). No significant differences were found between treatments for any taxa (ANOVA, $p > 0.05$ in all cases, Appendix IV).

Although not statistically significant, there were some apparent trends in taxonomic abundances between treatments (Figure 5.8). There was a higher abundance of the gastropod *Turitella communis* (Risso) in control sediments than sediments under complex blocks. *Turitella communis* was absent in sediments under simple blocks. The bivalve *Nucula nucleus* (L.) was present in higher numbers in control sediments

and those under complex blocks than in sediments under simple blocks. There was a greater abundance of the bivalve *Corbula gibba* (Olivi) in control sediments than in sediments under complex or simple blocks. *Corbula gibba* was present in just one core from under complex and simple blocks. The Maldanidae family (bristle worms) had a higher abundance in the controls than in sediments under complex or simple blocks. Maldanidae were only present in one complex block core and were absent from all simple block cores. The Eunicidae I family (bristle worms) had a higher abundance in control sediments than in sediments under simple blocks. There were no clear differences in abundance in control and complex or complex and simple block treatments. The Amparetidae family (bristle worms) were present in control sediments but absent from sediments under complex and simple blocks. The Terebellidae and Aphroditidae (bristle worms) had low abundances in all treatments. The Sabellidae (bristle worms) had low abundances in sediments from complex and control treatments but were absent in sediments from under simple blocks. However, the Idoteidae and Gammaridae (Isopod and Amphipod crustacea) were only present in sediments from under simple blocks.

5.3.3 Diversity

The epifauna on reef blocks had a significantly greater Shannon-Wiener diversity (H') than the infauna in the sediments under reef blocks (two-way ANOVA, $p < 0.05$, Figure 5.9, Table 5.3). When the diversity indices on and under reef blocks were considered together there was no significant difference between reef block type (two-way ANOVA, block type and faunal category both fixed; $p > 0.05$, Figure 5.9, Table 5.3). It is important to note that the diversity measures of epifauna on complex reef blocks only take into account the experimental surface of one face of each reef

block and not the inside surfaces of complex blocks. No interaction was found between where the diversity was measured (i.e. epifauna or infauna) and reef block type ($p > 0.05$).

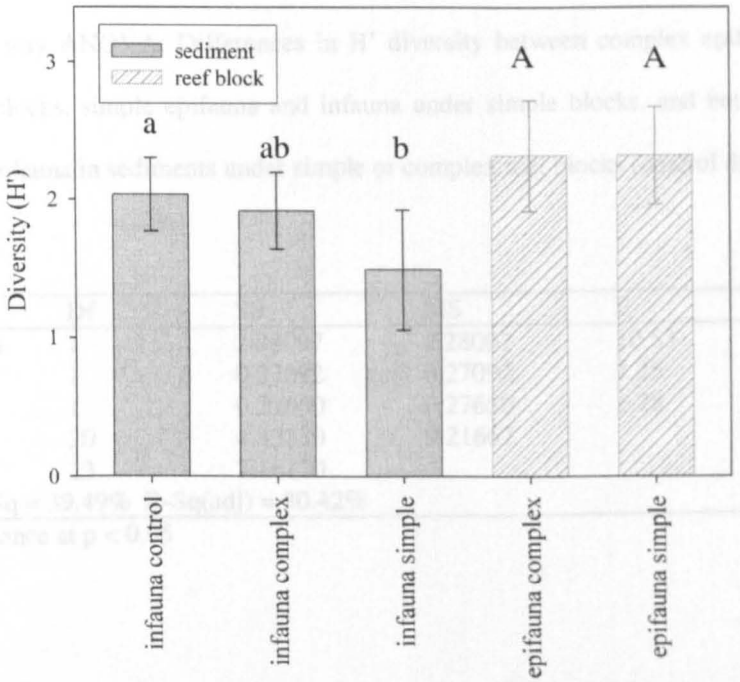

Figure 5.9 Mean Shannon-Wiener diversity indices (H') from different infaunal and epifaunal treatments with 95% confidence intervals (n = 6). Treatments are: infauna in control sediments, infauna in sediments under complex blocks, infauna in sediments under simple blocks, epifauna on complex blocks and epifauna on simple blocks. Different letters above data bars show significant differences between treatments (Fisher's pairwise comparisons, $p < 0.05$). Comparisons were made between treatments within sediment or block samples and not between sediment and block samples.

A one-way ANOVA with Fisher's pairwise comparison showed significant differences in the species diversity between infaunal treatments ($p < 0.05$, Appendix IV). There was a significantly higher species diversity (H') of infauna in control sediments than infauna in sediments under simple reef blocks ($p < 0.05$). No significant differences were found between the infauna in sediments under complex

reef blocks and either control or simple treatments ($p > 0.05$, Appendix IV) or between the species diversity (H') of assemblages on the north face of simple and complex reef blocks ($p > 0.05$, Appendix IV).

Table 5.3. Two-way ANOVA: Differences in H' diversity between complex epifauna and infauna under complex blocks, simple epifauna and infauna under simple blocks, and between epifauna on reef blocks and infauna in sediments under simple or complex reef blocks (control data not included in this analysis).

Source	Df	SS	MS	F	P
Infauna/epifauna	1	2.28097	2.28097	10.53	0.004*
Block type	1	0.27092	0.27092	1.25	0.277
Interaction	1	0.27650	0.27650	1.28	0.272
Error	20	4.33330	0.21667		
Total	23	7.16170			
S = 0.4655 R-Sq = 39.49% R-Sq(adj) = 30.42%					

* shows significance at $p < 0.05$

5.3.4 Biomass of epifauna on reef blocks and infauna in sediments

There was a significantly increased dry weight and ash free dry weight of biomass on reef blocks than in the sediment (two-way ANOVA, $p < 0.05$, Table 5.4, Table 5.5, Figure 5.10 and Figure 5.11). There was also a significant effect of reef block type when both epifaunal and infaunal biomass were considered together (epifauna on blocks combined with infauna in the underlying sediments); a significantly greater biomass was associated with complex rather than with simple reef blocks (two-way ANOVA, $p < 0.05$). There was no significant interaction between biomass type (infauna or epifauna) and block type (complex or simple).

Table 5.4 Mean dry weight and ash free dry weight of biomass with 95% confidence intervals (n = 6) per unit area of seabed (441cm^2).

	Dry weight (g)	Ash free dry weight (g)
Control infauna	24.59 ± 13.72	1.05 ± 0.55
Complex infauna	12.04 ± 11.91	0.39 ± 0.30
Simple infauna	0.23 ± 0.20	0.05 ± 0.03
Complex epifauna	245.70 ± 93.15	16.17 ± 5.42
Simple epifauna	82.36 ± 42.56	5.07 ± 2.39

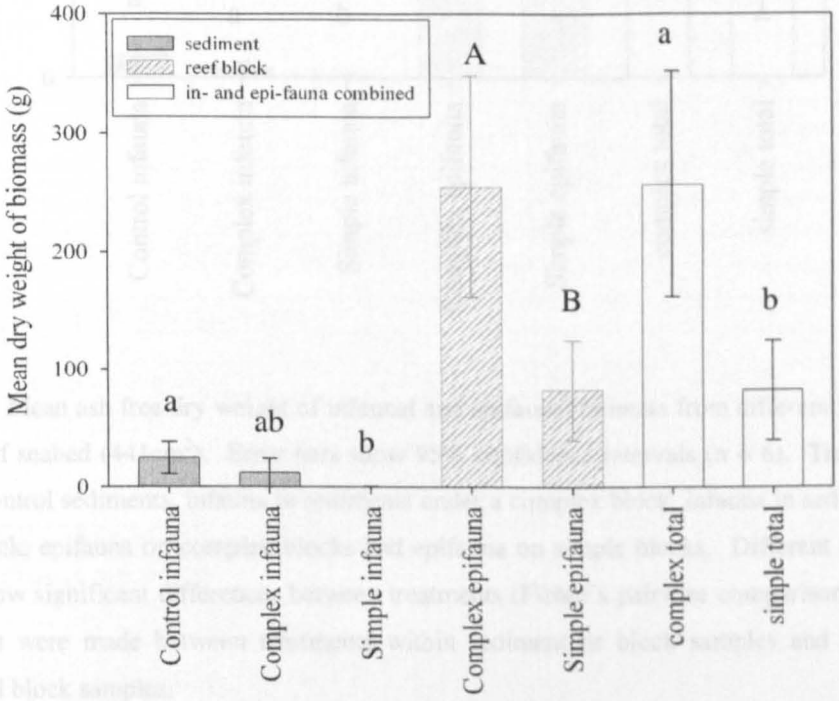

Figure 5.10 Mean dry weight of infaunal and epifaunal biomass from different treatments in a unit area of seabed (441cm^2). Error bars show 95% confidence intervals (n = 6). Treatments are: infauna in control sediments, infauna in sediments under a complex block, infauna in sediments under a simple block, epifauna on complex blocks and epifauna on simple blocks, combined epifauna and infauna on and under complex blocks and combined epifauna and infauna on and under simple blocks. Different letters above data bars show significant differences between treatments (Fisher's pairwise comparisons, $p < 0.05$). Comparisons were made between treatments within sediment or block samples and not between sediment and block samples.

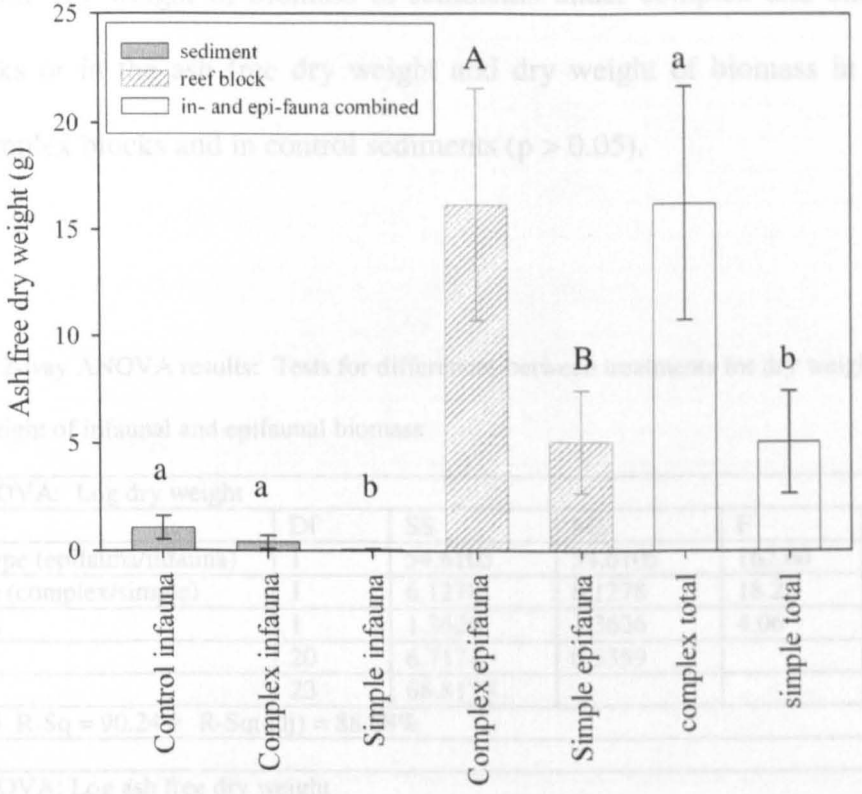

Figure 5.11 Mean ash free dry weight of infaunal and epifaunal biomass from different treatments in a unit area of seabed (441cm^2). Error bars show 95% confidence intervals (n = 6). Treatments are: infauna in control sediments, infauna in sediments under a complex block, infauna in sediments under a simple block, epifauna on complex blocks and epifauna on simple blocks. Different letters above data bars show significant differences between treatments (Fisher's pairwise comparisons, $p < 0.05$). Comparisons were made between treatments within sediment or block samples and not between sediment and block samples.

Infauna and epifauna were analysed separately using one-way ANOVA (Appendix IV) with 95% Fisher's pairwise comparisons. The dry weight and ash free dry weight of biomass in control sediments was significantly greater than in sediments under simple reef blocks (Fisher's pairwise comparisons, $p < 0.05$, Figure 5.10 and Figure 5.11). There was also a significantly greater ash free dry weight of biomass in sediments under complex blocks than sediments under simple reef blocks (Fisher's

pairwise comparisons, $p < 0.05$, Figure 5.11). No significant differences were found between the dry weight of biomass in sediments under complex and under simple reef blocks or in the ash free dry weight and dry weight of biomass in sediments under complex blocks and in control sediments ($p > 0.05$).

Table 5.5 2-way ANOVA results: Tests for differences between treatments for dry weight and ash free dry weight of infaunal and epifaunal biomass

2-way ANOVA: Log dry weight					
Source	Df	SS	MS	F	P
Biomass type (epifauna/infauna)	1	54.6105	54.6105	162.60	0.000*
Block type (complex/simple)	1	6.1278	6.1278	18.25	0.000*
Interaction	1	1.3626	1.3626	4.06	0.058
Error	20	6.7171	0.3359		
Total	23	68.8179			
S = 0.5795 R-Sq = 90.24% R-Sq(adj) = 88.78%					
2-way ANOVA: Log ash free dry weight					
Source	Df	SS	MS	F	P
Biomass type (epifauna/infauna)	1	50.0202	50.0202	95.77	0.000*
Block type (complex/simple)	1	4.0936	4.0936	7.84	0.011*
Interaction	1	0.4992	0.4992	0.96	0.340
Error	20	10.4460	0.5223		
Total	23	65.0590			
S = 0.7227 R-Sq = 83.94% R-Sq(adj) = 81.54%					

* shows significance at $p < 0.05$

The dry weight and ash free dry weight of epifaunal biomass were significantly greater on complex reef blocks than on simple reef blocks (one-way ANOVA, $p < 0.05$, Table 5.6, Figure 5.10 and Figure 5.11).

Table 5.6 One-way ANOVA: dry weight and ash free dry weight of epifauna on complex and simple reef blocks

Dry weight of epifauna on complex and simple reef blocks					
Source	Df	SS	MS	F	P
Epifaunal treatment (complex/simple)	1	89155	89155	10.88	0.008*
Error	10	81914	8191		
Total	11	171069			
S = 90.51 R-Sq = 52.12% R-Sq(adj) = 47.33%					
Ash free dry weight of epifauna on complex and simple reef blocks					
Source	Df	SS	MS	F	P
Epifaunal treatment (complex/simple)	1	369.8	369.8	13.5	0.004*
Error	10	273.9	27.4		
Total	11	643.7			
S = 5.233 R-Sq = 57.45% R-Sq(adj) = 53.20%					

* shows significance at $p < 0.05$

5.3.5 Surface area of simple and complex reef modules ($1m^2$ quadrat)

The mean surface area, with 95% confidence limits, of different orientations within a one m^2 quadrat area on complex and simple reef modules at the Loch Linnhe artificial reef complex are shown in Figure 5.12 and Table 5.7.

The majority of surfaces of reef blocks on both complex and simple reef modules were in the vertical orientation (63.9% and 57.8% respectively Table 5.7). The mean total surface area within a $1m^2$ area on a complex reef module was $3.08m^2 \pm 0.7m^2$ and $2.33m^2 \pm 0.44m^2$ on a simple reef module (Table 5.7). These mean values will be used in section 5.3.7 to estimate the epifaunal biomass within a $1m^2$ area of complex and simple reef module.

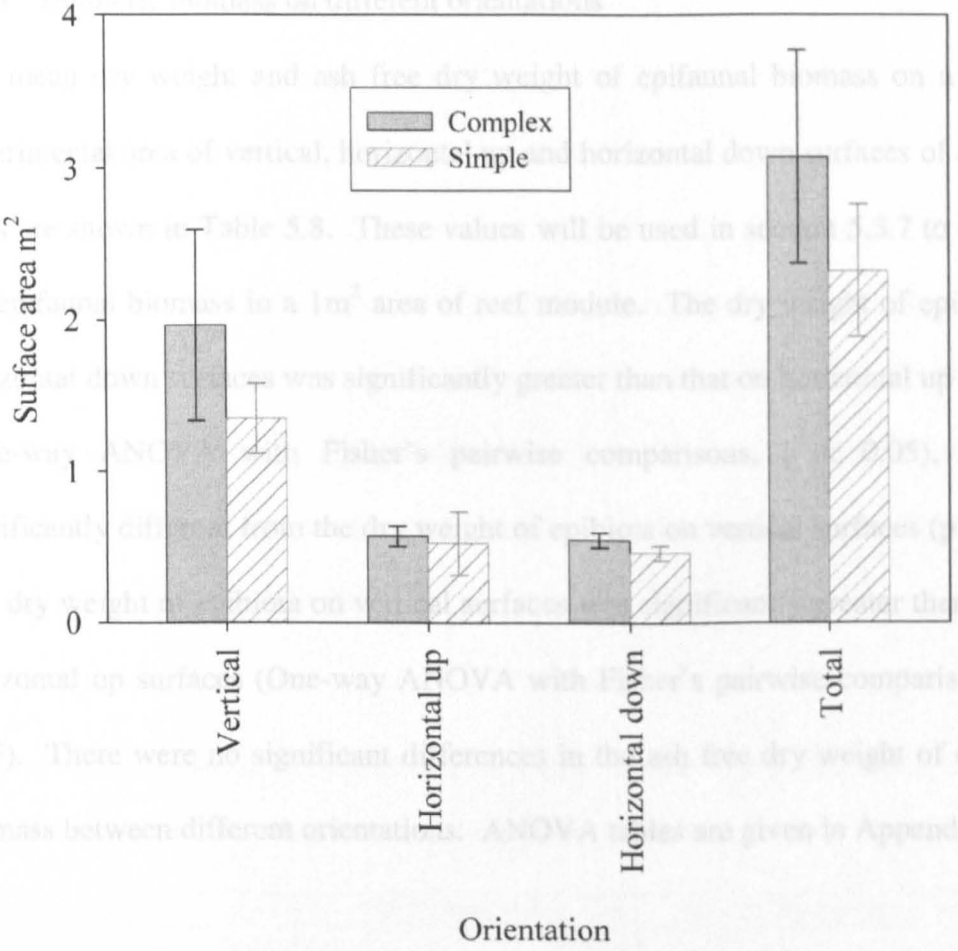

Figure 5.12 Mean surface area of different orientations within a $1m^2$ quadrat on a complex and simple reef module (n = 4). Error bars show 95% confidence intervals.

Table 5.7 Mean surface area, with 95% confidence intervals, of different orientations within a $1m^2$ quadrat on a complex and simple reef module (n = 4).

Reef type	Reef type/orientation	Mean surface area (m^2)	Approx. percentage contribution (%)
Complex	vertical	1.97 ± 0.63	63.9
	horizontal up	0.57 ± 0.07	18.4
	horizontal down	0.54 ± 0.05	17.7
	total	**3.08 ± 0.70**	**100.0**
Simple	vertical	1.35 ± 0.23	57.8
	horizontal up	0.52 ± 0.21	22.4
	horizontal down	0.46 ± 0.05	19.8
	total	**2.33 ± 0.44**	**100.0**

5.3.6 Epibiotic biomass on different orientations

The mean dry weight and ash free dry weight of epifaunal biomass on a $200cm^2$ experimental area of vertical, horizontal up and horizontal down surfaces of concrete units are shown in Table 5.8. These values will be used in section 5.3.7 to estimate the epifaunal biomass in a $1m^2$ area of reef module. The dry weight of epibiota on horizontal down surfaces was significantly greater than that on horizontal up surfaces (One-way ANOVA with Fisher's pairwise comparisons, $p < 0.05$), but not significantly different from the dry weight of epibiota on vertical surfaces ($p > 0.05$). The dry weight of epibiota on vertical surfaces was significantly greater than that on horizontal up surfaces (One-way ANOVA with Fisher's pairwise comparisons, $p < 0.05$). There were no significant differences in the ash free dry weight of epibiotic biomass between different orientations. ANOVA tables are given in Appendix IV.

Table 5.8. Mean weight of epifaunal biomass, rounded to 2 decimal places and shown with 95% confidence intervals (n = 4), on different orientations after 12 months of fouling. Size of scraped area of concrete units was $200cm^2$.

Surface orientation	Dry wt (g)	Ash free dry wt (g)
Vertical	31.99 ± 3.57	4.15 ± 0.80
Horizontal up	13.37 ± 3.74	3.02 ± 1.75
Horizontal down	26.54 ± 10.87	2.73 ± 1.11

5.3.7 Biomass estimate on reef modules per $1m^2$

A biomass estimate for each orientation (vertical, horizontal up or horizontal down) within a $1m^2$ area of reef module was calculated by multiplying the mean surface area (cm^2) of orientation in a $1m^2$ quadrat (Table 5.7) with the mean biomass per $1cm^2$ on the corresponding concrete experimental units (mean values in Table 5.8 divided by 200). Calculated estimates of biomass per $1m^2$ reef module are shown in

Table 5.9.

5.3.8 Estimates of the size and surface area of reef modules

Complex reef modules had a significantly smaller footprint than simple reefs (Table 5.10; one-way ANOVA, $F_{1,12} = 42.49$, $p < 0.05$, Appendix IV; see also Figure 1.5), but had a significantly higher profile (Table 5.10; one-way ANOVA, $F_{1,12} = 6.57$, $p < 0.05$, Appendix IV). The simple reef modules had a significantly greater estimated surface area of cone than complex reef modules (Table 5.10; one-way ANOVA, $F_{1,12} = 52.01$, $p < 0.05$, Appendix IV).

Table 5.9 Epifaunal biomass estimate within a $1m^2$ area of reef module after 12 months of fouling. Values in the table have been rounded up to 2 decimal places.

Orientation	Reef type	Dry weight (g) per $1m^2$	Ash free dry weight (g) per $1m^2$
Vertical	Complex	3143.40	408.09
	Simple	2155.16	279.79
Horizontal Up	Complex	379.15	85.57
	Simple	348.15	78.57
Horizontal Down	Complex	720.72	74.27
	Simple	611.91	63.06
Total	**Complex**	**4243.27**	**567.92**
	Simple	**3115.22**	**421.42**

5.3.9 Epifaunal biomass estimate on a complex and simple reef module.

An approximate estimate of epifaunal biomass on complex and simple artificial reef modules was calculated using the estimate of surface area of a cone for each reef type (Table 5.10) and the estimate of dry weight and ash free dry weight of epifaunal biomass per $1m^2$ (Table 5.9). The estimated net increase in dry weight of biomass 12 months after the deployment of a standard complex reef module, taking into account the potential loss in infaunal biomass in underlying sediments, at the Loch Linnhe

artificial reef complex is 545.16kg of dry weight (Table 5.11). A 12 month old simple reef module is estimated to enhance the dry weight of biomass by 733.33kg.

The estimated dry weight of epifaunal biomass on complex and simple reef modules was 9.8 and 5.9 times greater respectively than the estimated infaunal dry weight of biomass in the area of sediment covered by the respective reef type. There was a 30.8 and 18.7 times greater estimated ash free dry weight of epifaunal biomass on complex and simple reef modules respectively than the infaunal ash free dry weight of biomass in the area of sediment (Table 5.11).

Table 5.10. Estimates of the footprint (m^2) and height (m) of seven complex and simple Loch Linnhe artificial reef modules taken from a multibeam image and measured in ArcGIS 9. The surface area of each module was calculated assuming a conical shape.

Reef type	Reef module	**Footprint (m^2)**	**Height (m)**	**Surface area of cone (m^2)**
Complex	C1c	97.25	5.20	133.05
	C3c	105.00	4.48	132.48
	B3c	155.25	3.49	173.35
	B2c	105.50	4.11	129.35
	D3c	132.00	4.19	157.14
	A2c	101.75	3.80	122.31
	D1c	122.75	4.72	153.78
Complex mean		**111.07 ± 15.48**	**4.28 ± 0.39**	**143.07 ± 13.73**
Simple	C2s	293.00	2.37	301.67
	C1s	306.25	2.16	313.53
	C3s	344.75	1.92	350.49
	D2s	219.00	4.07	243.65
	D3s	203.75	4.78	236.96
	B3s	302.00	2.61	312.48
	B1s	204.00	3.68	224.30
Simple mean		**267.54 ± 42.51**	**3.08 ± 0.81**	**283.29 ± 35.55**

Table 5.11. Estimates of net biomass increase 12 months after the deployment of a standard complex and simple Loch Linnhe artificial reef module. The increase per unit area of seabed was calculated by dividing the estimate of epifaunal biomass on the reef module by the estimate of infaunal biomass in the footprint area of the reef.

Reef type		Dry weight (kg)	Ash free dry weight (kg)
Complex	Epifauna on reef module	607.09	81.25
	Infauna in footprint (111.07m^2) calculated using control infauna values Table 5.4)	61.93	2.64
	Increase per unit area of seabed	**x 9.8**	**x 30.8**
	Net increase in biomass	**545.16**	**78.618**
Simple	Epifauna on reef module	882.51	119.38
	Infauna in footprint (267.54m^2) calculated using control infauna values (Table 5.4)	149.18	6.37
	Increase per unit area of seabed	**x 5.9**	**x 18.7**
	Net increase in biomass	**733.33**	**113.01**

5.4 Discussion

This chapter has shown that the introduction of an artificial reef module in Loch Linnhe has the potential to increase the production of biomass per unit area, with respect to infauna and sessile epifauna, by up to 30.8 times (ash free dry weight on complex modules) after 12 months of fouling.

Steimle et al. (2002) showed reef epifauna to have a productivity estimate one to two orders of magnitude greater than that of infauna. The current study has estimated the production of biomass per unit area and not actual production and so cannot be directly compared to the work of Steimle et al. (2002). However, both studies showed the presence of an artificial reef module to support more kilocalories of production or grams of biomass than the surrounding natural soft sediments.

Simple reef modules within the Loch Linnhe artificial reef complex were estimated to produce a greater net increase in biomass than complex reef modules. However,

because of the different shapes of the two types of reef module, the increase in biomass per unit area of seabed was greater on complex than on simple reef modules. This estimate compares the increase in biomass on reef modules to the amount of infaunal biomass that is lost in the sediments under the reef modules. So, while the greater surface area of the simple reef modules means that the simple reef modules have the potential to produce a greater net increase in biomass than a complex reef module, the complex reef modules have a greater estimated increase in biomass per unit area of seabed.

Both dry weight and ash free dry weight of biomass were estimated in this study. Ash free dry weight is a measure of the amount of soft tissue that is burnt away when the sample is ashed in a muffle furnace and excludes calcareous deposits such as shells and worm tubes as well as any sand grains and fragments of concrete which may have been present in samples. An estimate of ash free dry weight of biomass, therefore, represents the amount of organic matter accessible for digestion by higher predators. The ash free dry weight of epifaunal biomass on complex and simple reef modules was estimated to be 30.8 and 18.7 times greater, respectively, than the infauna in the sediments covered by the respective reef module. Productivity has been defined as the rate of conversion of resources to biomass per unit area per unit time (Waide et al. 1999). Estimates of biomass after 12 months of fouling, therefore, suggest that complex reefs may be approximately 1.6 times more productive, with respect to epifauna, than simple reef modules.

There were no significant differences in the abundances of infaunal taxa in control, simple block and complex block sediments. This may be a result of very low

abundances of most taxa in the sediment cores. Nevertheless, there appeared to be a higher abundance of most taxa in control sediments than in sediments under reef blocks, especially in sediments under simple blocks. This was especially true of gastropods such as *T. communis* which were generally present at or towards the surface of the sediment cores (*pers. obs.*). This trend was backed up by the significantly lower Shannon-Wiener diversity indices in simple block sediments than in control sediments.

Sediments in control samples had a significantly higher infaunal biomass and diversity than sediments under simple reef blocks but not complex reef blocks. There was also a significantly greater biomass of infauna in sediments under complex than simple reef blocks. Simple reef blocks are heavier than complex blocks (45kg and 27.4kg respectively) and when blocks were recovered at the end of the experiment it was noted that the simple blocks had sunk further into the sediments than the complex blocks (*pers. obs.*). This may explain the differences in infaunal assemblage structure in sediment cores underneath simple and complex reef blocks. Estimates of the increase in biomass following the deployment of an artificial reef module were calculated using infaunal biomass estimates taken from control sediments as it was not possible to determine biomass in sediments under reef modules in this study. However, the differences in infaunal biomass in sediments under individual complex and simple reef blocks suggests that, at least at the reef edge where the total weight of reef blocks would be lower than in the centre of a reef module, there may be greater abundances of infauna in sediments under complex reefs than under simple reefs.

Following the results from the present study it would be expected that sediments under the centre of artificial reef modules would have a low infaunal species diversity, or may possibly be devoid of fauna. The dominant infaunal taxa, if any, might be composed of bivalves such as *N. nucleus* and *C. gibba*. This is in contrast to the sediments surrounding a reef module which have been shown to be dominated by the gastropod *T. communis* and with moderate abundances of both bivalves and bristle worms. It would be interesting to establish whether any infauna is present in sediments under an entire artificial reef module. While this would be logistically difficult, involving the partial destruction of reef modules, it may be possible to do using artificial reef modules at the Loch Linnhe artificial reef as these reefs are composed of reef blocks which can be moved by divers on SCUBA.

Estimates made in this study only take into account infaunal and sessile epifaunal communities on artificial reef modules and their surrounding sediments. However, there appears to be a greater abundance of mobile fauna on complex than simple reefs in Loch Linnhe (Hunter 2006 and pers. obs.). This may be a result of the increased epifaunal productivity, the greater habitat heterogeneity (e.g. Guichard et al. 2001) or the higher vertical relief of complex modules compared with simple modules. Whatever the explanation, the larger number of mobile fauna on complex reefs suggests that the estimate of differences in productivity between complex and simple reef modules in this study may be conservative.

5.4.1 Conclusions

This chapter has shown that the presence of an artificial reef module in Loch Linnhe has a negative impact on infauna in sediments under reef blocks. It has also been

shown that an artificial reef module has great potential to significantly enhance the productivity, with respect to infaunal/epifaunal biomass, of an area of seabed. Complex reef modules were estimated to be approximately 1.6 times more productive, with respect to epifaunal biomass, than simple reef modules in the Loch Linnhe artificial reef complex. The null hypothesis H_0 can, therefore, be rejected. This study, therefore, highlights the influence of habitat complexity on epifaunal productivity and complements the work of authors such as Guichard et al. (2001) who showed habitat complexity to influence the associated biological community. These findings also have implications for future commercial-scale artificial reef developments as the productivity increase of 1.6 times from simple to complex reef modules is achieved despite the fact that 39 percent less concrete is required to build a complex than a simple reef module. Complex reef modules are, therefore, more economically viable, compared with simple reef modules, in terms of both construction costs and biological productivity.

Chapter 6 Trophic dynamics on natural and artificial reefs in Loch Linnhe

6.1 Introduction

Artificial reefs have been frequently used to mitigate the loss of natural habitat and to enhance degraded fisheries (Pratt 1994, Guidetti et al. 2005), but a key question remains as to whether these artificial habitats support biological communities comparable to those on natural reefs (Pratt 1994, Carr & Hixon 1997, Svane & Peterson 2001).

Results from previous chapters have shown there to be differences in the epifaunal predation pressure and, as a result, in epifaunal recruitment onto PVC recruitment panels deployed at concrete artificial reef modules and natural rocky reefs in Loch Linnhe (chapters 3 and 4). The actual epibiotic communities on the Loch Linnhe reefs themselves have not been characterised. However, the differences in epifaunal predation and epifaunal communities developing on PVC recruitment panels, combined with differences in habitat complexity and the effect of different substrata on the reef types (Rose 2005), may result in differences in the actual epifaunal communities and resulting food webs on the natural and artificial reefs in Loch Linnhe.

Of the few studies that have compared biotic interactions on artificial and natural reefs, the majority have found significant differences with respect to epifaunal communities (e.g. Butler & Connolly 1996, Connell & Glasby 1999, Glasby 1999a, Connell 2001, Bulleri 2005a, b). Those studies that have recorded fish abundances on artificial and natural reefs have generally reported higher abundances at artificial

reefs (e.g. Danner et al. 1994, Fujita et al. 1996, Carr & Hixon 1997). Where comparisons have been made of the diet of fish on artificial and natural reefs, a greater proportion of epibenthic prey items in fish gut contents was found at artificial reefs (e.g. Donaldson & Clavijo 1994, Lindquist et al. 1994, Pike & Lindquist 1994, Vose & Nelson 1994). However, there is a lack of information on the transfer of reef biomass from producers to consumers on subtidal reefs (Brickhill et al. 2005).

Stable isotope analysis is a relatively new technique which has been successfully used to investigate trophic relationships in many marine and freshwater ecosystems (e.g. Sholto-Douglas et al. 1991, Maruyama et al. 2001, Davenport & Bax 2002, Connolly 2003, Genner et al. 2003, Sotiropoulos et al. 2004). Isotopic abundances are expressed using δ notation as parts per thousand (‰) deviation from international standards (described further in section 6.4.2). The isotopic ratio of naturally occurring carbon ($^{13}C/^{12}C$) broadly reflects the isotopic composition of the diet of an organism and, therefore, provides information on the source of carbon to the food web (Sotiropoulos et al. 2004). For example, benthic algae have a $\delta^{13}C$ signature within the range of -10 to -20‰ and marine phytoplankton -18 to -24‰ (Lajtha & Michener 1994).

The $^{15}N/^{14}N$ ratio in consumer tissues tends to increase relative to that of the diet because of preferential excretion of the lighter isotope (^{14}N) during protein transamination and deamination (Steele & Daniel 1978, Macko et al. 1986, 1987). For example, the $\delta^{15}N$ of an consumer's tissue increases in the range of 2.8 to 3.4‰ from one trophic level to the next (Jacob et al. 2005), reflecting the animal's assimilated diet over a period determined by the turnover rate of the tissues (Tieszen

et al. 1983). This provides a more representative description of trophodynamics than more traditional methods. Gut content analysis (GCA), for example, only gives information on what the organism has eaten immediately prior to capture. The identification of partially digested prey items can also be problematic when using GCA and often results in an underestimation of the softer dietary components (Lajtha & Michener 1994, Grey et al. 2002).

Because the $\delta^{15}N$ signature of an organism gives information on the trophic level and, therefore, the diet of an organism, stable isotope analysis can be used to assess differences in diet between populations. The aims of this study were to use the stable isotope ratios of carbon and nitrogen to investigate the trophodynamics of some key taxa inhabiting artificial and natural reefs in Loch Linnhe.

Null hypotheses tested:

1. H_0: there are no effects of reef type on the trophodynamics of key reef-dwelling taxa on artificial and natural reefs in Loch Linnhe.
2. H_0: there are no effects of reef type on the somatic condition of reef-dwelling fish on artificial and natural reefs in Loch Linnhe.

6.2 Materials and methods

6.2.1 Study sites

Three complex artificial reef modules within the Loch Linnhe artificial reef complex were used in this study. The sites used were M1c (56°32.162N 5°26.972W), deployed 9/08/02 – 13/03/2003; B1c (56°32.079N 5°27.3441W), deployed 08/08/2003; and B3c (56°32.088N 5°27.256W), deployed 14/08/03 (Figure 6.1). All

reef modules were in approximately 15m of water and were approximately 2 years old with mobile communities dominated by reef-dwelling fish, urchins, starfish and crabs.

Natural reef selection proved to be difficult. Sites were selected to be as similar to the artificial reef complex as possible with respect to environmental variables such as depth, fresh water input, and relief. It was also important that communities inhabiting the selected natural reefs were similar to those on the artificial reef sites used in the study in order to be able to sample the same taxa from both reef types. Many local reef sites were sampled, including those sites used in previous chapters, but reef-dwelling fish were caught only at Eilean Mor (56° 27.348N 5° 26.034W) and Rubha Garbh-aird (56° 28.415N 5° 27.571W) (Figure 6.1). These two sites were, therefore, used in this study instead of the natural reef sites used in previous chapters.

6.2.2 Sample collection

Reef-dwelling fish and crabs were caught using creels deployed and recovered using a small research vessel. Creels were baited with the opened urchin, *Echinus esculentus* (L.). As the target fish species, the wrasse family, are generally crepuscular the creels were initially deployed late afternoon, left overnight and recovered as early as possible the following morning; the aim being to catch fish during the morning feeding period to minimise time for the digestion of stomach contents. However, while some fish were caught using this method it seemed that many fish were entering the creels to feed and then finding their way out again. The fishing technique was, therefore, changed to incorporate creeling during the day, leaving creels to fish for approximately one hour before hauling, and this proved

more successful.

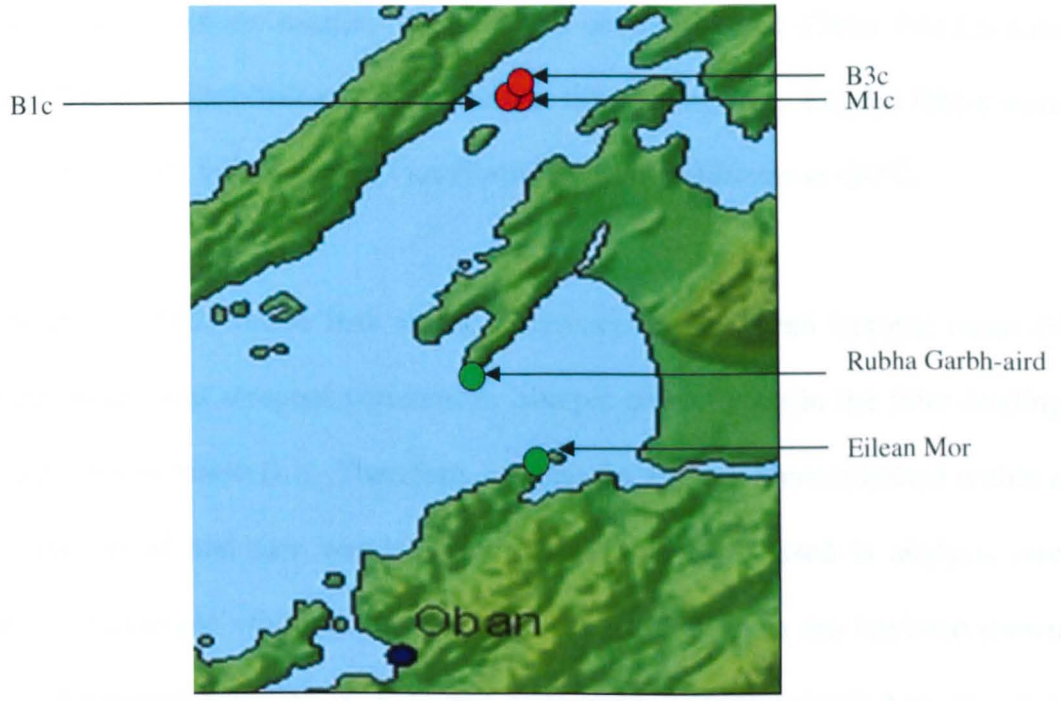

Figure 6.1 Map showing artificial ● and natural ● reef sites used in this study for stable isotope analyses.

On recovery of creels, fish were dispatched by prolonged immersion in anaesthetic (ethyl *p*-amino benzoate) before being eviscerated. The fish and guts were placed into separate bags, labelled and frozen immediately in a portable freezer. Two legs were removed from crabs caught in creels and these were also frozen to provide tissue samples for analysis. All samples were transferred to a chest freezer (-20°C) on return to the laboratory at the end of each day to preserve tissue for analysis and to prevent further digestion of stomach contents.

SCUBA was used to collect invertebrate and algal samples from reefs. Many

different taxa were collected to represent as many trophic levels as possible. All samples were frozen at -20°C until they were processed. Taxa used in this study are detailed below. Plankton was collected from each site using a plankton net with a 20 micron mesh. Plankton samples were filtered onto pre-ashed 13mm PALLS Life Science A/E glass fibre filters using a vacuum filtration system. Loaded filters were placed individually in Eppendorfs (small plastic vials) and frozen at -20°C.

Lorrain et al. (2002) found both strong differences in the mean isotopic ratios of different organs and seasonal variation in isotopic composition in the filter feeding scallop *Pecten maximus* (L.). Therefore, samples for analysis were collected within a short time period and care was taken over choice of organ used in analysis (see below). For example, white fish muscle was used for analysis as this has been shown to have the lowest variation in $\delta^{13}C$ and $\delta^{15}N$ isotope ratios exhibited by any fish tissue (Pinnegar & Polunin 1999).

6.2.3 Sample preparation for stable isotope analysis

Muscle tissue was used in the analysis of most faunal groups, as described below. Samples were prepared for both carbon and nitrogen stable isotope analysis. Lipid and carbonate-rich tissues were treated prior to analysis because both components are known to affect the carbon stable isotope ratio of a sample (DeNiro & Epstein 1978, Sotiropoulos et al. 2004). However, the process of lipid extraction and carbonate removal has been shown to increase the nitrogen stable isotope ratio of a sample (Sotiropoulos et al. 2004). Samples requiring treatment for lipid or carbonate removal were, therefore, divided into untreated and treated samples so that nitrogen and carbon isotope ratios could be analysed respectively.

Samples not requiring treatment for the removal of lipid or carbonate (samples for nitrogen analysis and samples for carbon analysis naturally poor in lipid and carbonate, see Figure 6.2) were defrosted, oven dried at 50°C and homogenised using a small pestle and mortar. Samples were then weighed into small foil capsules using a microbalance (0.7mg ± 0.2mg for animal tissue and 1.5-2.0mg for plant/algae samples). The exact weight of each sample was recorded. Carbon and nitrogen analysis was carried out simultaneously for these samples.

Table 6.1 Summary table of pre-treatment of samples for stable isotope analysis

	Pre-analysis treatment	
Taxa	Lipid extraction	Acidification (carbonate removal)
Plankton	No	No
Macroalgae	No	No
Barnacle	Yes	Yes
Gastropod	No	No
Starfish	Yes	Yes
Urchin	Yes	No
Crab	No	No
Fish	No	No

Lipid extraction

Samples were homogenised in 2:1 chloroform:methanol and left to extract overnight in a fume cupboard. All homogenising tubes and rods were cleaned thoroughly between each sample to avoid cross-contamination. Following extraction, the lipid-rich extract was carefully pipetted into a glass vial, preserved with Butylated Hydroxytoluene (BHT, $C_{15}H_{24}O$) in nitrogen gas and stored in a freezer at -20°C for future fatty acid analysis. The remaining solid, lipid extracted, tissue was placed in a clean glass vial and oven dried at 50°C.

Carbonate removal

Following lipid extraction, carbonate in tissues was removed by acidification with 1M Hydrochloric acid (HCl). The acid was dropped onto the tissue, drop by drop, in a test tube until the sample had completely stopped effervescing. The sample was then filtered onto GF/F Whatman filter paper and rinsed thoroughly with millipure water before being placed into a glass vial and oven dried at 50°C.

Plankton

No attempt was made to differentiate between zooplankton and phytoplankton. Each dried sample was scraped off the filter and weighed into tin capsules. No pre-treatment was carried out. Five filters of plankton from each site were analysed for stable isotope ratios.

Macroalgae

Samples of the kelp *Laminaria saccharina* (L.) and a red filamentous algae *Ptilota plumosa* (Hudson) were analysed. No pre-treatment was carried out on macroalgal samples. See Table 6.2 for sample numbers.

Barnacle, *Balanus crenatus* (Bruguière).

Barnacles were defrosted and the soft tissue was plucked out of the shell with forceps. All barnacles (approximately 25) from each site were pooled together, homogenised and split into half. One half was analysed for nitrogen isotope ratios. The other half of each sample was lipid extracted and acidified to remove any remaining carbonate. Three replicates were taken from each sample.

The grey top shell, *Gibbula cineraria* (L.)

The foot of each gastropod was used for analysis. Each foot was placed into a glass vial and oven dried at 50°C. No lipid extraction was carried out on *G. cineraria* samples as they were too small to be divided into treated and untreated samples. The nitrogen stable isotope ratio is more important than carbon when identifying trophic levels and so none of the tissue was lipid extracted. See Table 6.2 for sample numbers.

The sea urchin, *E. esculentus* (L.)

Sea urchins with a test diameter of approximately 100mm were selected for analysis. The gonad tissue was separated from the test on return to the laboratory and immediately frozen at -20°C. Half of the gonad sample from each urchin was oven dried at 50°C for the analysis of nitrogen stable isotope ratios; the other half of the sample was lipid extracted. See Table 6.2 for sample numbers.

The starfish, *Asterias rubens* (L.)

Five starfish approximately 100mm in length were selected for analysis from each site. A section of the arm was cut off each starfish with a scalpel. The arm section was then cut open longitudinally to expose the gut contents. Gut contents were washed away with millipore water so as not to contaminate the sample of arm tissue (DeNiro & Epstein 1978). Half of the sample was oven dried for nitrogen isotope ratio analysis and half was both lipid extracted and acidified to remove carbonate.

The velvet swimming crab, *Necora puber* (L.)

Leg tissue from each crab was used for analysis. Five crabs were sampled from each

site. No pre-treatment was carried out.

Rock cook, *Centrolabrus exoletus* (L.)

Two main species of reef dwelling fish were caught at both artificial and natural reef sites in this study. These were *C. exoletus*, and the corkwing wrasse (*Crenilabrus melops* L.). However, although many *C. melops* were caught at both of the natural sites this species was not used in the analysis because of lack of samples from artificial reef sites. Unfortunately, while many *C. exoletus* were caught at all the artificial reef sites, data were only available for this species from Rubha Garbh-aird and not from the second natural reef site, Eilean Mor.

Fish samples were defrosted, measured for total length and weighed (eviscerated weight) to enable estimates of condition indices of fish to be made. The guts and otoliths of all fish were kept frozen for future analysis of gut contents and possible age determination. Approximately 0.5g of white muscle tissue was dissected from each fish for analysis. No pre-treatment was carried out. See Table 6.2 for sample numbers.

See Table 6.1 for a summary of which samples were treated prior to analysis and Table 6.2 for information on sample numbers.

6.2.4 Sample analysis

Carbon and nitrogen isotope analyses were carried out by continuous flow isotope ratio mass spectrometry (CF-IRMS), using a Costech (model ECS 4010) elemental analyser (EA) interfaced with a ThermoFinnigan Delta Plus XP mass spectrometer.

For each sample, approximately 0.7mg (± 0.2mg) of animal material and 1.5-2.0mg of plant material was loaded into a 4 x 6mm tin capsule and combusted in the EA at 1020°C for simultaneous determination of carbon and nitrogen isotope ratios. Three internal standards (Gel, Alanine 14 and Alanine 15) were used throughout each run to allow for linearity effects and instrument drift. Analyses were carried out at the Scottish Universities Environmental Research Centre at East Kilbride.

Table 6.2 Sample numbers of each taxa analysed for stable isotope analysis

	Artificial sites			Natural sites	
Taxa	B1c	B3c	M1c	Rubha Garbh-aird	Eilean Mor
Plankton (no. of filters)	5	5	5	5	5
L. saccharina			5	4	4
P. plumose		1	5	5	
G. cineraria < 1cm		1	7	6	4
G. cineraria > 1cm		1	2	4	4
B. crenatus (each sample comprised approximately 25 animals)	3	3	3	3	3
E. esculentus	6	6	6	7	5
A. rubens	5	5	5	5	5
N. puber	5	5	5	5	5
E. exoletus < 10cm	4	2	6		
E. exoletus > 10cm	16	12	11	8	

All isotope abundances were expressed using δ notation as parts per thousand (‰) deviation from international standards, V-Pee dee belemnite (carbon) and AIR (nitrogen), according to the equation

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1000$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Standard deviation of both $\delta^{15}N$ and $\delta^{13}C$ is around 0.2‰ and 0.1‰ respectively for all standards.

6.2.5 Data analysis

Study sites were initially characterised using primary producers (phytoplankton and macroalgae) to establish whether there were baseline differences in $\delta^{13}C$ and $\delta^{15}N$ between reef types.

Comparisons were made between reef types for $\delta^{15}N$ and $\delta^{13}C$ for all taxa using a nested ANOVA model: 'reef type' 'site (reef type)' where site was a random factor and reef type was fixed. Prior to analysis data were checked for normality and homogeneity of variance within the Minitab software package. As ontogentic shifts in diet have been recorded for many taxa (e.g. Letourneur et al. 1997, Genner et al. 2003) those taxa sampled with a broad range in size were separated into size classes for analysis. These were *G. cineraria* and *C. exoletus* which were separated into animals smaller than and larger than 1cm and 10cm respectively. A study by Sayer et al. (1996) showed the diets of male and female *C. exoletus* to be predominantly composed of the same prey items and so all fish within each size class were analysed together to keep samples numbers as large as possible.

In cases where there may be differences in the source of carbon and nitrogen to the base of the food web, such as comparisons between different locations, stable isotope values are more meaningful when used in conjunction with a trophic baseline (Vander Zanden et al. 1999). The use of a primary consumer as a trophic baseline level has been shown to have a lower error term than when a primary producer is used (Vander Zanden & Rasmussen 2001). For example, plankton samples usually include a mix of phytoplankton, detritus, microzooplankton and bacteria and so it is difficult to obtain clean samples of phytoplankton for particulate organic carbon

(POC) or particulate organic nitrogen (PON) analysis (Lajtha & Michener 1994). Therefore, although primary producers such as plankton and macroalgae were characterised in this study, the grey top shell *G. cineraria* was used as a $\delta^{15}N$ baseline for trophic position calculations.

Trophic position of taxa were calculated *sensu* Vander Zanden and Ramussen (2001) using the formula:

$$\text{Trophic position} = (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})/3.4 + 2$$

where the consumer was the taxa under investigation and the primary consumer, *G. cineraria,* was the trophic baseline. Data for *G. cineraria* were only available for artificial sites M1c and B3c and natural sites Eilean Mor and Rubha Garbh-aird and so trophic position of taxa was only calculated for these sites.

The somatic condition factor (K_s) of each fish was calculated using the formula

$$K_s = EW/aTL^b$$

where EW was eviscerated weight, TL was total length, and *a* and *b* were the intercept and slope of a fitted linear relationship between length and weight. Values of *a* and *b* in this study were taken from a previous study of wrasse in the Oban area by Sayer et al. (1996) because sample numbers in the present study were not always sufficient to generate a robust model of the relationship between length and weight of fish. Male and female *C. exoletus* were analysed separately.

6.3 Results

6.3.1 Site characterisation

The phytoplankton at all study sites were characterised for $\delta^{15}N$ and $\delta^{13}C$ (Figure 6.2). No significant differences were found in $\delta^{15}N$ between reef types or sites (ANOVA, $p > 0.05$). There were no significant differences in $\delta^{13}C$ between reef types (ANOVA $p > 0.05$) although it is worth noting that the actual p value was 0.055 which is close to the critical significant value. There were significant differences in $\delta^{13}C$ between sites (ANOVA, $p < 0.05$).

Macroalgal samples, in the form of *L. saccharina* and *P. plumosa*, from artificial and natural reef sites were also characterised (Figure 6.3 and Figure 6.4). No significant differences were found in the $\delta^{15}N$ or $\delta^{13}C$ signature of *L. saccharina* between reef types or site (ANOVA, $p > 0.05$ in all cases, Figure 6.3, Appendix V). There were no significant differences in either the $\delta^{15}N$ or $\delta^{13}C$ signatures of *P. plumosa* between reef types (ANOVA, $p > 0.05$) but there was a significant difference in $\delta^{13}C$ signature between sites (ANOVA, $p < 0.05$, Figure 6.4, Appendix V).

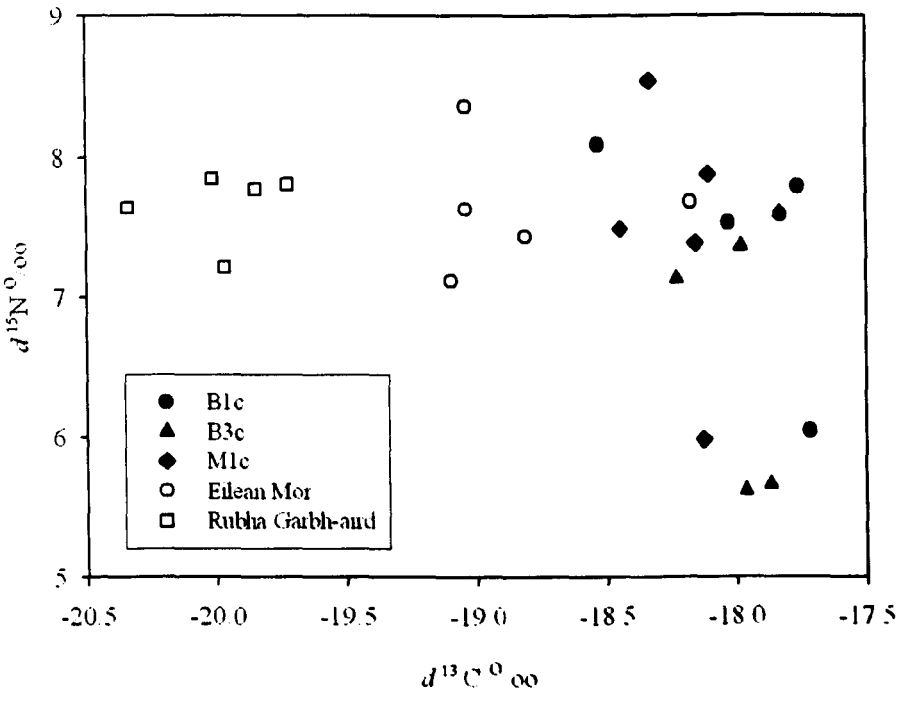

Figure 6.2 $\delta^{13}C$ and $\delta^{15}N$ of phytoplankton collected from artificial and natural study sites.

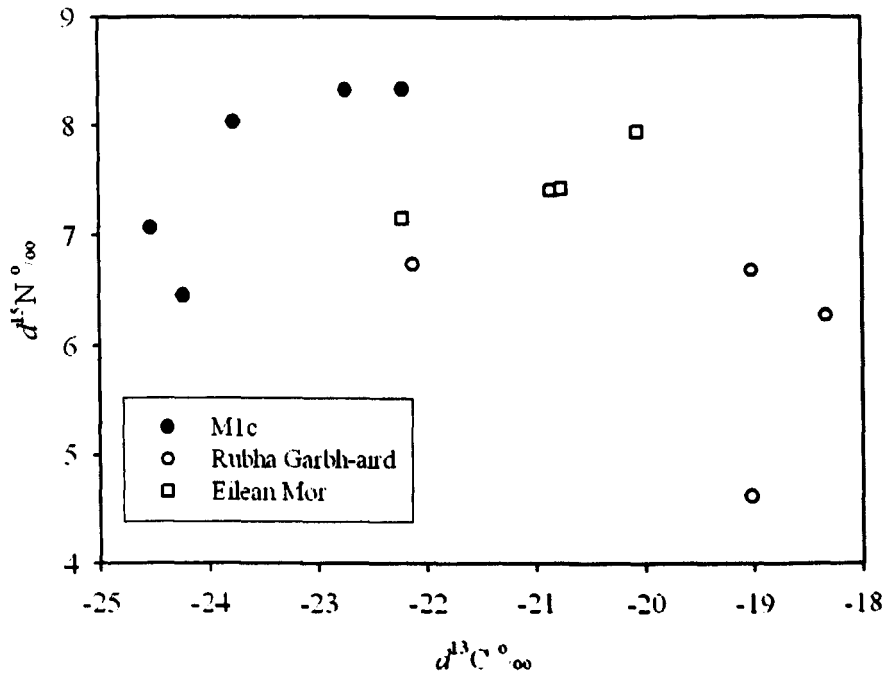

Figure 6.3 $\delta^{13}C$ and $\delta^{15}N$ of *L. saccharina* collected from artificial and natural study sites.

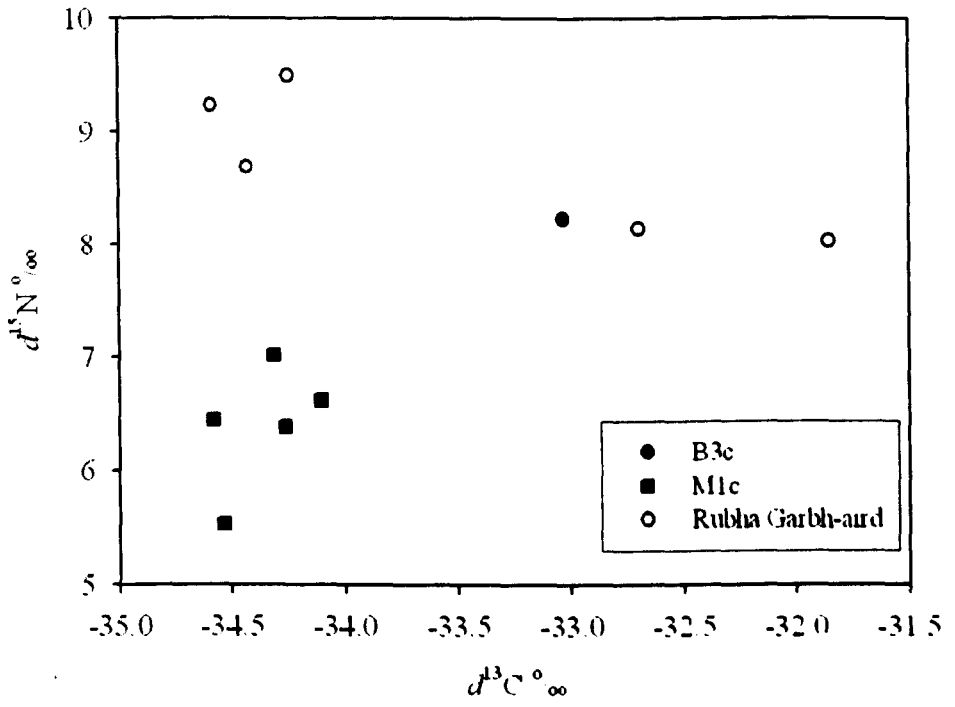

Figure 6.4 $\delta^{13}C$ and $\delta^{15}N$ of *P. plumosa* collected from artificial and natural study sites.

6.3.2 Stable isotope ratios of taxa at artificial and natural reefs in Loch Linnhe

The mean $\delta^{15}N$ at artificial and natural reef types of all taxa sampled are shown in Figure 6.5. It can be seen that the grey top shell, *G. cineraria*, and the urchin, *E. esculentus*, have the lowest $\delta^{15}N$ values and the rock cook, *C. exoletus*, have the highest $\delta^{15}N$ values of the taxa studied. The starfish, *A. rubens*, had a significantly higher $\delta^{15}N$ value at natural reefs than artificial reefs and the velvet swimming crab, *N. puber*, had a significantly higher $\delta^{15}N$ value at artificial than natural reefs (ANOVA, $p < 0.05$ in both cases). No significant differences in $\delta^{15}N$ were found between reef types for *G. cineraria*, *E. esculentus*, *B. crenatus* or *C. exoletus* (ANOVA, $p > 0.05$).

Mean $\delta^{13}C$ values are shown in Figure 6.6. No significant differences were found between the $\delta^{13}C$ value of any taxa at artificial and natural reefs (ANOVA, $p > 0.05$). However, it is worth noting that the actual p value for *E. esculentus* was 0.059 which is close to the critical significant level. There was little difference in $\delta^{13}C$ values between taxa studied with the exception of *A. rubens* and *N. puber* which had lower mean $\delta^{13}C$ than the other taxa.

The ANOVA results of differences in $\delta^{15}N$ and $\delta^{13}C$ for all taxa between artificial and natural reefs are summarised in Table 6.3. Mean $\delta^{15}N$ and $\delta^{13}C$ values and full ANOVA tables are given in Appendix V.

Table 6.3 Summary table showing two-way nested ANOVA results for differences between reef types and sites for $\delta^{15}N$ and $\delta^{13}C$. An 'X' shows significance at $p < 0.05$.

	$\delta^{15}N$		$\delta^{13}C$	
Taxa	Reef type	Site	Reef type	Site
Gibbula cineraria <1cm		X		X
Gibbula cineraria >1cm				X
Balanus crenatus		X		X
Echinus esculentus		X		
Asterias rubens	X			X
Necora puber	X			
Centrolabrus exoletus <10cm				
Centrolabrus exoletus >10cm				

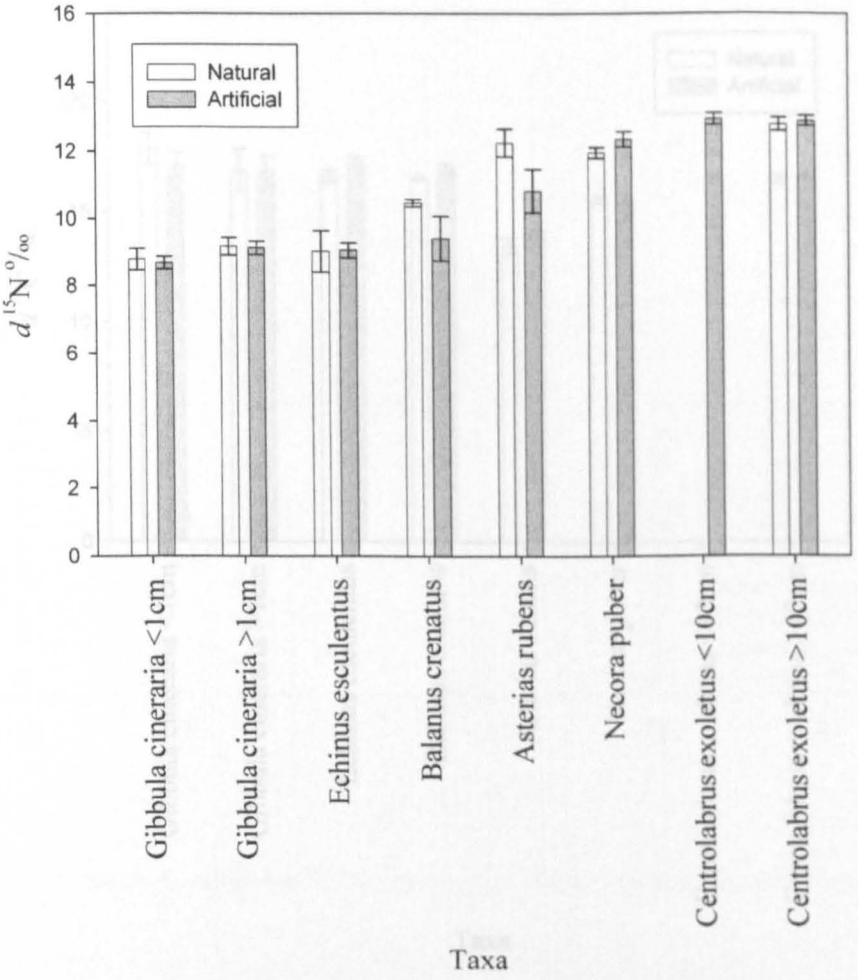

Figure 6.5 Mean $\delta^{15}N$ of all taxa at artificial and natural reef types in Loch Linnhe. Error bars show 95% confidence intervals. See Table 6.2 for sample numbers.

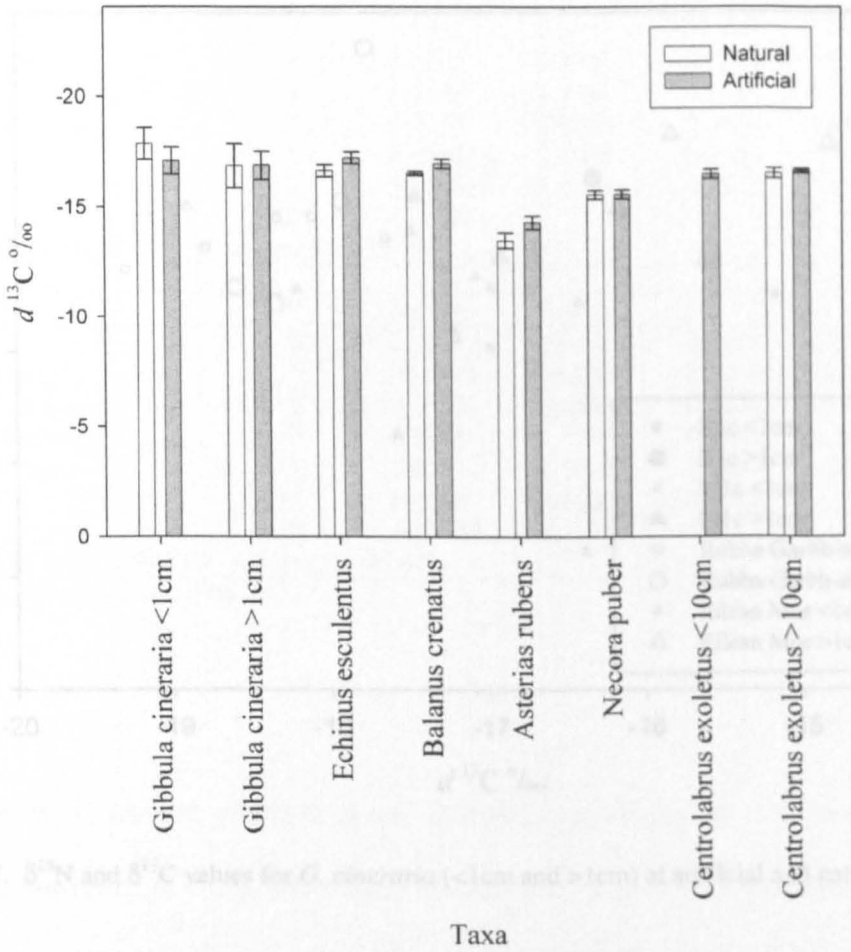

Figure 6.6 Mean $\delta^{13}C$ of all taxa at artificial and natural reef types in Loch Linnhe. Error bars show 95% confidence intervals. See Table 6.2 for sample numbers.

6.3.3 Trophic position

The grey top shell, *G. cineraria*, was used as a baseline level of $\delta^{15}N$ in order to calculate trophic position. The $\delta^{15}N$ and $\delta^{13}C$ of *G. cineraria* are characterised in Figure 6.7 and Table 6.4.

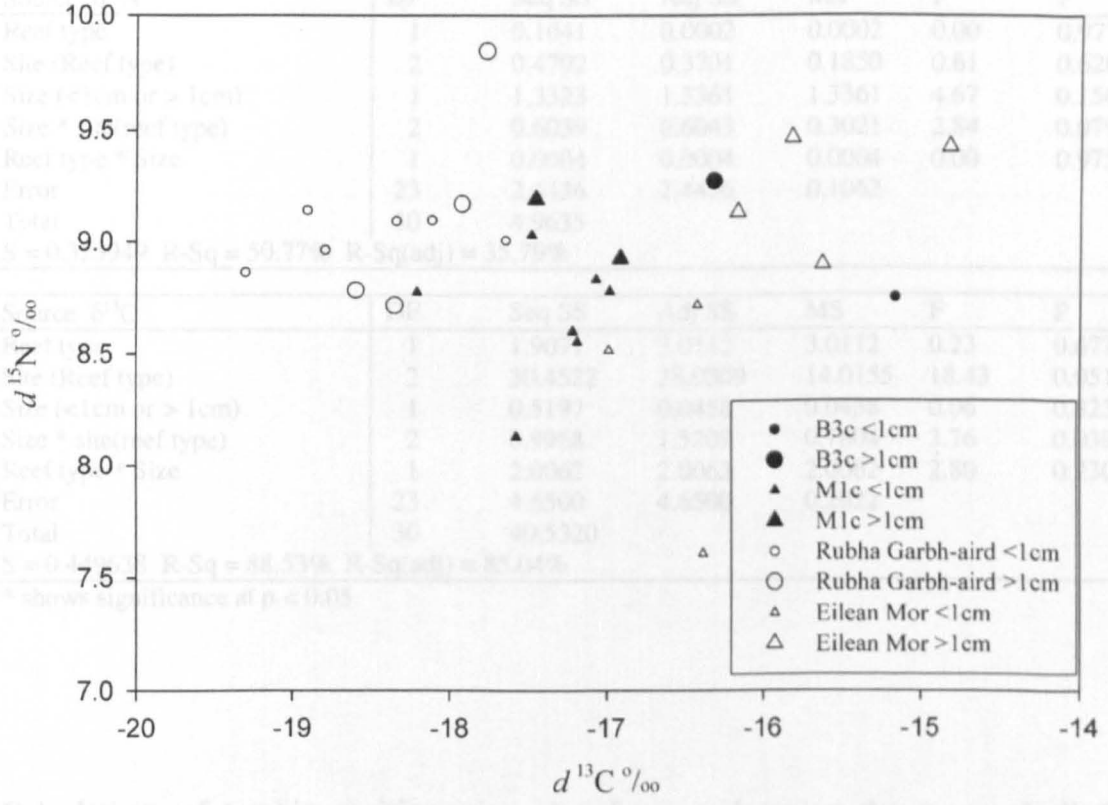

Figure 6.7. $\delta^{15}N$ and $\delta^{13}C$ values for *G. cineraria* (<1cm and >1cm) at artificial and natural sites.

No significant differences or interactions were found between reef type, site (nested within reef type), or size of *G. cineraria* for $\delta^{15}N$ values (ANOVA, $p < 0.05$, Table 6.4). There were no significant differences between the $\delta^{13}C$ at artificial and natural reef types ($p > 0.05$) or size ($p > 0.05$) of *G. cineraria.* There was no significant difference between the $\delta^{13}C$ at different sites although the p value was 0.051 which is only just above the critical significance value. There was, however, a significant interaction between size of *G. cineraria* and study site (ANOVA, $p < 0.05$).

Table 6.4 3 way nested ANOVA results for *G. cineraria* $\delta^{15}N$ and $\delta^{13}C$

Source $\delta^{15}N$	DF	Seq SS	Adj SS	MS	F	P
Reef type	1	0.1041	0.0002	0.0002	0.00	0.977
Site (Reef type)	2	0.4792	0.3701	0.1850	0.61	0.620
Size (<1cm or > 1cm)	1	1.3323	1.3361	1.3361	4.67	0.156
Size * site(reef type)	2	0.6039	0.6043	0.3021	2.84	0.079
Reef type * Size	1	0.0004	0.0004	0.0004	0.00	0.975
Error	23	2.4436	2.4436	0.1062		
Total	30	4.9635				
S = 0.325949 R-Sq = 50.77% R-Sq(adj) = 35.79%						

Source $\delta^{13}C$	DF	Seq SS	Adj SS	MS	F	P
Reef type	1	1.9071	3.0112	3.0112	0.23	0.677
Site (Reef type)	2	30.4522	28.0309	14.0155	18.43	0.051
Size (<1cm or > 1cm)	1	0.5197	0.0458	0.0458	0.06	0.823
Size * site(reef type)	2	0.9968	1.5209	0.7604	3.76	0.039 *
Reef type * Size	1	2.0062	2.0062	2.0062	2.80	0.230
Error	23	4.6500	4.6500	0.2022		
Total	30	40.5320				
S = 0.449638 R-Sq = 88.53% R-Sq(adj) = 85.04%						

* shows significance at $p < 0.05$

Calculations of trophic position were, therefore, made using the mean of all *G. cineraria* (individuals <1cm and >1cm) at each site. The trophic position and rank of study taxa at each reef type are shown in Table 6.5 and Figure 6.8.

Although there were significant differences between sites for *B. crenatus*, *E. esculentus* and *C. exoletus* (ANOVA, $p < 0.05$, Table 6.6), no significant differences were found between reef types for any taxa (ANOVA, $p > 0.05$, Table 6.6). There were, however differences in the rank order of taxa with respect to trophic position at artificial and natural reef types Table 6.5. The urchin, *E. esculentus* had the lowest trophic position of the study taxa at both artificial and natural reefs, with a mean trophic position of 2.06 and 2.00 respectively.

Table 6.5 Mean trophic position, ± standard deviation, and rank of study taxa at artificial and natural reefs in Loch Linnhe. The $\delta^{15}N$ baseline used in calculations was the mean value of all *G. cineraria* (<1cm and >1cm) $\delta^{15}N$ at each site ($\delta^{15}N$ at M1c = 8.76 ± 0.37, B3c = 9.01 ± 0.31, Rubha Garbh-aird = 9.07 ± 0.31 and Eilean Mor = 8.82 ±0.64).

Taxa	Artificial				Natural			
	Site	$\delta^{15}N_{consumer} - \delta^{15}N_{baseline}$	Trophic position	Rank	Site	$\delta^{15}N_{consumer} - \delta^{15}N_{baseline}$	Trophic position	Rank
E. esculentus	M1c	0.40 ± 0.43	2.12 ± 0.13		Rubha Garbh-aird	0.80 ± 0.23	2.24 ± 0.07	
	B3c	-0.01 ± 0.29	2.00 ± 0.08		Eilean Mor	-0.97 ± 0.44	1.72 ± 0.13	
	Artificial ALL	0.19 ± 0.41	2.06 ± 0.12	1	Natural ALL	-0.02 ± 1.0	2.00 ± 0.28	1
B. crenatus	M1c	-0.67 ± 0.09	1.80 ± 0.03		Rubha Garbh-aird	1.34 ± 0.14	2.39 ± 0.04	
	B3c	1.14 ± 0.25	2.33 ± 0.07		Eilean Mor	1.71 ± 0.12	2.50 ± 0.04	
	Artificial ALL	0.23 1.00	2.07 ± 0.30	2	Natural ALL	1.52 ± 0.24	2.45 ± 0.07	2
A. rubens	M1c	1.98 ± 1.10	2.58 ± 0.32		Rubha Garbh-aird	3.70 ± 0.29	3.09 ± 0.08	
	B3c	2.10 ± 1.49	2.62 ± 0.44		Eilean Mor	2.89 ± 0.41	2.85 ± 0.12	
	Artificial ALL	2.04 ± 1.24	2.60 ± 0.36	3	Natural ALL	3.29 ± 0.54	2.97 ± 0.16	4
N. puber	M1c	3.57 ± 0.35	3.05 ± 0.11		Rubha Garbh-aird	2.78 ± 0.19	2.82 ± 0.06	
	B3c	3.32 ± 0.60	2.98 ± 0.18		Eilean Mor	3.23 ± 0.28	2.95 ± 0.08	
	Artificial ALL	3.45 ± 0.48	3.01 ± 0.14	4	Natural ALL	3.00 ± 0.33	2.88 ± 0.10	3
C. exoletus >10cm	M1c	4.16 ± 0.36	3.22 ± 0.10		Rubha Garbh-aird	3.70 ± 0.29	3.09 ± 0.08	
	B3c	3.85 ± 0.33	3.13 ± 0.10		Eilean Mor	-	-	
	Artificial ALL	4.00 ± 0.37	3.18 ± 0.11	5	Natural ALL	-	-	5
C. exoletus <10cm	M1c	4.22 ± 0.38	3.24 ± 0.11		Rubha Garbh-aird	-	-	
	B3c	-	-		Eilean Mor	-	-	
	Artificial ALL	-	-	6	Natural ALL	-	-	

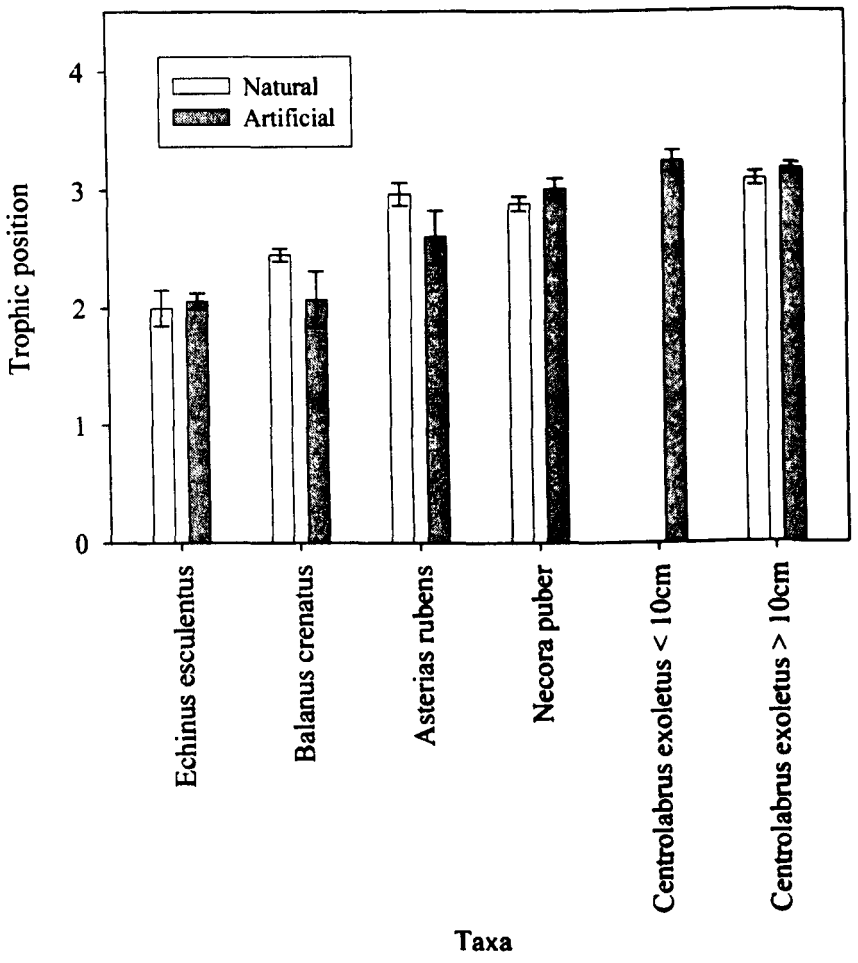

Figure 6.8 Mean trophic position of taxa at artificial and natural reef types. Error bars show 95% confidence intervals. See Table 6.2 for sample numbers.

Table 6.6 Summary table showing significant differences in trophic position for taxa at different reef types and sites. Full ANOVA tables are given in Appendix V.

	Trophic position	
Taxa	Reef type	Site
Balanus crenatus		X
Echinus esculentus		X
Asterias rubens		
Necora puber		
Centrolabrus exoletus >10cm		X

The barnacle, *B. crenatus,* was ranked second with scores of 2.07 and 2.45 at artificial and natural reef sites respectively. At artificial reefs, *A. rubens* held the next lowest trophic position with a score of 2.60; however, at natural sites the third ranked taxa was *N. puber*, with a score of 2.88. The forth ranked taxon with respect to trophic position at artificial reefs was *N. puber* with a mean score of 3.01 and at natural sites was *A. rubens* with a score of 2.97. *C. exoletus* had the highest rank with respect to trophic position at both artificial and natural reefs with scores of 3.18 and 3.09 respectively.

6.3.4 Fish condition indices

No significant differences were found in the somatic condition indices (K_s) of male or female rock cook, *C. exoletus*, between artificial and natural reef types or sites (ANOVA, $p > 0.05$, Figure 6.9 and Table 6.7). There was, however, a significant difference in K_s between male and female fish at all sites (ANOVA, $p < 0.05$).

Table 6.7 3 way nested ANOVA results for Somatic condition indices (K_s) for rock cook wrasse, *C. exoletus*, at artificial and natural reef types.

Source	DF	Seq SS	Adj SS	MS	F	P
Reef type	1	0.001214	0.000017	0.000017	0.00	0.949
Site (Reef type)	2	0.013578	0.006113	0.003056	0.57	0.638
Sex	1	0.099101	0.041178	0.041178	7.99	0.029 *
Sex * site(reef type)	2	0.010853	0.010794	0.005397	1.11	0.338
Reef type * Sex	1	0.000022	0.000022	0.000022	0.00	0.950
Error	51	0.248361	0.248361	0.004870		
Total	58	0.373129				
S =0.0697842 R-Sq = 33.44% R-Sq(adj) = 24.30%						

* shows significance at $p < 0.05$

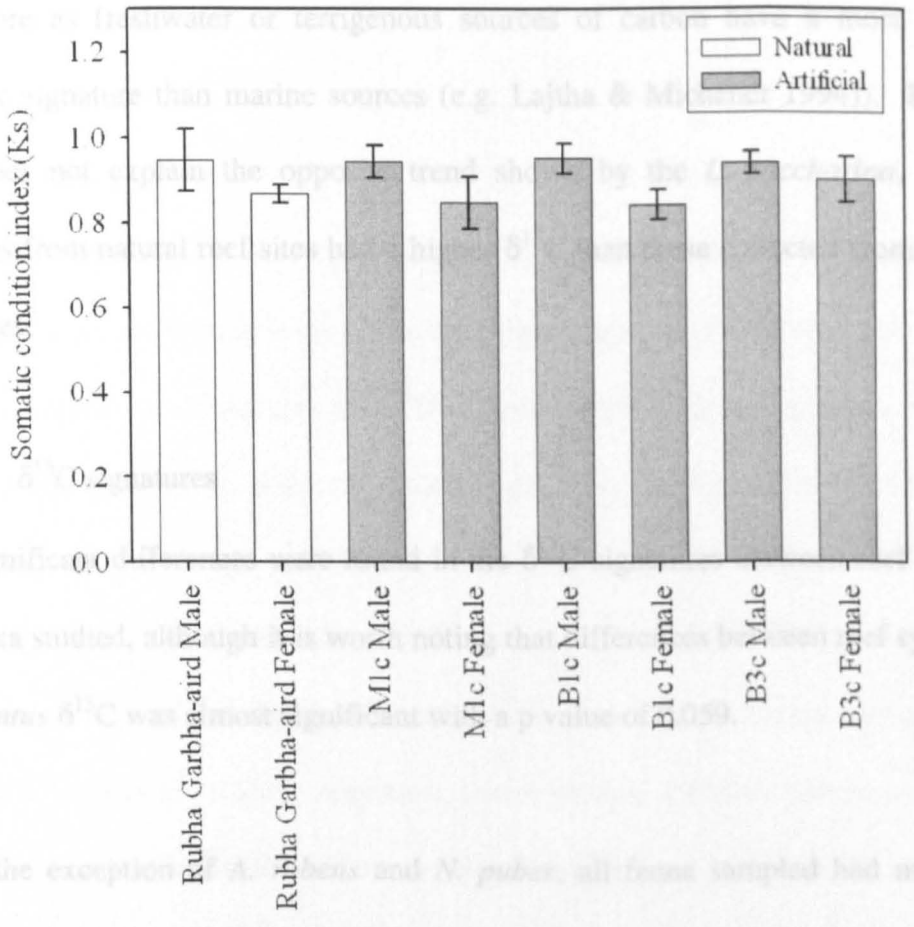

Figure 6.9 Mean somatic condition index (K_s) of male and female rock cook wrasse (*C. exoletus*) at artificial and natural reef sites in Loch Linnhe. Error bars show 95% confidence intervals (see Table 6.2 for sample numbers).

6.4 Discussion

6.4.1 Site characterisation

There were no significant differences in the $\delta^{15}N$ or $\delta^{13}C$ of phytoplankton, *L. saccharina* or *P. plumosa* between artificial reefs and natural reefs in Loch Linnhe. However, there were significant differences in the $\delta^{13}C$ between sites for both phytoplankton and *P. plumosa*. Although not significant, the phytoplankton from natural reef sites appeared to have a lower $\delta^{13}C$ signature compared with artificial

reef sites. This could be explained by the closer proximity of the natural reef sites to the shore as freshwater or terrigenous sources of carbon have a more negative isotopic signature than marine sources (e.g. Lajtha & Michener 1994)). However, this does not explain the opposite trend shown by the *L. saccharina*, whereby samples from natural reef sites had a higher $\delta^{13}C$ than those collected from artificial reef sites.

6.4.2 $\delta^{13}C$ signatures

No significant differences were found in the $\delta^{13}C$ signatures between reef types for any taxa studied, although it is worth noting that differences between reef type for *E. esculentus* $\delta^{13}C$ was almost significant with a p value of 0.059.

With the exception of *A. rubens* and *N. puber*, all fauna sampled had mean $\delta^{13}C$ signatures between -16.5 and -18‰. These values are at the top end of the $\delta^{13}C$ signatures of the primary producers sampled in this study. Phytoplankton had a $\delta^{13}C$ signature range of -17.5 to -20.5‰, *L. saccharina* from -18 to -25‰. These values are within the $\delta^{13}C$ signatures in the literature for macroalgae and marine phytoplankton (Lajtha & Michener 1994). *P. plumosa* had a mean $\delta^{13}C$ signature ranging from -31 to -35‰, much more negative than any consumer $\delta^{13}C$ signatures, and so was not likely to have been a major constituent of the diet of fauna sampled in this study. *A. rubens* and *N. puber* had $\delta^{13}C$ signatures of approximately -14 and -15.5‰ respectively; well above the signatures of those primary producers characterised in this study. However, Lajtha and Michener (1994) reported benthic algae to have a $\delta^{13}C$ signature ranging from -10 to -20‰. It can, therefore, be concluded that benthic algae formed a greater part of the diet, or more likely the diet

of prey items, of *A. rubens* and *N. puber* than it did for *G. cineraria*, *E. esculentus*, *B. crenatus* or *C. exoletus*.

6.4.3 $\delta^{15}N$ signatures

The $\delta^{15}N$ signature of an organism increases with trophic level and so gives information on the trophic level of the organism within an ecosystem. The only taxa to have significant differences in $\delta^{15}N$ signatures between reef types in this study were *A. rubens* and *N. puber*. *Asterias rubens* is known to have a varied diet consisting of bivalves, polychaetes, other echinoderms and small crustacea, especially barnacles (Mortenson 1927, Hayward & Ryland 2003) and it had a significantly lower $\delta^{15}N$ signature at artificial compared with natural reef sites. The diet of *A. rubens* at artificial reef sites, therefore, had a higher component of prey items from lower trophic levels than at natural reef sites.

Although the biological communities on artificial and natural reefs in this study have not been compared, previous studies have suggested that there may be a greater density of epifaunal predators such as *A. rubens* at artificial than natural reef sites in Loch Linnhe (chapter 3). If differences in $\delta^{15}N$ between reef types were caused by the increased density of *A. rubens* at artificial reefs sites then it would be expected that $\delta^{15}N$ signatures would be enhanced at artificial reefs as a result of nutritional stress (Gannes et al. 1997). The $\delta^{15}N$ signature of *A. rubens* at artificial reef sites was lower than that at natural reef sites and so nutritional stress can be discounted as a reason for the difference in $\delta^{15}N$ between reef types. However, there appears to be a greater available biomass of epifauna on artificial reefs than natural reefs in Loch Linnhe (*pers. obs.*) perhaps as a result of the greater surface area to volume ratio and

higher complexity of habitat offered by the artificial reefs (Rose 2005, and see chapter 5). A higher epibiotic dietary component at artificial than natural reefs could perhaps explain the lower $\delta^{15}N$ signature of *A. rubens* at artificial reefs as many epifaunal taxa, such as barnacles and calcareous tube worms, are filter feeders and would, therefore, have a relatively low $\delta^{15}N$ signature.

There was also greater variation in the $\delta^{15}N$ values for *A. rubens* at artificial than natural sites. This could imply a greater heterogeneity in the diet at artificial than at natural reef sites, perhaps as a consequence of the greater habitat complexity of the artificial reef sites (e.g. Guichard & Bourget 1998, Guichard et al. 2001, Svane & Peterson 2001). Alternatively, this heterogeneity in the diet could be a result of the relatively newly established biological communities on artificial reefs compared to the existing natural rocky reefs, in agreement with the Intermediate Disturbance Hypothesis (Connell 1978).

Asterias rubens is known to form dense aggregations that move slowly along coastlines feeding voraciously (Sloan & Aldridge 1981, Saier 2001, Hayward & Ryland 2003). Populations of *A. rubens* on a reef can, therefore, be regarded as transient. As a result, the high variability in $\delta^{15}N$ signatures at artificial reef sites could be linked to residence times of individuals on reefs. For example, if the available prey items on an artificial reef module had a lower mean $\delta^{15}N$ signature than prey items on natural habitats, an individual that had been resident for a long time on an artificial reef module could be expected to have a lower $\delta^{15}N$ signature than those individuals that have recently arrived from natural habitats. The speed with which the stable isotope ratio of an animal's tissue changes to reach an

equilibrium with that of a new diet is dependent on the isotope turnover rate of both the tissue and taxa being studied (e.g. Gannes et al. 1997, Maruyama et al. 2001, Perga & Gerdeaux 2005, Sweeting et al. 2005). This has not been determined for *A. rubens*, however, Maruyama et al. (2001) found the half-change period of the $\delta^{15}N$ value of a migratory goby (*Rhinogobius* sp.) in Japan to be between one and three months depending on the age of the fish and concluded that growth rates were primarily responsible for determining isotopic turnover rates. Olive et al. (2003) showed the $\delta^{15}N$ value of the polychaete, *Nereis virens*, to reach a new equilibrium after just 7 days following the introduction of a depleted diet but that an asymptote had not been reached by day 70 following the introduction of an enriched diet. It is, therefore, likely that the isotopic turnover rate of *A. rubens* tissue is in the range of weeks to months.

The $\delta^{15}N$ signature of *N. puber* was also significantly different at artificial and natural reefs in Loch Linnhe suggesting differences in the diet of this species at the different reef types. However, in contrast to *A. rubens*, *N. puber* had a significantly higher $\delta^{15}N$ signature at artificial than natural reefs. Freire and González-Gurriarán (1995) investigated the feeding ecology of *N. puber* in NW Spain and found that, despite the variability in prey items taken, the small, anomuran decapod, *Pisidia longicornis* was the main prey item in all areas studied. Other dominant prey items included the mussel, *Mytilus galloprovincialis*, egg cases of Nassariidae gastropods, teleost fishes and the urchin *Psammechinus miliaris*.

The populations of *P. longicornis* at artificial and natural reefs in Loch Linnhe have not been quantified. However, *P. longicornis* is known to inhabit rock and gravel

and is often found living amongst the bryozoan *Pentapora fascialis* and other colonial forms (Hayward & Ryland 2003). *Pisidia longicornis* was abundant amongst epifaunal communities on PVC panels used in recruitment studies in previous chapters (*pers. obs.*), in particular on those panels heavily fouled with epifauna with high structural complexity such as solitary ascidia (*pers. obs.*). As a result of the greater habitat complexity on artificial reefs than natural reefs, with respect to both substrata and secondary fouling from epifaunal communities, *P. longicornis* could be expected to be more abundant at artificial than at natural reef sites. The higher $\delta^{15}N$ signature of *N. puber* at artificial than natural reefs in Loch Linnhe could perhaps be explained by differences in the availability of the preferred prey items of *N. puber* as a result of differences in habitat complexity of the reef types.

As described for *A. rubens*, the turnover rate of an organism will determine the speed with which a new diet is reflected in the isotopic signature of an organisms tissues. Many of the taxa sampled in this study were mobile and may have had varying residence times at the study sites prior to being sampled. It is possible, therefore, that the stable isotope ratios determined in this study do not fully reflect the community composition at the study sites but may be affected by previous areas inhabited by these mobile taxa. This source of error could perhaps be reduced in territorial taxa such as the corkwing wrasse, *C. melops*, a reef-dwelling fish that builds nests in crevices on reefs. Unfortunately sample numbers of *C. melops* from artificial reefs were not sufficient to make comparisons between reef types in this study. The use of complimentary gut content analysis, giving information on recently consumed prey items, could perhaps help to establish the error as a result of

varying residence times. Tagging and/or tethering experiments could also resolve some of these difficulties, but it was not possible to do this within the time and logistical constraints of this study.

The lipids that were extracted as part of the pre-treatment for stable isotope analysis were preserved for future fatty acid analysis. This analysis will give further information into the prey items consumed by the study taxa at artificial and natural reefs and may help to explain differences seen in $\delta^{15}N$ ratios of *A. rubens* and *N. puber*.

6.4.4 Trophic level

Stable isotope ratios offer an effective natural tracer for following energy and nutrient flows through ecosystems (Lajtha & Michener 1994) and $\delta^{15}N$ signatures have been used in many trophic studies (e.g. Sholto-Douglas et al. 1991, Maruyama et al. 2001, Davenport & Bax 2002, Connolly 2003, Genner et al. 2003). However, these data are more meaningful when used in conjunction with a trophic baseline (Vander Zanden & Rasmussen 2001, Post 2002, Jardine et al. 2003); this is particularly true when samples are being compared between locations where there may be differences in the source of carbon and nitrogen to the base of the food web (Vander Zanden et al. 1999). Although there were no significant differences in trophic position at artificial and natural reefs for any taxa, *A. rubens* and *N. puber* had different rank orders at the different reef types. *N. puber* had a higher rank with respect to trophic position than *A. rubens* at artificial reef sites, but a lower rank at natural reef sites. This reflects the differences seen in $\delta^{15}N$ between reef types for these taxa.

The trophic position of an organism can be thought of as the trophic level, detected using $\delta^{15}N$, calibrated to a baseline in order to allow direct comparison between sampling locations which may have different background levels of $\delta^{15}N$ and $\delta^{13}C$. In this way trophic position can be used to assess differences in the trophic level and, therefore, the diet of taxa at different reef sites. As the taxa analysed in this study were omnivorous, differences or similarities in trophic position of taxa can be used to infer the diet and, therefore, the composition of prey items available to the study taxa. Taxa analysed in the current study were mostly secondary consumers with a predominantly epifaunal diet. The similarity of trophic position of taxa at artificial and natural reef sites in Loch Linnhe, therefore, suggests that the epifaunal communities on these reefs are also similar.

Complimentary fatty acid analysis would help to investigate differences in rank order with respect to trophic level at artificial and natural reef sites for *A. rubens* and *N. puber*. This was not possible within the time frame for this study but samples remain for future analysis.

6.4.5 Somatic condition indices

No significant differences in fish condition of *C. exolutus* were found between artificial and natural reefs in Loch Linnhe. However, male fish had a significantly higher somatic condition index than female fish at both reef types (approximately 0.95 and 0.85 respectively). This is in contrast to a study by Sayer et al. (1996) who found no significant annual difference in K_s between sexes, although it appears that male *C. exoletus* had a higher K_s than female *C. exoletus* in September, with K_s values of approximately 1.0 and 1.1 respectively (Sayer et al. 1996). So not only

were K_s values in the current study lower than those reported in Sayer et al. (1996) but the trend was reversed.

The relationship between length and weight can provide information on the condition of fish (Jennings et al. 2001). An increase in the gonadosomatic index (GSI) together with a decrease in K_s and/or the hepatosomatic index (HSI) may be caused by the depletion of body reserves and/or the mobilization of proteins and lipids from the liver during gonadal development (Htun-Han 1978, Sayer et al. 1996). No information is available on the GSI or HSI of fish in this study; however, the lower K_s in female C. *exoletus* in this study could, perhaps, be explained by the fact that samples were collected in the autumn. All taxa in this study were sampled in September/October 2004 and so it is likely that female *C. exoletus* had a lower K_s because of the expenditure of energy for reproduction over the summer months (June to August). This is in agreement with a study by Htun-Han (1978) who showed a peak in somatic condition of the Dab, ***Limanda limanda***, in pre- and early-spawning periods and a trough in the post-spawning period.

Although not quantified at the sites used in this study, there did appear to be a greater population of *C. exoletus* at artificial than natural reefs in Loch Linnhe (***pers. obs.***). Hunter (2006) found approximately six times more C. *exoletus* on artificial reefs than natural reefs in Loch Linnhe in the summer and autumn seasons of 2005. That there was no significant difference in K_s between artificial and natural reef populations of *C. exoletus*, therefore, suggests that artificial reefs can provide resources to successfully support a greater population of these fish than natural reefs in Loch Linnhe. It is also worth noting that small individuals of C. *exoletus* (< 10cm) were

caught at each of the artificial sites but not at the natural sites. This may be coincidental, or it may be a result of the increased habitat complexity at artificial sites providing suitable settlement sites and habitat for juvenile fish (Brickhill et al. 2005).

This study would have benefited from greater sample numbers; however, uncharacteristically wet and windy weather in autumn 2004 made sampling difficult. The sea water in Loch Linnhe turned a deep peaty colour, as a result of fresh-water run-off, which may have reduced the available light and thus the foraging activity of fish in the area; thereby reducing the efficiency of creeling as a sampling method. This may also have made the reefs look similar in terms of baseline $\delta^{13}C$ and $\delta^{15}N$ thereby obscuring minor differences between the two reef types. It would also have been beneficial to have had a third natural reef site for comparison to the artificial reef modules in Loch Linnhe. In hindsight, it would have been interesting to have sampled fauna and flora from some of the natural sites used in previous chapters regardless of the lack of reef-dwelling fish at natural sites. This would have been particularly interesting as epifaunal recruitment work has shown there to be differences in epifaunal predation between reef types.

Nevertheless, this study has shown there to be many similarities in the trophic dynamics of artificial and natural reef sites in Loch Linnhe, but has also highlighted some interesting differences. Null hypotheses 1 and 2 can be, therefore, neither satisfactorily accepted nor rejected. It is hoped that the future analysis of fatty acid samples will clarify reasons behind any differences found between reef types.

Chapter 7 General discussion

Artificial reefs are widely used around the world for reasons which include habitat protection, fisheries enhancement, mitigation following the destruction of natural habitats, and structures solely for the benefit of recreational fishing and diving industries (Moreno et al. 1994, Pratt 1994, Bohnsack et al. 1997, Relini & Relini 1997, Baine 2001). This range of uses, combined with the prohibitive costs of prime materials and, therefore, the frequent use of materials of opportunity (Bohnsack & Sutherland 1985, Baine 2001), has resulted in a great variety in the design of artificial reefs. The vast majority of artificial reefs have also been constructed for economic or environmental, rather than scientific, purposes. This has resulted in a lack of artificial reefs with the replication levels required for in-depth scientific experiments (e.g. Lindberg 1997). This is, perhaps, one of the many reasons as to why, despite the numerous artificial reefs around our coastlines, there has been little robust scientific research into either the impacts or the ecological functioning of these structures (Grossman et al. 1997, Brickhill et al. 2005).

The work presented within this thesis has provided insights into both the impacts and the ecological functioning of a purpose-built experimental artificial reef in Loch Linnhe, west coast of Scotland.

7.1 Ecological functioning of the Loch Linnhe artificial reef: comparisons between artificial and natural reefs.

Similarities in the trophic position of key taxa at artificial and natural reefs in Loch Linnhe, estimated using stable isotope ratios, were interpreted in this thesis to show

that the base of the food webs was similar at both reef types (chapter 6). However, a detailed epifaunal recruitment study in Loch Linnhe showed there to be significant differences in the epibiotic communities after 15 months of fouling on PVC recruitment panels at artificial and local natural rocky reefs (chapter 4). This is in agreement with the majority of previous work in this field (e.g. Butler & Connolly 1996, Connell & Glasby 1999, Glasby 1999a, Connell 2001, Bulleri 2005a, b, Perkol-Finkel et al. 2006). However, little focus has been given to identifying processes controlling the epifaunal recruitment to artificial reefs in the literature (but see Bulleri 2005a, b).

Through the use of predator exclusion cages it was possible to determine that the differences presented in this thesis were the result of an increased epifaunal predation effect on the developing epifaunal assemblages on recruitment panels at artificial reef sites. This is shown in Figure 7.1 where the main conclusions from this thesis are summarised. It can be seen that, approximately two years post-deployment of the artificial reefs, epifaunal predation is higher at artificial than natural reefs. Epifaunal communities on recruitment panels inside predator exclusion cages were similar at artificial and natural reef sites suggesting that early recruitment of marine invertebrates was similar between reef types. It can, therefore, be concluded that post-settlement processes such as predation, rather than supply-side ecology (Lewin 1986, Underwood & Keough 2001) and pre-settlement processes, were influential in controlling the differences in epifaunal communities on PVC recruitment panels at the two reef types in Loch Linnhe. This is in contrast to (Bulleri 2005a, b) who showed that differences in epifaunal assemblages on recruitment panels were apparent from very early stages of succession.

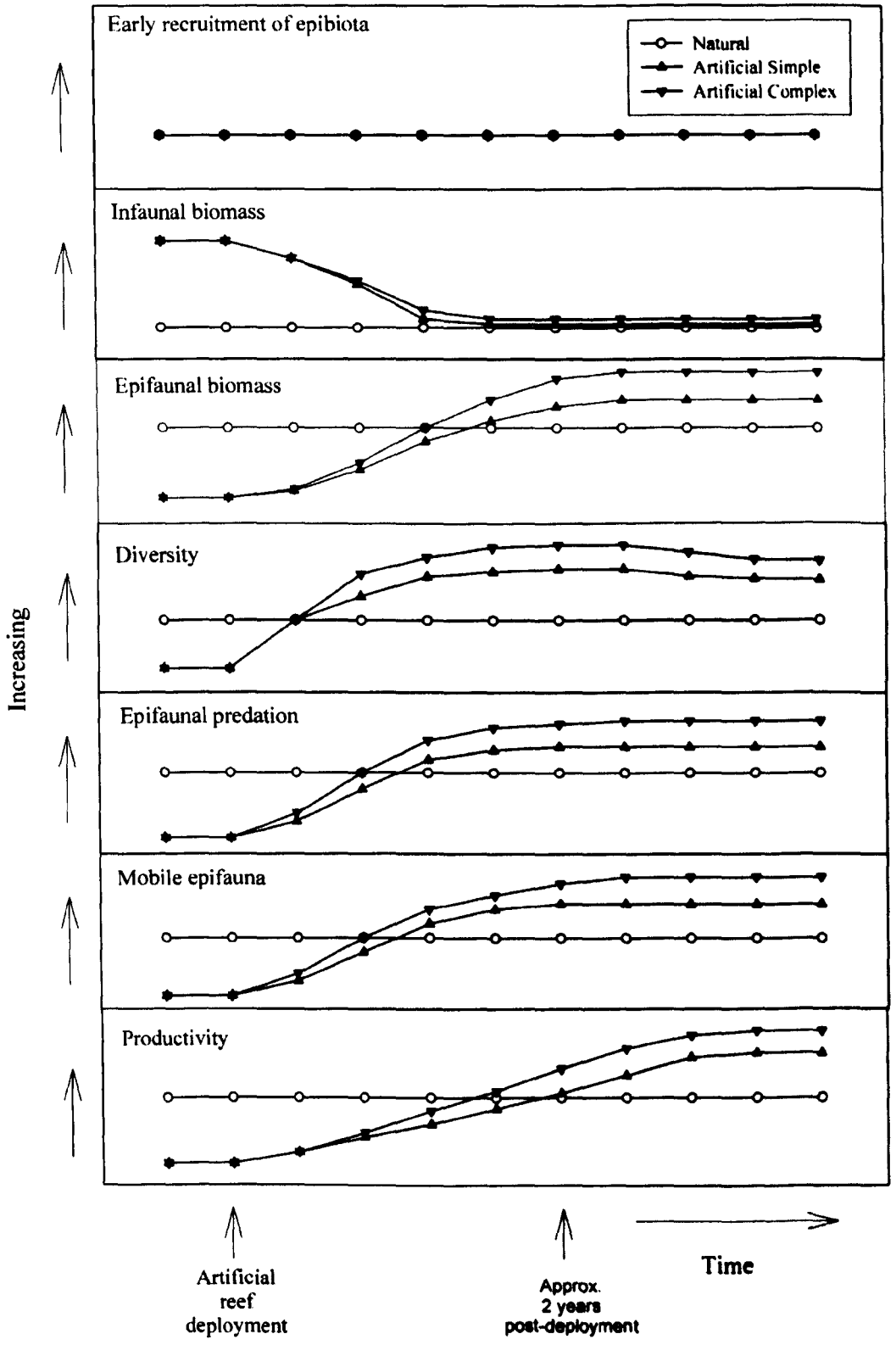

Figure 7.1 Graphical representation of the conclusions made, and hypotheses suggested, in this thesis with respect to differences in biotic interactions at artificial land natural reefs in Loch Linnhe. It should be noted that the scale of the graphs is variable e.g. the biomass of infauna lost is approximately 30 times less than the increase in epifaunal biomass.

It is widely acknowledged that care must be taken when inferring conclusions drawn from recruitment studies using artificial substrata onto natural substrata (e.g. McGuinness 1989, Glasby & Connell 2001). No attempt has been made in this study to relate the actual epifaunal communities on PVC recruitment panels to the respective artificial and natural reefs; however, it may be possible to infer processes observed on PVC panels to processes occurring on the reefs. For example, the effects of predation on developing epifaunal assemblages on recruitment panels have been shown to be greater at artificial reef sites compared with natural reef sites in Loch Linnhe. Making the assumption that predation is density-dependent (e.g. Connell & Anderson 1999) and that this was a result of higher predator densities on the artificial reefs, it seems likely that the observed differences in the influence of predation on epifaunal communities on recruitment panels is also true of communities on the reefs themselves. Although these epifaunal predators were not quantified directly within the work presented in this thesis, this is in agreement with observed greater abundances of many mobile taxa on the artificial than natural reefs in Loch Linnhe (Hunter 2006 and *pers. obs.*).

Two years post-deployment, it is proposed that a greater abundance of both epifaunal predators and mobile epifauna are present on the artificial than natural reefs in Loch Linnhe (Figure 7.1). A positive correlation is thought to exist between the structural complexity of reef habitat and its species diversity, abundance and biomass of inhabiting fish assemblages (e.g. Hixon & Beets 1993, Rilov & Benayahu 1998, Holbrook et al. 2002, Gratwicke & Speight 2005). It seems plausible that this could also be true of other mobile taxa such as epifaunal predators. Complex reef modules were estimated within this thesis to support a 1.6 times greater standing crop of

epifaunal biomass than the less structurally complex simple reef modules (chapter 5). The high structural complexity of the artificial reefs may also provide a greater surface area of hard substratum available for epifaunal fouling and, therefore, prey items for epifaunal predators, than the less complex local natural reefs (Rose 2005).

Perkol-Finkel et al. (2006) questioned whether epifaunal communities on artificial reefs will eventually mimic those on natural reefs as a result of structural and environmental differences between reef types. This is an important question as artificial reefs are often created in order to enhance fisheries or mitigate for the loss of natural habitat. It is, therefore, important to know whether these artificial structures support similar communities to local natural habitats or whether their use will have long-term consequences on the identity, diversity and abundance of subtidal biological communities (Carr & Hixon 1997, Connell 2001). It seems likely that the structural differences between the artificial and natural reef sites in Loch Linnhe may have contributed towards the differences in epifaunal predation pressures at the different reef types which resulted in post-settlement processes causing differences in the developing epibiotic communities on recruitment panels at the different reef types. As a result, it is suggested that where there are structural differences between reef types, differences in epifaunal community structure between reef types may persist through time even when early recruitment and larval supply are similar.

The Intermediate Disturbance Hypothesis (Connell 1978) states that species richness is highest at intermediate levels of disturbance. The increased disturbance resulting from greater predation pressures at the artificial reef sites, compared with the natural

reefs in Loch Linnhe, may, therefore, result in a higher species richness within the epifaunal community structure at artificial reef sites. This was observed in the data from open (uncaged) recruitment panels at artificial sites after 15 months of fouling. The high structural complexity of the artificial reef modules, compared with the low structural complexity of the local natural rocky reefs, may also result in a greater species richness of mobile taxa inhabiting the reefs (Dean & Connell 1987, Charbonnel et al. 2002, Holbrook et al. 2002, Gratwicke & Speight 2005). As such it is predicted that the artificial reefs in Loch Linnhe will have a greater species diversity than the local natural rocky reefs (Figure 7.1). Biological communities are known to change through time as a result of processes such as facilitation, whereby initial colonists alter the conditions and allow the entry of a new taxon (e.g. biofilm and the solitary ascidian *Ciona intestinalis;* Wieczorek & Todd 1998) and competitive exclusion, whereby dominant taxa out-compete early colonists (e.g. the Red Squirrelfish, *Sargocentron rubrum* and other reef-dwelling fish species; Spanier 2000). It is, therefore, anticipated that the species diversity will peak relatively early on in the development of the Loch Linnhe artificial reef communities before levelling off or even decreasing slightly as the communities mature (Connell 1978, Dean & Connell 1987).

Determining when or if a community has reached ecological maturity is a complicated issue and there is some question as to whether communities ever reach an ecological climax. Many communities have been shown to exhibit phase-shifts; for example coral reef communities changing from coral dominated to algal dominated assemblages (e.g. Bellwood et al. 2004). Other communities have been observed to alternate between apparently stable states (Sutherland 1974, Van de

Koppel et al. 2001). Perhaps it could be concluded that an ecological system cycling between alternate steady states could be considered as a mature community? Data gathered within this thesis has not allowed an estimate how long the Loch Linnhe artificial reefs will take to be able to be regarded as having ecologically mature biological communities associated with them. However, within this thesis, it has been shown that, just 2 years post-deployment, the artificial reef modules in Loch Linnhe support a diverse and comparable biological community to that of the nearby local natural rocky reefs.

7.2 The Loch Linnhe artificial reef and the attraction-production debate.

Whether artificial reefs are more productive or attractive with respect to biological communities is likely dependent on a wide range of factors including whether taxa are recruitment- or habitat-limited (Bohnsack 1989, Grossman et al. 1997). If habitat availability is limited then the introduction of new hard-bottom habitat in the form of artificial reefs should increase fish production through increased foraging, increased nesting habitat for adult fish and reduced mortality rates through the provision of resting habitat and refuge from predation (e.g. Hixon & Beets 1993, Relini & Relini 1997). No significant differences were found in the epifaunal recruitment to artificial and natural reef sites, in the absence of major epifaunal predators, which suggests that epibiotic taxa in Loch Linnhe are not recruitment-limited.

Productivity is the rate of conversion of resources to biomass per unit area per unit time; the rate at which organic matter is made available to higher trophic levels (Taylor 1998, Waide et al. 1999). Within this thesis the epifaunal biomass potential of a complex artificial reef module was estimated to be 1.6 times greater than a

simple artificial reef module in Loch Linnhe as a result of the differences in habitat complexity and available surface area. The natural reefs in Loch Linnhe have been shown previously to be less structurally complex than the artificial reef modules (Rose 2005), and so it can be hypothesised that the artificial reef modules may potentially support a greater epifaunal biomass than the natural reefs. This, combined with an observed greater epifaunal predation pressure at the artificial than natural reef sites in Loch Linnhe, can be interpreted to show that the Loch Linnhe artificial reef modules may be more productive, in terms of epifaunal biomass, than the local natural rocky reefs. This is summarised in Figure 7.1.

There were no significant differences in the somatic condition indices of the rockcook (*Centrolabrus exoletus*) between reef types in Loch Linnhe despite a greater observed population of this fish species at the artificial than natural reefs (Hunter 2006 and *pers. obs.*). This perhaps demonstrates that the artificial reef modules may be able to support a greater abundance of these fish; perhaps a result of the greater habitat complexity providing more shelter and nesting opportunities or a greater availability of epifaunal prey (e.g. Hixon & Beets 1993, Moring & Nicholson 1994, Gratwicke & Speight 2005). Again, this suggests that the Loch Linnhe artificial reef may be more productive than attractive with respect to habitat for *C. exoletus*.

The epifaunal biomass on a complex artificial reef module in Loch Linnhe was estimated within this thesis to be up to 30 times greater than the infaunal biomass lost in the underlying sediments after approximately 12 months of fouling (chapter 5). This represents a great increase in biomass at the base of the food-web which is

potentially available as prey items for taxa in higher trophic levels. This work complements that of Steimle et al. (2002) who estimated the epifauna on their artificial reef to be up to 44 times more productive than the infauna in nearby sandy sediments. These studies demonstrate that the addition of an artificial reef module can increase the productivity of the local area. Figure 7.1 shows that prior to the deployment of an artificial reef module there is expected to be a high infaunal biomass at the artificial reef site. Following the deployment of a reef module, the infaunal biomass in the underlying sediments is expected to decrease substantially with time. A small amount of infaunal biomass is expected to remain in the sediments at the edge of reef modules (chapter 5), particularly under complex reef blocks which are lighter and so sink into the sediment to a lesser extent than the heavier simple reef blocks. The infaunal biomass at the natural reef sites remains low (probably zero) through time.

Although no direct comparisons in productivity between artificial and natural reefs in Loch Linnhe have been made within this thesis, there is indirect evidence to show that the Loch Linnhe artificial reef modules are productive habitats and may well be more productive than their local natural rocky reefs (as summarised in Figure 7.1). Habitat complexity appears to be an influential factor in the productivity of the Loch Linnhe artificial reef.

7.3 Limitations of this study and recommended methodology/protocols.

There are many inherent difficulties associated with artificial reef research. Firstly, as mentioned previously, there are few artificial reefs with replication suitable for robust scientific research and little standardisation of artificial reef design making

comparisons between artificial reefs and between research programmes difficult (e.g. Grossman et al. 1997, Lindberg 1997, Brickhill et al. 2005).

The importance of detailed comparisons between artificial and natural reefs has been discussed throughout this thesis. Although the size, shape, design and replication of experimental artificial reefs can be carefully planned (depending on funding, resources, licensing agreements etc.), researchers have to make the best use of available nearby natural rocky reefs. Comparisons between artificial and natural reefs are, therefore, often problematic with many confounding factors including differences in depth, size, shape, age and reef topography between reefs (Carr & Hixon 1997). Many artificial reefs are also constructed of artificial materials such as steel or concrete and so could support quite different epibiotic communities as a result of differences in substrata (Keough & Downes 1982, Walters & Wethey 1996, Glasby 2000, Brown 2005). All of these factors contribute to difficulties in interpreting the results of comparisons between the biological communities on artificial and natural reefs.

If all these challenges associated with artificial reef research were not enough, there is also a lack of standardisation with respect to the methods used in artificial reef studies making it difficult to compare the results between different research programmes (Relini & Relini 1997, Qiu et al. 2003). Within this thesis, PVC recruitment panels, combined with wire mesh predator exclusion cages, were used to assess and compare early epifaunal recruitment, longer-term epifaunal recruitment and the effects of epifaunal predation on developing epifaunal assemblages at artificial and natural reef sites. This method enabled comparisons despite differences

in substrata and ecological age of the reef types. Stable isotope analysis was used to identify differences in the trophic levels and dietary source of some key taxa inhabiting both artificial and natural reef types in Loch Linnhe. This technique failed to detect any major differences in reef types suggesting that the epifaunal community structures of the artificial and natural reefs were similar. However, this technique would be more useful with complementary gut content analysis of some key taxa, perhaps combined with fatty acid analysis, in order to identify the major prey items (e.g. Gurney et al. 2001, Grey et al. 2002, Jones & Waldron 2003). The taxa selected for stable isotope analysis in this study included some highly mobile and potentially transient species, such as the starfish, *Asterias rubens*. This made interpretation of results difficult as the residence times of these individuals on the study reefs were not known. Therefore, in future, it is recommended that sessile and territorial taxa should be used whenever possible.

On completion, the Loch Linnhe artificial reef complex will comprise 42 artificial reef modules within a 0.4 km^2 licensed area. The majority of these modules are arranged in sets of six replicates, approximately 30m apart, as shown in Figure 1.2. Within this thesis it has been shown that the increased effects of epifaunal predation on developing communities on recruitment panels at artificial reef sites was also apparent at sites 100m distant from artificial reef modules (chapter 3). This complements previous work that has found mobile predators impacting epifaunal and infaunal communities at distances in excess of 100m from artificial reefs (e.g. Davis et al. 1982, Frazer & Lindberg 1994). This is an important finding in that it suggests that any "replicate" reef module in the Loch Linnhe artificial reef complex within 100m of another reef module cannot be regarded as an independent reef.

At the start of the recruitment study, the Loch Linnhe artificial reef complex was still under construction with just 13 reef modules in place. However, by the end of the study many more reef modules had been deployed and the study reefs (M2s, M1c, and M1s) had nearest neighbours at 53, 54 and 36m, respectively. All three of the reef modules used as replicates in the epifaunal recruitment study may, therefore, have been compromised with respect to independence. The same is true of the reef modules used in the trophic dynamics study. This issue of independence is important for the future construction of experimental artificial reefs if truly robust research is to be carried out. However, artificial reef construction is, in general, heavily influenced by financial constraints and licensing issues so this may not always be achievable.

This lack of independence of artificial reefs presents a problem similar to that faced by researchers looking into the environmental impact of anthropogenic disturbances such as sewage outfalls, whereby there is often just one impacted area under investigation. Some researchers have resolved this problem through the use of a Beyond BACI experimental design, whereby one impacted area is compared to multiple control areas (Underwood 1992, Chapman et al. 1995). In this way the spatial variability within an impacted location can be contrasted with levels of variation found in replicated control locations and should, therefore, identify any differences that could be attributed to the disturbance. This technique could, perhaps, be used to access differences in the ecology of artificial and natural reefs when no independent artificial reef replicates are available.

Added to the non-independence issues of artificial reef modules used as replicates within this thesis, there were also pseudoreplication issues (Hurlbert 1984) within the

recruitment studies (chapters 3 and 4). All four "replicate" recruitment panels were mounted on the same PVC frame. This means that it was not possible to determine the within-site variability in epibiotic recruitment as a result of factors such as the patchy distribution of larvae. Where predator exclusion cages were used, it was one single cage that was used to exclude predators from all four panels. The problems with this experimental design are discussed in chapter 3 (section 3.4.6). Working in the subtidal environment using SCUBA introduces many logistical limitations and all experimental designs within this thesis were planned within the logistical constraints of the project. However, in hindsight, and with greater time and resources, the experimental design could have been improved with replicate sets of panels at each site in order to estimate the inter-site variability of recruitment and with separate predator exclusion cages over recruitment panels in order to control for the patchiness of predator abundances.

7.4 The challenges for future artificial reef research

The importance of the independence of study sites is also relevant to the stable isotope work from chapter 6. Problems associated with the use of key taxa which are mobile and, therefore, may have varying residence times on the study reefs may be heightened if these taxa are also moving between reefs. Further work is needed to establish the influence area of an artificial reef module to determine which, if any, sites within the Loch Linnhe artificial reef complex can be used as independent replicates. In the case of mobile fauna this can be achieved through a detailed tagging study across the Loch Linnhe artificial reef complex.

As discussed previously, species richness on the Loch Linnhe artificial reefs may

decrease with time after deployment as a result of competitive exclusion. It is widely accepted that there is a relationship between species diversity, or species richness, and productivity (Huston 1979, Rosenzweig & Abramsky 1993, Wright et al. 1993, Waide et al. 1999, Fukami & Morin 2003). As such, it would be interesting to re-address many of the issues examined within this thesis once the communities on the Loch Linnhe artificial reef have had more time to mature.

Several studies have reported the presence of an artificial reef to have an impact on the infaunal communities in sediments near to artificial reefs, either as a result of changes in sediment properties or reef-dwelling predators (e.g. Davis et al. 1982, Ambrose & Anderson 1990, Frazer & Lindberg 1994, Barros et al. 2001, Fabi et al. 2002). As the artificial reefs in Loch Linnhe appear to harbour a greater mobile faunal community than the local natural reefs it would be interesting to see if this has any effects on the infauna in surrounding sediments. This thesis has shown that the placement of an artificial reef block reduces the infaunal biomass in underlying sediments, but no comparisons have been carried out on the differences between the effects of reef-dwelling predators on infauna next to and away from natural and artificial reefs.

The artificial reefs in Loch Linnhe have been shown to be more productive than the local natural reefs and natural soft sediment with respect to epifaunal (and infaunal) biomass. The increased habitat complexity of the artificial reefs appears to be fundamental to the success of the Loch Linnhe project. The effects of habitat complexity on reef productivity have not been tested within this thesis, with the exception of chapter 5 which showed the higher complexity reef modules to support

a greater epifaunal biomass. However, the design of the Loch Linnhe artificial reef complex, with two known complexities of reef module (simple and complex), provides an ideal setting for this type of investigation assuming issues of non-independence of study sites can be overcome.

Although this thesis has shown that, and has attempted to quantify the scale with which, the Loch Linnhe artificial reef has enhanced the productivity in the local area, it may be that a similar reef deployed in a more or less productive natural system would alter the production in an area to a different extent. Although the majority of artificial reefs are sited in areas of low productivity for the purpose of enhancing productivity, care needs to be taken when making comparisons between the functioning of man-made structures deployed in very different systems (i.e. temperate and tropical, high and low energy). Research into the efficacy of artificial structures would, therefore, benefit from studies on a series of similar structures deployed across a broader range of systems.

7.5 Thesis conclusions

The work presented in this thesis has contributed quantified information to the attraction-production debate, showing that the Loch Linnhe artificial reef not only has a mobile community associated with it but that it appears to be highly productive in its own right with respect to epibiotic biomass. It would seem logical that if a reef is highly productive at the base of the food web then this energy may be passed up the food chain to result in a highly productive system. Many different aspects of the ecological functioning of the Loch Linnhe artificial reef complex have been assessed within this thesis and, as a result, it is concluded that just two years post-deployment,

the artificial reefs in Loch Linnhe may already be more productive per unit area/volume than the natural rocky reefs in Loch Linnhe. The reefs constructed of complex reef blocks are expected to be more productive than those made from simple reef blocks as a result of the high habitat complexity and heterogeneity provided by the complex reef modules. This thesis, therefore, lends weight to the argument that the placement of a well designed artificial reef can increase the productivity of a local area, as summarised in Figure 7.1. Conclusions drawn from this thesis support the hypothesis that artificial reefs provide additional critical habitat that increases the environmental carrying capacity and eventually the abundance and biomass of reef-dwelling fauna (*sensu* Bohnsack 1989).

Results from this thesis suggest that the artificial reefs in Loch Linnhe could be a suitable replacement for, or addition to, the existing natural rocky reefs in the area. As such it would appear that the materials and construction design of these artificial reefs would be a sensible option, with respect to biological communities, for other man-made structures such as breakwaters which often have a significant subtidal component. Through the careful use of such structures, it may be possible to fulfil the practical requirements of a breakwater, or other similar structure, while at the same time augmenting biological productivity and, potentially, local inshore fisheries.

The main conclusions from this thesis are summarised below:

Methods

- The combination of laboratory-based abundance and biomass determinations is recommended for future artificial reef studies of epifaunal assemblage development
- Vertically orientated PVC recruitment panels are recommended for use inartificial reef studies of epifaunal development to assess and/or control for variation in epifaunal predation pressures

Biotic interactions

- Epibiotic larval supply tended toward uniformity across the artificial and natural reef study sites
- Significantly greater effects of epifaunal predation on epifaunal assemblage structure on PVC recruitment panels were found at artificial than natural reef sites
- Significant differences were found in epifaunal assemblage structure on open PVC panels at artificial and natural reef sites, probably as a result of epifaunal predation
- Post-settlement processes and not supply-side ecology appear to be controlling differences in the developing epifaunal assemblages at artificial and natural reefs in Loch Linnhe
- The increased effects of epifaunal predation on epifaunal assemblage structure extend to at least 100m distant from the artificial reefs in Loch Linnhe
- Complex artificial reef modules are estimated to be 1.6 times more productive in terms of epifaunal/infaunal biomass than simple artificial reef

modules in Loch Linnhe

- The presence of a simple reef block significantly reduced the infaunal biomass in sediments
- A complex reef module was estimated to support up to 30.8 times more standing crop of epifaunal/infaunal biomass than the natural soft sediments on which is lies prior to deployment
- Results from stable isotope analysis suggested that similar community structures exist on the artificial and natural reefs in Loch Linnhe
- Fish condition indices, combined with an observed greater abundance of fish on artificial than natural reefs, suggest that the artificial reef modules in Loch Linnhe can support a greater population of fish than the local natural rocky reefs
- Approximately two years following deployment of the Loch Linnhe artificial reef complex, the artificial reefs appear to be more productive than the local natural rocky reefs
- Habitat complexity is proposed as a key factor in the high productivity of the Loch Linnhe artificial reefs
- The design of the Loch Linnhe artificial reef has provided a habitat that appears to support a comparable, but more productive, biological community to that on the local natural rocky reefs.
- Issues of non-independence of artificial reef "replicate" sites are a problem as a result of the logistical constraints of artificial reef creation within Loch Linnhe.

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Appendix I Results tables from chapter 2

ANOVA and Kruskall Wallis tables from tests of significant differences between substrata.

ANOVA table : ABUNDANCE

Source of variation		Df	MS	F	P
Barnacle *in situ*	Substratum	1	83000	16.09	0.002*
	Error	10	5158		
	Total	11			
Barnacle laboratory	Substratum	1	267605	35.43	0.000*
	Error	10	7552		
	Total	11			
Barnacle image	Substratum	1	113296	44.58	0.000*
	Error	10	2541		
	Total	11			
Solitary ascidian *in situ*	Substratum	1	56	0.20	0.668
	Error	10	288		
	Total	11			
Solitary ascidian laboratory	Substratum	1	0.0210	0.50	0.497
	Error	10	0.0423		
	Total	11			
Solitary ascidian image	Substratum	1	108	0.58	0.466
	Error	10	188		
	Total	11			
Calcareous tube worm *in situ*	Substratum	1	4.7533	98.88	0.000*
	Error	10	0.0481		
	Total	11			
Calcareous tube worm laboratory	Substratum	1	5808	22.76	0.001*
	Error	10	255		
	Total	11			
Calcareous tube worm image	Substratum	1	51.886	82.39	0.000*
	Error	10	0.630		
	Total	11			
Erect bryozoan *in situ*	Substratum	1	14.1	0.54	0.479
	Error	10	26.1		
	Total	11			
Erect bryozoan laboratory	Substratum	1	225	1.41	0.262
	Error	10	159		
	Total	11			
Erect bryozoan image	Substratum	1	1.3	0.06	0.808
	Error	10	21.4		
	Total	11			
Green algae *in situ*	Substratum	1	3.425	33.88	0.000*
	Error	10	0.101		
	Total	11			
Green algae laboratory	Substratum	1	2.3256	28.12	0.000*
	Error	10	0.0827		
	Total	11			
Green algae image	Substratum	1	4.166	35.11	0.000*
	Error	10	0.119		
	Total	11			
Red algae laboratory	Substratum	1	768.0	13.24	0.005*
	Error	10	58.0		
	Total	11			
Red algae image	Substratum	1	1.5714	64.72	0.000*
	Error	10	0.0243		

	Total	11			
S *in situ*	Substratum	1	21.33	20.00	0.001*
	Error	10	1.07		
	Total	11			
S laboratory	Substratum	1	0.33	0.23	0.640
	Error	10	1.43		
	Total	11			
S image	Substratum	1	5.333	12.31	0.006*
	Error	10	0.433		
	Total	11			

* indicates significant at $p < 0.017$ (Bonferroni correction for multiple tests)

Kruskall Wallis table

	Substrata	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Red algae *in situ*	1 (PVC)	6	0.000	4.0	-2.40	7.17	1	0.007*
	2 (Concrete)	6	4.000	9.0	2.40			
	Overall	12		6.5				

* indicates significant at $p < 0.017$ (Bonferroni correction for multiple tests)

FREQUENCY

ANOVA table

Source of variation		Df	MS	F	P
Barnacle *in situ*	Substratum	1	8480	16.59	0.002*
	Error	10	511		
	Total	11			
Barnacle image	Substratum	1	6674	31.98	0.000*
	Error	10	209		
	Total	11			
Solitary ascidian *in situ*	Substratum	1	16	0.06	0.813
	Error	10	276		
	Total	11			
Solitary ascidian laboratory	Substratum	1	0	0.00	0.985
	Error	10	211		
	Total	11			
Solitary ascidian image	Substratum	1	120	0.36	0.561
	Error	10	333		
	Total	11			
Calcareous tube worm *in situ*	Substratum	1	58.098	109.28	0.000*
	Error	10	0.532		
	Total	11			
Calcareous tube worm laboratory	Substratum	1	51.67	45.04	0.000*
	Error	10	1.15		
	Total	11			
Calcareous tube worm image	Substratum	1	63.503	78.72	0.000*
	Error	10	0.807		
	Total	11			
Erect bryozoan *in situ*	Substratum	1	1.146	1.56	0.241
	Error	10	0.936		
	Total	11			
Erect bryozoan laboratory	Substratum	1	3.17	2.29	0.161

	Error	10	1.38		
	Total	11			
Erect bryozoan image	Substratum	1	0.075	0.12	0.732
	Error	10	0.603		
	Total	11			
Green algae *in situ*	Substratum	1	3.211	23.88	0.001*
	Error	10	0.134		
	Total	11			
Green algae laboratory	Substratum	1	1.7441	27.15	0.000*
	Error	10	0.0642		
	Total	11			
Green algae image	Substratum	1	3.504	23.28	0.001*
	Error	10	0.151		
	Total	11			
Red algae laboratory	Substratum	1	19.24	18.52	0.002*
	Error	10	1.04		
	Total	11			
Red algae image	Substratum	1	15.374	22.58	0.001*
	Error	10	0.681		
	Total	11			
S *in situ*	Substratum	1	0.9003	19.35	0.001*
	Error	10	0.0465		
	Total	11			
S laboratory	Substratum	1	0.000	0.00	0.981
	Error	10	0.0279		
	Total	11			
S image	Substratum	1	0.40845	46.13	0.000*
	Error	10	0.00885		
	Total	11			

* indicates significant at $p < 0.017$ (Bonferroni correction for multiple tests)

Kruskall Wallis table

	Substrata	N	Median	Av Rank	Z	H	Df	P (adjusted for ties)
Barnacle laboratory	1 (PVC)	6	97.5	9.3	2.64	7.03	1	0.008*
	2 (Concrete)	6	47.0	3.8	-2.64			
	Overall	12		6.5				
Red algae *in situ*	1 (PVC)	6	0.0	4.0	-2.40	7.21	1	0.007*
	2 (Concrete)	6	1.98406	9.0	2.40			
	Overall	12		6.5				

* indicates significant at $p < 0.017$ (Bonferroni correction for multiple tests)

PERCENT COVER GRID

ANOVA table

Source of variation		Df	MS	F	P
Solitary ascidian *in situ*	Substratum	1	46.0	0.58	0.465
	Error	10	79.9		
	Total	11			
Solitary ascidian image	Substratum	1	75.0	0.86	0.376
	Error	10	87.5		
	Total	11			
Calcareous tube worm *in situ*	Substratum	1	20.918	199.26	0.000*
	Error	10	0.105		
	Total	11			
Calcareous tube worm laboratory	Substratum	1	9.794	12.80	0.005*
	Error	10	0.765		
	Total	11			
Calcareous tube worm image	Substratum	1	7.313	41.95	0.000*
	Error	10	0.174		
	Total	11			
Erect bryozoan *in situ*	Substratum	1	3.52	1.33	0.276
	Error	10	2.65		
	Total	11			
Erect bryozoan laboratory	Substratum	1	17.52	4.20	0.068
	Error	10	4.17		
	Total	11			
Erect bryozoan image	Substratum	1	0.26	0.14	0.715
	Error	10	1.81		
	Total	11			
Green algae *in situ*	Substratum	1	1.948	14.68	0.003*
	Error	10	0.133		
	Total	11			
Green algae laboratory	Substratum	1	1.3853	21.34	0.001*
	Error	10	0.0649		
	Total	11			
Green algae image	Substratum	1	1.560	13.94	0.004*
	Error	10	0.112		
	Total	11			
Red algae laboratory	Substratum	1	0.3018	11.87	0.006*
	Error	10	0.0254		
	Total	11			
Red algae image	Substratum	1	0.1912	8.34	0.016*
	Error	10	0.0229		
	Total	11			
S *in situ*	Substratum	1	21.33	20.00	0.001*
	Error	10	1.07		
	Total	2			
S laboratory	Substratum	1	0.75	0.65	0.438
	Error	10	1.15		
	Total	11			
S image	Substratum	1	10.083	46.54	0.000*
	Error	10	0.217		
	Total	11			

* indicates significant at $p < 0.017$ (Bonferroni correction for multiple tests)

Kruskall Wallis table

	Substrata	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Barnacle *in situ*	1 (PVC)	6	1.8261	9.5	2.88	8.34	1	0.004*
	2 (Concrete)	6	0.8702	3.5	-2.88			
	Overall	12		6.5				
Barnacle laboratory	1 (PVC)	6	1.799	9.5	2.88	8.31	1	0.004*
	2 (Concrete)	6	1.000	3.5	-2.88			
	Overall	12		6.5				
Barnacle image	1 (PVC)	6	1.6152	9.5	2.88	8.34	1	0.004*
	2 (Concrete)	6	0.6946	3.5	-2.88			
	Overall	12		6.5				
Red algae *in situ*	1 (PVC)	6	0.000	4.0	-2.4	7.21	1	0.007*
	2 (Concrete)	6	0.39794	9.0	2.4			
	Overall	12		6.5				

* indicates significant at $p < 0.017$ (Bonferroni correction for multiple tests)

PERCENT COVER RANDOM POINT

ANOVA table

Source of variation		Df	MS	F	P
Barnacle laboratory	Substratum	1	6165.3	361.25	0.000*
	Error	10	17.1		
	Total	11			
Barnacle image	Substratum	1	5808.0	93.88	0.000*
	Error	10	61.9		
	Total	11			
Solitary ascidian laboratory	Substratum	1	5	0.03	0.859
	Error	10	161		
	Total	11			
Calcareous tube worm image	Substratum	1	2.5717	31.55	0.000*
	Error	10	0.0815		
	Total	11			
Erect bryozoan laboratory	Substratum	1	5.3	0.22	0.651
	Error	10	24.5		
	Total	11			
Erect bryozoan image	Substratum	1	5.3	0.45	0.515
	Error	10	11.7		
	Total	11			
Green algae laboratory	Substratum	1	2.068	7.54	0.021*
	Error	10	0.274		
	Total	11			
Green algae image	Substratum	1	588.0	10.16	0.010*
	Error	10	57.9		
	Total	11			
Red algae image	Substratum	1	33.3	2.36	0.156
	Error	10	14.1		
	Total	11			
S laboratory	Substratum	1	0.5733	23.05	0.000*
	Error	10	0.0249		
	Total	11			
S image	Substratum	1	10.08	5.99	0.034*
	Error	10	1.68		
	Total	11			

* indicates significant at $p < 0.05$

Kruskall Wallis table

	Substrata	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Solitary ascidian image	1 (PVC)	6	16.00	6.6	0.08	0.01	1	0.935
	2 (Concrete)	6	16.00	6.4	-0.08			
	Overall	12		6.5				
Calcareous tube worm laboratory	1 (PVC)	6	0.000	3.5	-2.88	10.29	1	0.001*
	2 (Concrete)	6	8.000	9.5	2.88			
	Overall	12		6.5				
Red algae laboratory	1 (PVC)	6	0.000	4.5	-1.92	5.28	1	0.022*
	2 (Concrete)	6	4.000	8.5	1.92			
	Overall	12		6.5				

* indicates significant at $p < 0.05$

Appendix II Results tables for chapter 3

Frequency distribution curves of the 0-1mm fraction of sediments from the 12 recruitment sites.

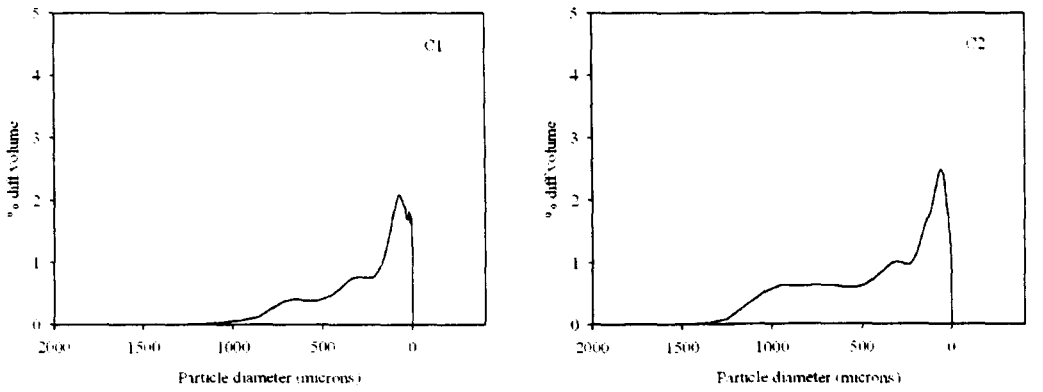

Figure 1 Frequency distribution plots for the 0-1mm size particle fraction of sediments from control sites. Both sites show poor to moderate sediment sorting.

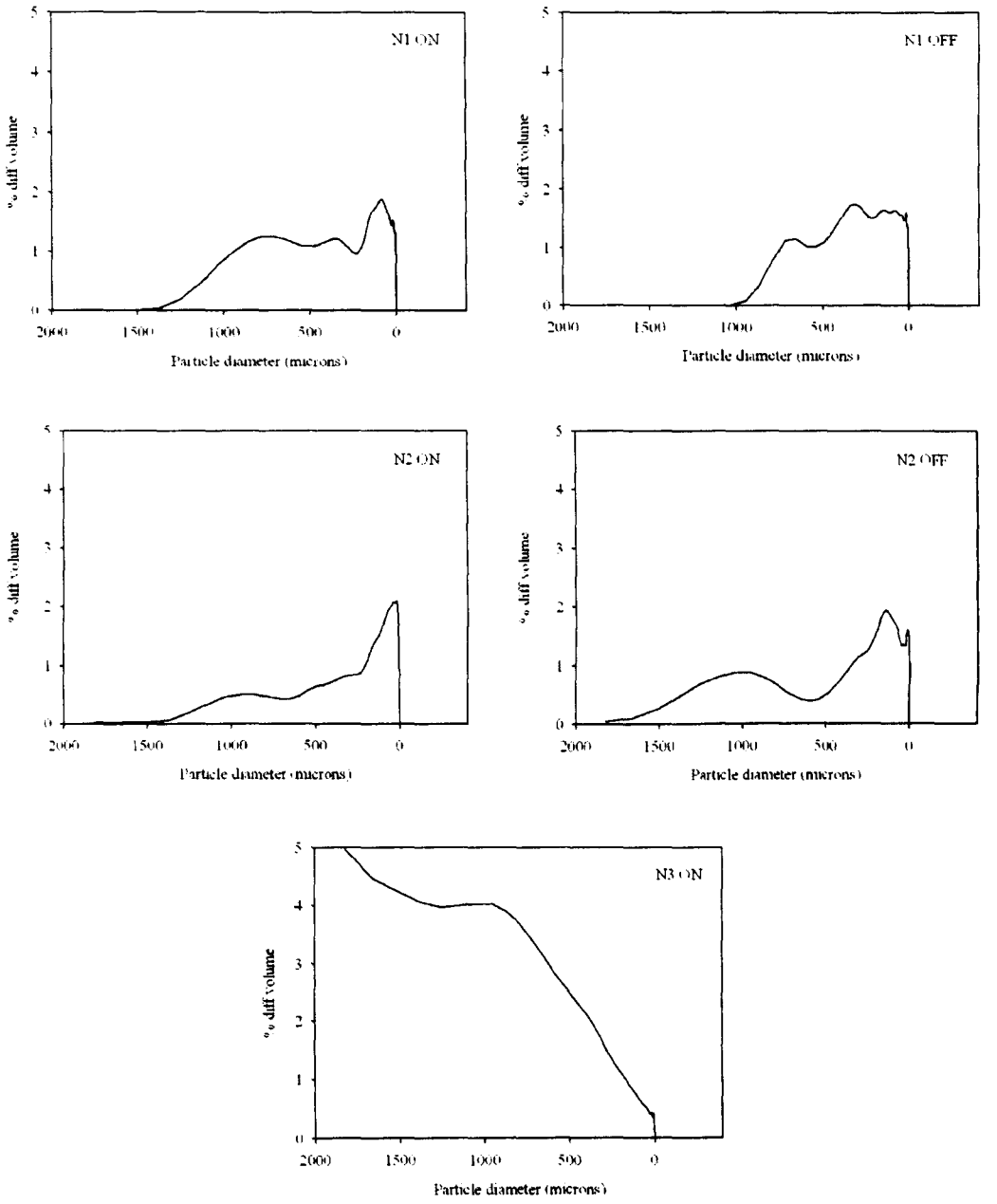

Figure 2 Frequency distribution plots for the 0-1mm size particle fraction of sediments from natural and natural off-reef sites. N1 ON and N2 OFF reef sites show bimodal and N1 OFF, N2 ON and N3 ON show poor sediment sorting.

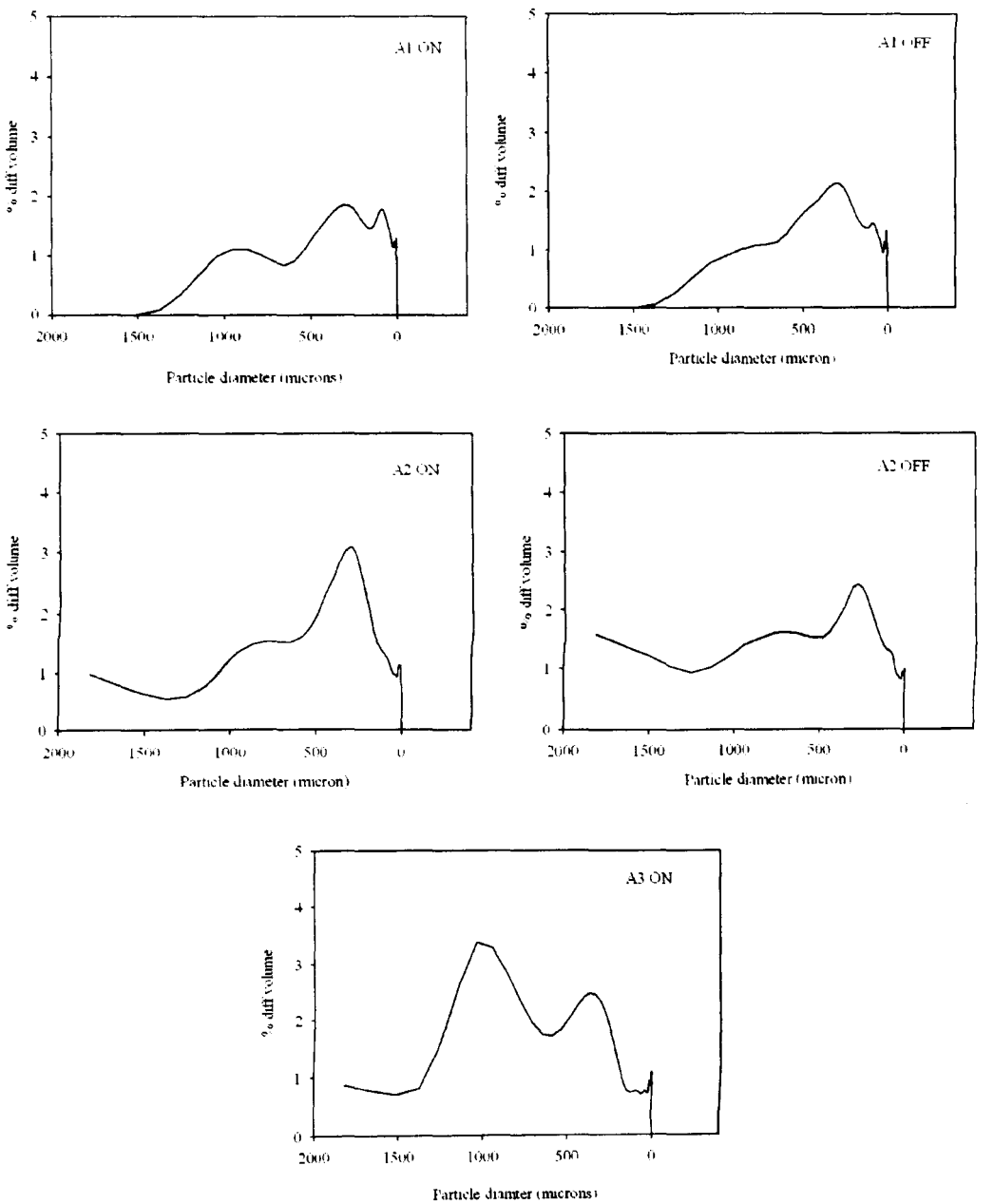

Figure 3 Frequency distribution plots for the 0-1mm size particle fraction of sediments from artificial and artificial off-reef sites. A1 ON and A3 ON show bimodal sediment sorting. A2 ON and A2 OFF reef sites show poor sorting and sediments from A1 OFF are poor to moderately sorted.

ANOVA TABLES

Epifaunal biomass results

Natural Dry weight					
Source	DF	SS	MS	F	P
Reef type	2	2261	1131	2.48	0.099
Error	33	15047	456		
Total	35	17308			
S = 21.35 R-Sq = 13.07% R-Sq(adj) = 7.80%					
Natural off-reef Dry weight					
Reef type	2	2927	1464	6.36	0.007*
Error	21	4834	230		
Total	23	7761			
S = 15.17 R-Sq = 37.72% R-Sq(adj) = 31.78%					
Artificial Dry weight					
Reef type	2	6642.3	3321.1	98.50	0.000*
Error	33	1112.7	33.7		
Total	35	7754.9			
S = 5.807 R-Sq = 85.65% R-Sq(adj) = 84.78%					
Artificial off-reef Dry weight					
Reef type	2	3308.7	1654.4	152.67	0.000*
Error	21	227.6	10.8		
Total	23	3536.3			
S = 3.292 R-Sq = 93.57% R-Sq(adj) = 92.95%					
Control Dry weight					
Reef type	2	537	287	1.71	0.205
Error	21	3523	168		
Total	23	4096			
S = 12.95 R-Sq = 13.99% R-Sq(adj) = 5.80%					
Natural Ash free dry wt					
Reef type	2	172.9	86.4	1.60	0.218
Error	33	1786.5	54.1		
Total	35	1959.3			
S = 7.358 R-Sq = 8.82% R-Sq(adj) = 3.30%					
Natural off-reef Ash free dry wt					
Reef type	2	204.9	102.4	1.92	0.172
Error	21	1123.0	53.5		
Total	23	1327.8			
S = 7.313 R-Sq = 15.43% R-Sq(adj) = 7.37%					
Artificial Ash free dry weight					
Reef type	2	27.837	13.919	70.92	0.000*
Error	33	6.477	0.196		
Total	35	34.314			
S = 0.4430 R-Sq = 81.12% R-Sq(adj) = 79.98%					
Artificial off-reef Ash free dry weight					
Reef type	2	22.882	11.441	82.58	0.000*
Error	21	2.910	0.139		
Total	23	25.791			
S = 0.3722 RSq = 88.72% R-Sq(adj) = 87.64%					

Control Ash free dry weight					
Reef type	2	17.96	8.98	2.17	0.140
Error	21	87.06	4.15		
Total	23	105.02			
S = 2.036 R-Sq = 17.10% R-Sq(adj) = 9.21%					

* indicates significance at $p < 0.05$

Kruskall Wallis tables for differences in species abundance between treatments.

Artificial sites

	Treatment	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Pomatoceros triqueter	Caged	12	154.0	11.8	-0.52	0.27	1	0.603
	Open	12	148.5	13.3	0.52			
	Caged	12	154.0	13.5	0.69	0.48	1	0.488
	Partial	12	135.0	11.5	-0.69			
	Open	12	148.5	14.3	1.27	1.61	1	0.204
	Partial	12	135.0	10.7	-1.27			
Hydroides elegans	Caged	12	46.0	9.0	-2.4	5.75	1	0.016*
	Open	12	64.0	16.0	2.4			
	Caged	12	46.0	12.0	-0.35	0.12	1	0.729
	Partial	12	50.0	13.0	0.35			
	Open	12	64.0	14.9	1.65	2.71	1	0.100
	Partial	12	50.0	10.1	-1.65			
Sinistral spirorbid	Caged	12	25.0	11.3	-0.84	0.70	1	0.402
	Open	12	36.0	13.7	0.84			
	Caged	12	25.0	12.2	-0.23	0.05	1	0.817
	Partial	12	32.5	12.8	0.23			
	Open	12	36.5	13.2	0.46	0.21	1	0.644
	Partial	12	32.5	11.8	-0.46			
Balanus crenatus	Caged	12	295.0	18.5	4.16	17.31	1	0.000*
	Open	12	5.50	6.5	-4.16			
	Caged	12	295.0	18.3	3.98	15.88	1	0.000*
	Partial	12	4.0	6.8	-3.98			
	Open	12	5.50	12.4	-0.09	0.01	1	0.931
	Partial	12	4.0	12.6	0.09			
Balanus crenatus scar	Caged	12	4.5	6.8	-3.98	15.89	1	0.000*
	Open	12	36.5	18.3	3.98			
	Caged	12	4.5	7.1	-3.75	14.10	1	0.000*
	Partial	12	82.5	17.9	3.75			
	Open	12	36.5	10.8	-1.15	1.33	1	0.248
	Partial	12	82.5	14.2	1.15			

Anomiidae	Caged	12	191.0	14.1	1.10	1.20	1	0.273
	Open	12	225.0	10.9	-1.10			
	Caged	12	191.0	10.6	-1.33	1.76	1	0.184
	Partial	12	341.5	14.4	1.33			
	Open	12	225.0	9.1	-2.34	5.47	1	0.019*
	Partial	12	341.5	15.9	2.34			
Bugula sp.	Caged	12	41.5	18.1	3.87	14.98	1	0.000*
	Open	12	9.5	6.9	-3.87			
	Caged	12	41.5	17.5	3.49	12.20	1	0.000*
	Partial	12	12.5	7.5	-3.49			
	Open	12	9.5	11.3	-0.84	0.70	1	0.402
	Partial	12	12.5	13.7	0.84			
Serpula vermicularis	Caged	12	22.00	12.1	-0.26	0.07	1	0.795
	Open	12	22.50	12.9	0.26			
	Caged	12	22.0	14.7	1.53	2.35	1	0.125
	Partial	12	9.5	10.3	-1.53			
	Open	12	22.5	14.8	1.56	2.44	1	0.119
	Partial	12	9.5	10.3	-1.56			
Filograna implexa	Caged	12	104.5	17.2	3.23	10.55	1	0.001*
	Open	12	6.5	7.8	-3.23			
	Caged	12	104.5	17.8	3.7	13.69	1	0.000*
	Partial	12	4.0	7.2	-3.7			
	Open	12	6.5	12.8	0.20	0.04	1	0.837
	Partial	12	4.0	12.2	-0.20			
Porifera sp.	Caged	12	43.0	18.5	4.16	17.36	1	0.000*
	Open	12	5.5	6.5	-4.16			
	Caged	12	43.0	18.5	4.16	17.31	1	0.000*
	Partial	12	8.0	6.5	-4.16			
	Open	12	5.50	10.8	-1.21	1.49	1	0.223
	Partial	12	8.00	14.3	1.21			
Ascidiella aspersa	Caged	12	0.00	10.3	-1.56	3.49	1	0.062
	Open	12	0.50	14.8	1.56			
	Caged	12	0.00	11.9	-0.40	0.33	1	0.568
	Partial	12	0.00	13.1	0.40			
	Open	12	0.50	14.2	1.18	1.87	1	0.171
	Partial	12	0.00	10.8	-1.18			
Fenestrulina malusii	Caged	12	5.0	6.8	-3.93	15.41	1	0.000*
	Open	12	21.0	18.2	3.93			
	Caged	12	5.0	6.5	-4.16	17.39	1	0.000*
	Partial	12	35.5	18.5	4.16			

	Open	12	21.0	8.8	-2.54	6.48	1	0.011*
	Partial	12	35.5	16.2	2.54			

* indicates significance at $p < 0.05$

Artificial off-reef sites

	Treatment	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Pomatoceros triqueter	Caged	8	142.5	7.9	-0.53	0.28	1	0.600
	Open	8	196.0	9.1	0.53			
	Caged	8	142.5	9.1	0.53	0.28	1	0.600
	Partial	8	68.5	7.9	-0.53			
	Open	8	196.0	12.5	3.36	11.31	1	0.001*
	Partial	8	68.5	4.5	-3.36			
Hydroides elegans	Caged	8	49.5	7.1	-1.16	1.34	1	0.247
	Open	8	56.5	9.9	1.16			
	Caged	8	49.50	11.5	2.52	6.35	1	0.012*
	Partial	8	31.50	5.5	-2.52			
	Open	8	56.50	11.8	2.78	7.77	1	0.005*
	Partial	8	31.50	5.2	-2.78			
Sinistral spirorbid	Caged	8	19.50	6.1	-2.0	3.98	1	0.046*
	Open	8	59.00	10.9	2.0			
	Caged	8	19.50	7.3	-1.05	1.10	1	0.293
	Partial	8	33.50	9.8	1.05			
	Open	8	59.0	9.9	1.21	1.46	1	0.226
	Partial	8	33.50	7.1	-1.21			
Balanus crenatus	Caged	8	497.0	12.5	3.36	11.29	1	0.001*
	Open	8	8.0	4.5	-3.36			
	Caged	8	497.0	12.5	3.36	11.48	1	0.001*
	Partial	8	1.5	4.5	-3.36			
	Open	8	8.0	11.2	2.26	5.10	1	0.022*
	Partial	8	1.5	5.8	-2.26			
Balanus crenatus scar	Caged	8	43.5	10.3	1.47	2.16	1	0.141
	Open	8	23.0	6.8	-1.47			
	Caged	8	43.5	9.2	0.58	0.33	1	0.563
	Partial	8	29.50	7.8	-0.58			
	Open	8	23.0	9.0	0.42	0.18	1	0.674
	Partial	8	29.5	8.0	-0.42			
Anomiidae	Caged	8	230.5	11.5	2.52	6.35	1	0.012*
	Open	8	71.0	5.5	-2.52			

	Caged	8	230.5	12.1	3.05	9.28	1	0.002*
	Partial	8	59.0	4.9	-3.05			
	Open	8	71.0	8.9	0.37	0.14	1	0.713
	Partial	8	59.0	8.1	-0.37			
Bugula sp.	Caged	8	67.0	12.1	3.05	9.28	1	0.002*
	Open	8	21.5	4.9	-3.05			
	Caged	8	67.0	12.5	3.36	11.33	1	0.001*
	Partial	8	9.0	4.5	-3.36			
	Open	8	21.5	9.9	1.21	1.47	1	0.226
	Partial	8	9.0	7.1	-1.21			
Serpula vermicularis	Caged	8	27.0	9.2	0.58	0.33	1	0.563
	Open	8	23.5	7.8	-0.58			
	Caged	8	27.0	11.4	2.42	5.85	1	0.016*
	Partial	8	12.0	5.6	-2.42			
	Open	8	23.5	10.1	1.37	1.87	1	0.171
	Partial	8	12.0	6.9	-1.37			
Fenestrulina malusii	Caged	8	10.5	5.3	-2.73	7.46	1	0.006*
	Open	8	73.5	11.8	2.73			
	Caged	8	10.5	9.4	0.74	0.54	1	0.461
	Partial	8	10.5	7.6	-0.74			
	Open	8	73.5	12.3	3.15	9.96	1	0.002*
	Partial	8	10.5	4.8	-3.15			
Filograna implexa	Caged	8	4.3 E+01	12.5	3.36	12.31	1	0.000*
	Open	8	0.00	4.5	-3.36			
	Caged	8	4.3 E+01	11.9	2.89	8.61	1	0.003*
	Partial	8	0.00	5.1	-2.89			
	Open	8	0.00	7.3	-1.0	1.72	1	0.190
	Partial	8	0.00	9.7	1.0			
Porifera sp.	Caged	8	15.0	11.4	2.47	6.12	1	0.013*
	Open	8	1.5	5.6	-2.47			
	Caged	8	15.0	11.2	2.26	5.12	1	0.024*
	Partial	8	3.5	5.8	-2.26			
	Open	8	1.5	7.1	-1.21	1.48	1	0.223
	Partial	8	3.5	9.9	1.21			
Ascidiella aspersa	Caged	8	1.0	11.5	2.52	.57	1	0.003*
	Open	8	0.0	5.5	-2.52			
	Caged	8	1.0	11.5	2.52	8.57	1	0.003*
	Partial	8	0.0	5.5	-2.52			
	Open	8	0.0	8.5	0.00	0.00	1	1.000
	Partial	8	0.0	8.5	0.00			

* indicates significance at $p < 0.05$

Control

	Treatment	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Pomatoceros triqueter	Caged	8	103.5	8.5	0.0	0.0	1	1.000
	Open	8	153.5	8.5	0.0			
	Caged	8	103.5	7.6	-0.79	0.62	1	0.431
	Partial	8	168.0	9.4	0.79			
	Open	8	153.5	7.0	-1.26	1.59	1	0.208
	Partial	8	168.0	10.0	1.26			
Hydroides elegans	Caged	8	98.0	11.4	2.42	5.84	1	0.016*
	Open	8	34.5	5.6	-2.42			
	Caged	8	98.0	8.6	0.11	0.01	1	0.916
	Partial	8	98.5	8.4	-0.11			
	Open	8	34.5	5.6	-2.42	5.84	1	0.016*
	Partial	8	98.5	11.4	2.42			
Sinistral spirorbid	Caged	8	18.5	8.5	0.0	0.00	1	1.000
	Open	8	21.0	8.5	0.0			
	Caged	8	18.5	7.9	-0.53	0.28	1	0.599
	Partial	8	22.5	9.1	0.53			
	Open	8	21.0	7.4	-0.89	0.80	1	0.371
	Partial	8	22.5	9.6	0.89			
Balanus crenatus	Caged	8	23.0	6.0	-2.10	4.41	1	0.036*
	Open	8	328.5	11.0	2.10			
	Caged	8	23.0	7.3	-1.05	1.10	1	0.294
	Partial	8	63.5	9.8	1.05			
	Open	8	328.5	10.4	1.63	2.65	1	0.103
	Partial	8	63.5	6.6	-1.63			
Balanus crenatus scar	Caged	8	0.5	4.6	-3.31	11.19	1	0.001*
	Open	8	42.0	12.4	3.31			
	Caged	8	0.5	5.4	-2.63	7.21	1	0.007*
	Partial	8	9.5	11.6	2.63			
	Open	8	42.0	10.3	1.52	2.33	1	0.127
	Partial	8	9.5	6.7	-1.52			
Anomiidae	Caged	8	294.5	9.3	0.63	0.40	1	0.528
	Open	8	256.5	7.8	-0.63			
	Caged	8	294.5	8.9	0.32	0.10	1	0.753
	Partial	8	283.5	8.1	-0.32			
	Open	8	256.5	8.5	0.00	0.00	1	1.000
	Partial	8	283.5	8.5				

Bugula sp.	Caged	8	15.0	7.4	-0.89	0.8	1	0.371
	Open	8	29.5	9.6	0.89			
	Caged	8	15.0	7.0	-1.26	1.59	1	0.207
	Partial	8	27.5	10.0	1.26			
	Open	8	29.5	7.9	-0.53	0.28	1	0.598
	Partial	8	27.5	9.1	0.53			
Serpula vermicularis	Caged	8	30.0	9.0	0.42	0.18	1	0.673
	Open	8	23.0	8.0	-0.42			
	Caged	8	30.0	8.5	0.0	0.00	1	1.000
	Partial	8	36.5	8.5	0.0			
	Open	8	23.0	6.8	-1.47	2.17	1	0.141
	Partial	8	36.5	10.3	1.47			
Fenestrulina malusii	Caged	8	6.0	8.4	-0.05	0.00	1	0.958
	Open	8	29.0	8.6	0.05			
	Caged	8	6.0	8.4	-0.11	0.01	1	0.916
	Partial	8	8.0	8.6	0.11			
	Open	8	29.0	9.1	0.53	0.28	1	0.594
	Partial	8	8.0	7.9	-0.53			
Filograna implexa	Caged	8	0.00	7.9	-0.53	0.41	1	0.523
	Open	8	0.00	9.1	0.53			
	Caged	8	0.00	8.5	0.00	0.00	1	1.000
	Partial	8	0.00	8.5	0.00			
	Open	8	0.00	9.1	0.53	0.41	1	0.523
	Partial	8	0.00	7.9	-0.53			
Porifera sp.	Caged	8	15.5	10.1	1.31	1.76	1	0.184
	Open	8	2.5	6.9	-1.31			
	Caged	8	15.5	10.3	1.52	2.36	1	0.124
	Partial	8	3.0	6.7	-1.52			
	Open	8	2.5	9.4	0.74	0.55	1	0.458
	Partial	8	3.0	7.6	-0.74			
Ascidiella aspersa	Caged	8	0.0	8.1	-0.37	0.16	1	0.685
	Open	8	0.5	8.9	0.37			
	Caged	8	0.0	9.3	0.63	0.59	1	0.442
	Partial	8	0.0	7.8	-0.63			
	Open	8	0.5	9.9	1.16	1.78	1	0.183
	Partial	8	0.0	7.1	-1.16			

* indicates significance at $p < 0.05$

Natural sites

	Treatment	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Pomatoceros triqueter	Caged	12	246.0	14.4	1.33	1.76	1	0.184
	Open	12	109.5	10.6	-1.33			
	Caged	12	246.0	11.0	-1.04	1.08	1	0.299
	Partial	12	293.5	14.0	1.04			
	Open	12	109.5	9.9	-1.79	3.21	1	0.073
	Partial	12	293.5	15.1	1.79			
Hydroides elegans	Caged	12	68.5	13.8	0.89	0.80	1	0.371
	Open	12	64.5	11.2	-0.89			
	Caged	12	68.5	14.3	1.27	1.61	1	0.204
	Partial	12	57.5	10.7	-1.27			
	Open	12	64.5	12.0	-0.38	0.14	1	0.707
	Partial	12	57.5	13.0	0.38			
Sinistral spirorbid	Caged	12	8.5	9.4	-2.17	4.73	1	0.030*
	Open	12	44.0	15.6	2.17			
	Caged	12	8.5	9.5	-2.11	4.43	1	0.035*
	Partial	12	34.5	15.5	2.11			
	Open	12	44.0	14.3	1.27	1.62	1	0.203
	Partial	12	34.5	10.7	-1.27			
Balanus crenatus	Caged	12	65.0	14.1	1.10	1.20	1	0.272
	Open	12	32.5	10.9	-1.10			
	Caged	12	65.0	14.7	1.53	2.35	1	0.126
	Partial	12	10.0	10.3	-1.53			
	Open	12	32.5	13.4	0.61	0.37	1	0.544
	Partial	12	10.0	11.6	-0.61			
Balanus crenatus scar	Caged	12	3.0	11.5	-0.69	0.51	1	0.477
	Open	12	25.5	13.5	0.69			
	Caged	12	3.0	11.9	-0.40	0.17	1	0.684
	Partial	12	6.0	13.1	0.40			
	Open	12	25.5	14.2	1.15	1.35	1	0.246
	Partial	12	6.0	10.8	-1.15			
Anomiidae	Caged	12	179.5	16.4	2.71	7.36	1	0.007*
	Open	12	61.5	8.6	-2.71			
	Caged	12	179.5	13.8	0.92	0.85	1	0.356
	Partial	12	77.5	11.2	-0.92			
	Open	12	61.5	11.0	-1.07	1.14	1	0.285
	Partial	12	77.5	14.0	1.07			

Bugula sp.	Caged	12	6.5	14.0	1.04	1.09	1	0.297
	Open	12	5.5	11.0	-1.04			
	Caged	12	6.5	12.5	0.0	0.0	1	1.000
	Partial	12	9.0	12.5	0.0			
	Open	12	5.5	9.8	-1.85	3.44	1	0.064
	Partial	12	9.0	15.2	1.85			
Serpula vermicularis	Caged	12	27.0	14.0	1.07	1.14	1	0.285
	Open	12	12.0	11.0	-1.07			
	Caged	12	27.0	10.3	-1.5	2.26	1	0.133
	Partial	12	34.0	14.7	1.5			
	Open	12	12.0	9.2	-2.31	5.35	1	0.021*
	Partial	12	34.0	15.8	2.31			
Fenestrulina malusii	Caged	12	7.0	9.7	-1.96	3.95	1	0.047
	Open	12	39.0	15.3	1.96			
	Caged	12	7.0	11.0	-1.07	1.17	1	0.279
	Partial	12	12.0	14.0	1.07			
	Open	12	39.0	14.5	1.36	1.88	1	0.171
	Partial	12	12.0	10.5	-1.36			
Filograna implexa	Caged	12	0.0	14.2	1.15	2.64	1	0.104
	Open	12	0.0	10.8	-1.15			
	Caged	12	0.0	14.2	1.15	2.64	1	0.104
	Partial	12	0.0	10.8	-1.15			
	Open	12	0.0	12.5	0.03	0.00	1	0.952
	Partial	12	0.0	12.5	-0.03			
Porifera sp.	Caged	12	1.5	15.0	1.73	3.36	1	0.067
	Open	12	0.0	10.0	-1.73			
	Caged	12	1.5	11.6	-0.64	0.41	1	0.520
	Partial	12	3.0	13.4	0.64			
	Open	12	0.0	8.3	-2.94	9.32	1	0.002*
	Partial	12	3.0	16.8	2.94			
Ascidiella aspersa	Caged	12	18.5	13.8	0.87	0.76	1	0.383
	Open	12	8.0	11.3	-0.87			
	Caged	12	18.5	15.0	1.73	3.17	1	0.075
	Partial	12	0.5	10.0	-1.73			
	Open	12	8.0	14.5	1.39	2.03	1	0.154
	Partial	12	0.5	10.5	-1.39			

* indicates significance at $p < 0.05$

Natural off-reef sites

	Treatment	N	Median	Ave Rank	Z	H	Df	P (adjusted for ties)
Pomatoceros triqueter	Caged	8	174.0	10.9	2.0	3.98	1	0.046*
	Open	8	58.5	6.1	-2.0			
	Caged	8	174.0	11.4	2.42	5.87	1	0.015*
	Partial	8	54.0	5.6	-2.42			
	Open	8	58.5	9.7	1.0	1.0	1	0.317
	Partial	8	54.0	7.3	-1.0			
Hydroides elegans	Caged	8	135.5	12.1	3.05	9.29	1	0.002*
	Open	8	62.0	4.9	-3.05			
	Caged	8	135.5	11.4	2.42	5.83	1	0.016*
	Partial	8	59.0	5.6	-2.42			
	Open	8	62.0	9.0	0.42	0.18	1	0.674
	Partial	8	59.0	8.0	-0.42			
Sinistral spirorbid	Caged	8	22.0	7.7	-0.68	0.47	1	0.495
	Open	8	40.0	9.3	0.68			
	Caged	8	22.0	8.3	-0.16	0.02	1	0.875
	Partial	8	23.5	8.7	0.16			
	Open	8	40.0	9.3	0.68	0.47	1	0.495
	Partial	8	23.5	7.7	-0.68			
Balanus crenatus	Caged	8	30.0	11.7	2.68	7.33	1	0.007*
	Open	8	0.5	5.3	-2.68			
	Caged	8	30.0	9.9	1.16	1.34	1	0.247
	Partial	8	10.5	7.1	-1.16			
	Open	8	0.5	6.1	-2.05	4.29	1	0.038*
	Partial	8	10.5	10.9	2.05			
Balanus crenatus scar	Caged	8	0.0	6.8	-1.47	3.2	1	0.074
	Open	8	4.9E+01	10.3	1.47			
	Caged	8	0.0	6.8	-1.47	3.2	1	0.074
	Partial	8	6.85E+01	10.3	1.47			
	Open	8	49.0	8.5	0.0	0.0	1	1.000
	Partial	8	68.5	8.5	0.0			
Anomiidae	Caged	8	162.5	10.5	1.68	2.82	1	0.093
	Open	8	42.5	6.5	-1.68			
	Caged	8	162.5	10.8	1.89	3.57	1	0.059
	Partial	8	32.0	6.3	-1.89			
	Open	8	42.5	8.5	0.0	0.0	1	1.000
	Partial	8	32.0	8.5	0.0			

Bugula sp.	Caged	8	4.0	9.7	1.0	1.05	1	0.305
	Open	8	3.0	7.3	-1.0			
	Caged	8	4.0	8.6	0.05	0.0	1	0.958
	Partial	8	4.5	8.4	-0.05			
	Open	8	3.0	8.0	-0.42	0.18	1	0.669
	Partial	8	4.5	9.0	0.42			
Serpula vermicularis	Caged	8	24.5	9.9	1.21	1.46	1	0.226
	Open	8	6.0	7.1	-1.21			
	Caged	8	24.5	10.5	1.68	2.88	1	0.090
	Partial	8	3.5	6.5	-1.68			
	Open	8	6.0	9.4	0.79	0.63	1	0.426
	Partial	8	3.5	7.6	-0.79			
Fenestrulina malusii	Caged	8	5.0	8.0	-0.42	0.20	1	0.654
	Open	8	19.0	9.0	0.42			
	Caged	8	5.0	8.3	-0.21	0.05	1	0.829
	Partial	8	7.0	8.8	0.21			
	Open	8	19.0	9.0	0.42	0.19	1	0.666
	Partial	8	7.0	8.0	-0.42			
Filograna implexa	Caged	8	3.0	10.0	1.26	2.10	1	0.147
	Open	8	0.0	7.0	-1.26			
	Caged	8	3.0	10.5	1.68	4.87	1	0.027*
	Partial	8	0.0	6.5	-1.68			
	Open	8	0.0	9.5	0.84	2.14	1	0.143
	Partial	8	0.0	7.5	-0.84			
Porifera sp.	Caged	8	12.5	9.3	0.63	0.43	1	0.510
	Open	8	1.0	7.8	-0.63			
	Caged	8	1.25E+01	10.1	1.26			
	Partial	8	0.0	7.0	-1.26	2.10	1	0.148
	Open	8	1.0	9.9	1.21	1.79	1	0.181
	Partial	8	0.0	7.1	-1.21			
Ascidiella aspersa	Caged	8	10.0	7.8	-0.63	0.43	1	0.510
	Open	8	25.0	9.3	0.63			
	Caged	8	10.0	9.7	1.0	1.09	1	0.297
	Partial	8	4.5	7.3	-1.0			
	Open	8	25.0	9.5	0.84	0.81	1	0.369
	Partial	8	4.5	7.5	-0.84			

* indicates significance at $p < 0.05$

SIMPER RESULTS:

Natural sites

Open		Caged		Partial	
Taxa	% Cont.	Taxa	% Cont.	Taxa	% Cont.
Pomatoceros triqueter	15.85	Anomiidae	15.57	*Pomatoceros triqueter*	15.44
Hydroides elegans	13.34	*Pomatoceros triqueter*	15.43	Anomiidae	12.74
Anomiidae	12.92	*Hydroides elegans*	13.90	*Hydroides elegans*	12.39
Sinistral spirorbid	7.59	*Balanus crenatus*	8.41	*Serpula vermicularis*	8.85
Serpula vermicularis	7.18	*Serpula vermicularis*	6.47	Sinistral spirorbid	6.61
Balanus crenatus	6.99	*Ascidiella aspersa*	5.73	*Bugula* sp.	5.94
Fenestrulina malusii	5.33	*Bugula* sp.	5.58	*Balanus crenatus*	5.45
Bugula sp.	4.66	Sinistral spirorbid	3.91	*Balanus crenatus* scar	4.36
Balanus crenatus scar	4.33	Terebellid	2.87	*Callopora dumerilii*	4.10
Asicidella aspersa	4.14	*Fenestrulina malusii*	2.60	*Fenestrulina malusii*	3.62
Microporella ciliata	3.51	Tubulipora	2.35	Tubulipora	3.20
Modiolarka tumida	3.21	*Balanus crenatus* scar	2.25	*Microporella ciliata*	3.15
Callopora dumerillii	2.53	*Callopora dumerillii*	2.23	Porifera spp.	2.86
		Modiolarka tumida	2.20	Dextral spirorbid	1.75
		Porifera spp.	1.77		

Species causing dissimilarity between open and caged:
Balanus crenatus scar, *Balanus crenatus, Fenestrulina malusii, Modiolarka tumida*, Sinistral spirorbid, *Ascidiella aspersa, Microporella ciliata*, Byrozoan ancestrulae, Anomiidae, Terebellid, Porifera spp., *Serpula vermicularis*, Tubulipora, *Bugula* sp., *Filograna implexa, Pomatoceros triqueter*, Dextral spirorbid, *Callopora dumerilii, Ascidiella scabra, Smittoidea reticulata, Corella paralelogramma, Protula tubularia, Escharoides coccinea, Hydroides elegans*, Scallop, *Verruca stroemia, Electra pilosa, Botryllus schlosseri*, Didemnid/tridídemnid, *Escharella immersa*, Lichenopora, Juv mussel, Bivalve (long, oblong),

Species causing dissimilarity between open and partial:
Balanus crenatus scar, *Fenestrulina malusii, Balanus crenatus, Modiolarka tumida, Ascidiella aspersa*, sinistral spirorbid, *Microporella ciliata*, Porifera spp,.Tubulipora, bryozoan ancestrulae, anomiidae, terebellid, *Serpula vermicularis*, dextral spirorbid, *Botryllus schlosseri, Callopora dumerilii, Pomatoceros triqueter, Bugula* sp., Didembid/tridídemnid, Lichenopora, *Hydroides elegans*, scallop, *Escharella immersa, Ascidiella scabra, Electra pilosa, Pomatoceros lamarki, Elminius modestus, Verruca stroemia*, newly settled colonial ascidian, *Smittoidea reticulata, Clavelina lepadiformis, Haplopoma sciaphilum, Escharoides coccinea.*

Species causing dissimilarity between caged and partial:
Balanus crenatus, Ascidiella aspersa, Balanus crenatus scar, *Modiolarka tumida, Fenestrulina malusii*, sinistral spirorbid, *Microporella ciliata*, Porifera spp., *Tubulipora, terebellid, Serpula vermicularis*, anomiidae, *dextral spirorbid*, bryozoan ancestrulae, *Bugula* sp., *Callopora dumerilii, Filograna implexa, Botryllus schlosseri, Pomatoceros triqueter, Smittoidea reticulata, Ascidiella scabra*, Lichenopora, scallop, *Escharoides coccinea, Verruca stroemia, Protula tubularia*, didemnid/tridídemnid, *Corella paralelogramma, Escharella immersa, Hydroides elegans, Pomatoceros lamarki, Electra pilosa, Dendrodoa grossularia, Haplopoma sciaphilum, Hiatella arctica.*

Natural off-reef sites

Open		Caged		Partial	
Taxa	% Cont.	Taxa	% Cont.	Taxa	% Cont.
Hydroides elegans	18.70	*Hydroides elegans*	17.38	*Pomatoceros triqueter*	16.34
Pomatoceros triqueter	17.14	*Pomatoceros triqueter*	17.16	Anomiidae	14.23
Anomiidae	11.01	Anomiidae	14.18	*Hydroides elegans*	12.43
Sinistral spirorbid	9.80	*Balanus crenatus*	7.44	Sinistral spirorbid	9.86
Modiolarca tumida	5.66	Sinistral spirorbid	7.22	*Balanus crenatus*	6.83
Ascidiella aspersa	5.23	*Serpula vermicularis*	6.83	*Serpula vermicularis*	6.23
Serpula vermicularis	4.64	Tubulipora	4.54	*Balanus crenatus* scar	4.91
Balanus crenatus scar	3.68	*Ascidiella aspersa*	3.84	*Bugula* sp.	4.83
Terebellid	3.50	*Modiolarka tumida*	3.18	*Fenestrulina malusii*	3.58
Tubulipora	2.96	Terebellid	2.64	Tublipora	3.58
Fenestrulina malusii	2.71	*Bugula* sp.	2.35	Bryozoan ancestrulae	3.09
Callopora dumerillii	2.46	Porifera spp.	2.00	*Ascidiella aspersa*	2.57
Bryozoan ancestrulae	1.70	*Fenestrulina malusii*	1.61	*Callopora dumerilii*	2.55
Dextral spirorbid	1.69				

Species causing dissmiliarity between caged and partial:
Balanus crenatus scar, *Balanus crenatus, Ascidiella aspersa, Modiolarca tumida, Fenestrulina malusii*, Porifera spp., *Hydroides elegans*, Bryozoan ancestrulae, *Filograna implexa, Bugula* sp., Terebellid, *Serpula vermicularis*, Sinistral spirorbid, Anomiidae, Tubulipora, *Pomatoceros triqueter*, dextral spirorbid, *Microporella ciliata, Callopora dumerilii*, polychaete in mud tube, juv. Mussel, *Verruca stroemia, Escharoides coccinea, Sabella pavonia*, scallop, *Lichenopora,,Haplopoma sciaphilum*

Species causing dissimilarity between caged and open:
Balanus crenatus, Balanus crenatus scar, *Modiolarka tumida, Ascidiella aspersa, Fenestrulina malusii*, anomiidae, sinistral spirorbid, Porifera spp., *Serpula vermicularis, Bugula* sp., *Filograna implexa*, Terebellid, dextral spirorbid, bryozoan ancestrulae, *Microporella ciliata*, Tubulipora, *Pomatoceros triqueter, Callopora dumerillii*, polychaete in mud tube, juv mussel, *Hydroides elegans, Escharoides elegans, Escharoides coccinea, Sabella pavonia, Sipunculid, Escharella ventricosa*, bivalve (long, oblong), Lichenopora, *Verruca stroemia*

Species causing dissimilarity between partial and open:
Balanus crenatus scar, *Modiolarka tumida, Ascidiella aspersa, Balanus crenatus, Fenestrulina malusii*, sinistral spirorbid, Terebellid, bryozoan ancestrulae, Anomiidae, dextral spirorbid, *Bugula* sp., *Microporella ciliata, Hydroides elegans, Serpula vermicularis, Callopora dumerillii, Pomatoceros triqueter*, Porifera spp., Tubulipora, *Sabella pavonia, Escharella ventricosa*, bivalve (long, oblong), Sipunculid, Lichenopora, scallop, *Haplopoma sciaphilum*

Artificial off-reef sites

Open		Caged		Partial	
Taxa	% Cont.	Taxa	% Cont.	Taxa	% Cont.
Pomatoceros triqueter	11.61	*Balanus crenatus*	13.19	*Pomatoceros triqueter*	12.76
Hydroides elegans	9.08	Anomiidae	10.72	Anomiidae	12.12
Fenestrulina malusii	8.46	*Pomatoceros triqueter*	8.94	*Hydroides elegans*	9.93
Sinistral spirorbid	8.17	*Bugula* sp.	8.59	Sinistral spirorbid	9.60
Anomiidae	8.14	*Hydroides elegans*	8.43	*Serpula vermicularis*	7.20
Balanus crenatus scar	6.90	*Balanus crenatus* scar	7.73	Tubulipora	6.45
Serpula vermicularis	5.99	*Filograna implexa*	7.11	*Bugula* sp.	6.01
Microporella ciliata	5.20	*Serpula vermicularis*	6.39	*Fenestrulina malusii*	5.14
Bugula sp.	4.85	Porifera spp.	4.68	*Microporella ciliata*	4.31
Bryozoan ancestrulae	4.41	*Fenestrulina malusii*	4.45	Bryozoan ancestrulae	4.23
Tubulipora	4.34	Sinistral spirorbid	4.19	*Balanus crenatus* scar	4.23
Balanus crenatus	4.25	Tubulipora	3.10	Dextral spirorbid	3.73
Callopora dumerilii	4.00	*Callopora dumerilii*	2.71	Porifera spp.	3.65
Dextral spirorbid	3.23			Lichenopora	2.79
Electra pilosa	1.58				

Species causing dissimilarity between caged and partial:
Balanus crenatus, Filograna implexa, Bugula sp., *Balanus crenatus* scar, *Microporella ciliata,* dextral spirorbid, bryozoan ancestrulae, sinistral spirorbid, Porifera spp., Anomiidae, *Escharoides coccinea, Fenestrulina malusii, Pomatoceros triqueter, Escharella immersa,* Lichenopora, *Haplopoma sciaphilum,* juv mussel, *Serpula vermicularis,* Tubulipora, *Modiolarka tumida, Ascidiella aspersa, Verruca stroemia, Callopora dumerilii, Hiatella arctica, Hydroides elegans, Callopora aurita,* scallop, *Smittoidea reticulata, Escharella ventricosa*

Species causing dissimilarity between caged and open:
Filograna implexa, Balanus crenatus, Microporella ciliata, Porifera spp., *Fenestrulina malusii,* sinistral spirorbid, *Bugula* sp., dextral spirorbid, Anomiidae, *Electra pilosa,* bryozoan ancestrulae, *Escharoides coccinea, Pomatoceros triqueter, Escharella ventricosa,* Lichenopora, Tubulipora, *Haplopoma sciaphilum,* juv mussel, *Balanus crenatus* scar, *Escharella immersa, Modiolarka tumida, Callopora dumerillii, Serpula vermicularis, Ascidiella aspersa, Veruca stroemia, Hiatella arctica,* scallop, *Botryllus schlosseri, Callopora craticula, Hippoporina pertusa,* didemnid/tridemnid

Species causing dissimilarity between partial and open:
Fenestrulina malusii, Balanus crenatus, Balanus crenatus scar, *Electra pilosa, Filograna implexa, Callopora dumerilii,* Porifera spp., *Bugula* sp., *Pomatoceros triqueter,* dextral spirorbid, *Haplopoma sciaphilum, Microporella ciliata, Escharella immersa,* bryozoan ancestrulae, *Escharella ventricosa,* sinistral spirorbid, *Serpula vermicularis,* Anomiidae, *Escharoides coccinea, Hydroides elegans,* Lichenpora, *Callopora aurita, Botryllus schlosseri, Hippoporina pertusa,* Tubulipora, *Callopora craticula, Modiolarca tumida,* scallop.

Artificial sites

Open		Caged		Partial	
Taxa	% Cont.	Taxa	% Cont.	Taxa	% Cont.
Anomiidae	10.96	*Balanus crenatus*	10.91	Anomiidae	12.12
Pomatoceros triqueter	10.76	Anomiidae	10.90	*Pomatoceros triqueter*	9.54
Hydroides elegans	8.93	*Pomatoceros triqueter*	10.10	*Hydroides elegans*	7.96
Balanus crenatus scar	7.17	*Filograna implexa*	7.80	*Fenestrulina malusii*	7.91
Sinistral spirorbid	6.97	Porifera spp.	7.54	*Balanus crenatus* scar	7.91
Serpula vermicularis	6.57	*Hydroides elegans*	7.53	Sinistral spirorbid	6.75
Fenestrulina malusii	6.41	*Bugula* sp.	7.11	*Serpula vermicularis*	4.93
Mcroporella ciliata	4.40	*Serpula vermicularis*	6.07	Tubulipora	4.85
Tubulipora	4.28	Sinistral spirorbid	5.56	*Bugula* sp.	4.74
Bugula sp.	4.08	*Fenestrulina malusii*	3.33	Bryozoan ancestrulae	4.14
Bryozoan ancestrulae	3.78	Tubulipora	3.16	*Callopora dumerilii*	4.13
Callopora dumerilii	3.75	*Escharoides coccinea*	2.92	Porifera spp.	3.90
Porifera spp.	3.30	*Balanus crenatus*	2.03	*Escharoides coccinea*	3.51
Balanus crenatus	2.92	*Hiatella arctica*	1.98	*Microporella ciliata*	2.84
Electra pilosa	2.65	Scallop	1.68	*Balanus crenatus*	2.64
Escharoides coccinea	1.85	Juv mussel	1.53	Dextral spirorbid	2.41
Filograna implexa	1.72				

Species causing differences between partial and caged:
Balanus crenatus, Filograna implexa, Balanus crenatus scar, *Fenestrulina malusii*, Porifera spp., *Microporella ciliata, Bryozoan ancestrulae, Bugula* sp., *Callopora dumerilii, Smittoidea reticulata, Hiatella arctica*, Scallop, Juv mussel, *Escharoides coccinea*, Sinistral spirorbid, Lichenopora, *Serpula vermicularis, Verruca stroemia*, Anomiidae, Tubulipora, Dextral spirorbid, *Modiolarca tumida, Escharella ventricosa, Callopora aurita, Pomatoceros triqueter, Escharella immersa, Haplopoma sciaphilum, Hydroides elegans, Pomatoceros lamarki, Hippoporina pertusa, Corella paralelogramma*, Polychaete in sand tube

Species causing dissimilarity between partial and open:
Filograna implexa, Balanus crenatus, Electra pilosa, Balanus crenatus scar, *Escharoides coccinea, Microporella ciliata, Smittoidea reticulata*, Anomidea, *Serpula vermicularis*, Lichenopora, *Haplopoma sciaphilum, Bugula* sp., Porifera spp., *Pomatoceros triqueter*, Sinistral spirorbid, *Callopora dumerilii, Callopora aurita, Escharella immersa*, Tubulipora, *Escharella ventricosa*, Bryozoan ancestrulae, Didemnid/tridemnid, Dextral spirorbid, *Modiolarka tumida, Fenestrulina malusii, Ascidiella aspersa, Callopora craticula, Hydroides elegans, Botryllus schlosseri, Corella paralelogramma*, Polychaete in sand tube, *Hippoporina pertusa*, UID bryozoan, Scallop, *Dendrodoa grossularia*

Species causing dissimilarity between caged and open:
Balanus crenatus, Filograna implexa, Balanus crenatus scar, Porifera spp., *Bugula* sp., *Electra pilosa, Microporella ciliata, Fenestrulina malusii*, Bryozoan ancestrulae, *Hiatella arctica*, Juv mussel, *Smittoidea reticulata, Callopora dumerilii*, sinistral spirorbid, scallop, *Haplopoma sciaphilum*, Tubulipora, Lichenopora, *Escharella ventricosa, Verruca stroemia, Modiolarka tumida, Escharoides coccinea*, dextral spirorbid, didemnid/tridemnid, *Escharella immersa*, Anomiidae, *Callopora craticula, Ascidiella aspersa, Pomatoceros lamarki, Botryllus schlosseri, Callopora aurita, Hydroides elegans*, polychaete in sand tube

Control sites

Open		Caged		Partial	
Taxa	% Cont.	Taxa	% Cont.	Taxa	% Cont.
Anomiidae	15.44	Anomiidae	16.73	Anomiidae	16.34
Balanus crenatus	15.04	*Hydroides elegans*	13.76	*Hydroides elegans*	13.05
Pomatoceros triqueter	10.06	*Pomatoceros triqueter*	13.18	*Pomatoceros triqueter*	12.82
Balanus crenatus scar	9.90	*Serpula vermicuaris*	10.42	*Balanus crenatus*	8.76
Hydroides elegans	8.87	Sinistral spirorbid	8.58	*Serpula vermicularis*	8.73
Bugula sp.	5.56	*Callopora dumerilii*	6.61	Sinistral spirorbid	7.12
Serpula vermicularis	5.27	Tubulipora	5.36	*Callopora dumerilii*	6.45
Porifera spp.	3.39	Porifera spp.	4.99	*Bugula* sp.	5.84
Sinistral spirorbid	3.20	*Balanus crenatus*	4.35	*Balanus crenatus* scar	4.94
Ascidiella scabra	3.02	*Bugula* sp.	3.94	Tubulipora	4.64
Fenestrulina malusii	2.66	*Fenestrulina malusii*	3.59	Bryozoan ancestrulae	2.87
Callopora dumerilii	1.97				
Tubulipora	1.83				
Polychaete in sand tube	1.48				
Lichenopora	1.38				
Scallop	1.37				

Species causing dissimilarity between caged and partial:
Balanus crenatus scar, *Balanus crenatus*, Porifera spp. *Bugula* sp., *Fenestrulina malusii*, *Pomatoceros triqueter*, *Sinistral spirorbid*, Bryozoan ancestrulae, *Filograna implexa*, Tubulipora, *Callopora dumerilii*, *Microporella ciliata*, *Ascidiella scabra*, *Serpula vermicularis*, Anomiidae, *Ascidiella aspersa*, *Corella paralelogramma*, *Hydroides elegans*, *Protula tubularia*, *Modiolarca tumida*, Juv mussel, *Verruca stroemia*, dextral spirorbid, Lichenopora, *Escharoides coccinea*, *Apomatis similes*, *Dendrodoa grossularia*, *Sabella pavonia*, scallop, *Elminius modestus*, UID bryozoan, Terebellid, *Haplopoma sciaphilum*

Species causing dissimilarity between caged and open:
Balanus crenatus scar, *Balanus crenatus*, *Fenestrulina malusii*, Sinistral spirorbid, *Bugula* sp., *Callopora dumerilii*, *Pomatoceros triqueter*, *Hydroides elegans*, Tubulipora, *Serpula vermicualaris*, Porifera spp., *Filograna implexa*, Anomiidae, Byrozoan ancestrulae, *Microporella ciliata*, *Ascidiella scabra*, *Verruca stroemia*, *Ascidiella aspersa*, Polychaete in sand tube, *Sabella pavonia*, Scallop, *Hiatella arctica*, Lichenopora, Dextral spirorbid, *Electra pilosa*, *Corella paralelogramma*, *Apomatis similis*, Juv mussel, *Protularia tubuliaria*, *Modiolarca tumida*, *Dendrodoa grossularia*

Species causing dissimilarity between partial and open:
Balanus crenatus, *Fenestrulina malusii*, Sinistral spirorbid, *Balanus crenatus* scar, *Pomatoceros triqueter*, *Callopora dumerilii*, *Bugula* sp., *Hydroides elegans*, *Serpula vermicularis*, *Ascidiella scabra*, Porifera spp., *Filograna implexa*, Anomiidae, bryozoan ancestrulae, Tubulipora, *Microporella ciliata*, *Sabella pavonia*, polychaete in sand tube, *Verruca stroemia*, scallop, *Ascidiella aspersa*, dextral spirorbid, *Hiatella arctica*, *Electra pilosa*, juv mussel, Lichenopora, *Apomatis similis*, *Modiolarca tumida*, *Dendrodoa grossularia*, *Escharoides coccinea*

Appendix III Results tables for chapter 4

Seasonal predation

One-way ANOVA tables: Epifaunal biomass

Autumn (August to October 2003)

Natural Dry weight					
Source	DF	SS	MS	F	P
Treatment	2	29.57	14.79	9.05	0.001 *
Error	33	53.97	1.63		
Total	35	83.49			
S = 1.278 R-Sq = 35.42% R-Sq (adj) = 31.50%					
Artificial Dry weight					
Treatment	2	7.11	3.55	3.32	0.049 *
Error	33	35.36	1.07		
Total	35	42.47			
S = 1.035 R-Sq = 16.73% R-Sq (adj) = 11.69%					
Natural Ash free dry weight					
Treatment	2	0.2850	0.1425	3.32	0.049 *
Error	33	1.4178	0.0430		
Total	35	1.7028			
S = 0.2073 R-Sq = 16.74% R-Sq(adj) = 11.69%					
Artificial Ash free dry weight					
Treatment	2	0.0821	0.0410	2.03	0.147
Error	33	0.6659	0.0202		
Total	35	0.7480			
S = 0.1421 R-Sq = 10.97% R-Sq(adj) = 5.58%					

* indicates significance at $p < 0.05$

Winter (October 03 to January 04)

Natural Dry weight					
Source	DF	SS	MS	F	P
Treatment	2	0.000321	0.000160	0.64	0.535
Error	33	0.008317	0.000252		
Total	35	0.008638			
S = 0.01588 R-Sq = 3.71% R-Sq (adj) = 0.00%					
Artificial Dry weight					
Treatment	2	0.005712	0.002856	11.92	0.000 *
Error	33	0.007910	0.000240		
Total	35	0.013623			
S = 0.01548 R-Sq = 41.93% R-Sq (adj) = 38.41%					
Natural Ash free dry weight					
Treatment	2	0.0000155	0.0000078	0.49	0.615
Error	33	0.0005185	0.0000157		
Total	35	0.005340			
S = 0.003964 R-Sq = 2.90% R-Sq(adj) = 0.00%					
Artificial Ash free dry weight					
Treatment	2	0.0000549	0.0000274	1.75	0.190
Error	33	0.0005187	0.0000157		
Total	35	0.0005736			
S = 0.003964 R-Sq = 9.57% R-Sq(adj) = 4.09%					

* indicates significance at $p < 0.05$

Spring (January to April 04)

Natural Dry weight					
Source	DF	SS	*MS*	*F*	*P*
Treatment	2	0.000567	0.000284	*2.03*	*0.148*
Error	33	0.004616	0.000140		
Total	35	0.005184			
S = 0.01183 R-Sq = 10.95% R-Sq (adj) = 5.55%					
Artificial Dry weight					
Treatment	2	0.0374	0.0187	1.05	0.362
Error	33	0.5882	0.0178		
Total	35	0.6256			
S = 0.1335 R-Sq = 5.97% R-Sq (adj) = 0.27%					
Natural Ash free dry weight					
Treatment	2	0.0000682	0.0000341	0.66	0.526
Error	33	0.0017168	0.0000520		
Total	35	0.0017850			
S = 0.007213 R-Sq = 3.82% R-Sq(adj) = 0.00%					
Artificial Ash free dry weight					
Treatment	2	0.0003012	0.0001506	3.82	0.032
Error	33	0.0013016	0.0000394		
Total	35	0.0016028			
S = 0.006280 R-Sq = 18.79% R-Sq(adj) = 13.87%					

* indicates significance at $p < 0.05$

Summer (April to August 04)

Natural Dry weight					
Source	DF	SS	MS	F	P
Treatment	2	0.40	0.20	0.11	0.897
Error	33	53.05	1.83		
Total	35	53.45			
S = 1.353 R-Sq = 0.74% R-Sq (adj) = 0.00%					
Artificial Dry weight					
Treatment	2	14.33	7.17	4.34	0.021 *
Error	33	54.48	1.65		
Total	35	68.81			
S = 1.285 R-Sq = 20.83% R-Sq (adj) =16.03%					
Natural Ash free dry weight					
Treatment	2	0.031	0.015	0.12	0.891
Error	33	3.841	0.132		
Total	35	3.872			
S = 0.3639 R-Sq = 0.79% R-Sq(adj) = 0.00%					
Artificial Ash free dry weight					
Treatment	2	0.9241	0.4620	6.41	0.004 *
Error	33	2.3772	0.0720		
Total	35	3.3013			
S = 0.2684 R-Sq = 27.99% R-Sq(adj) = 23.63%					

* indicates significance at $p < 0.05$

Seasonal larval supply (caged data)
2-way nested ANOVA: Epifaunal biomass

Autumn

Dry weight					
Source	DF	SS	Adj MS	F	P
Reef type	1	6.5846	6.5846	1.06	0.362
Site (Reef type)	4	24.9410	6.2352	16.78	0.000 *
Error	18	6.6890	0.3716		
Total	23	38.2145			
S = 0.609599 R-Sq = 82.50% R-Sq (adj) = 77.63%					
Ash free dry weight					
Reef type	1	0.055970	0.055970	0.55	0.500
Site (Reef type)	4	0.408402	0.102100	10.50	0.000 *
Error	18	0.274946	0.009719		
Total	23	0.630318			
S = 0.0985862 R-Sq = 72.64% R-Sq(adj) = 65.03%					

* indicates significance at $p < 0.05$

Winter

Dry weight					
Source	DF	SS	MS	F	P
Reef type	1	0.0010010	0.0010010	2.11	0.220
Site (Reef type)	4	0.0018982	0.0004745	2.20	0.110
Error	18	0.0038797	0.0002155		
Total	23	0.0067790			
S = 0.0146813 R-Sq = 42.77% R-Sq(adj) = 26.87%					
Ash free dry weight					
Reef type	1	0.0000060	0.0000060	0.29	0.617
Site (Reef type)	4	0.0000820	0.0000205	1.30	0.308
Error	18	0.0002840	0.0000158		
Total	23	0.0003720			
S = 0.00397213 R-Sq = 23.66% R-Sq(adj) = 2.45%					

* indicates significance at $p < 0.05$

Spring

Dry weight					
Source	DF	SS	MS	F	P
Reef type	1	0.03060	0.03060	1.08	0.358
Site (Reef type)	4	0.11359	0.02840	1.08	0.394
Error	18	0.47178	0.02621		
Total	23	0.61598			
S = 0.161895 R-Sq = 23.41% R-Sq(adj) = 2.13%					
Ash free dry weight					
Reef type	1	0.0000667	0.0000667	3.16	0.150
Site (Reef type)	4	0.0000843	0.0000211	0.47	0.755
Error	18	0.0008035	0.0000446		
Total	23	0.0009545			
S = 0.00668123 R-Sq = 15.82% R-Sq(adj) = 0.00%					

* indicates significance at $p < 0.05$

Summer

Dry weight					
Source	DF	SS	MS	F	P
Reef type	1	1.192	1.192	0.23	0.659
Site (Reef type)	4	21.127	5.282	3.33	0.033 *
Error	18	28.530	1.585		
Total	23	50.849			
S = 1.25896 R-Sq = 43.89% R-Sq(adj) = 28.31%					
Ash free dry weight					
Reef type	1	0.06752	0.06752	0.13	0.741
Site (Reef type)	4	2.14456	0.53614	6.51	0.002 *
Error	18	1.48307	0.08239		
Total	23	3.69515			
S = 0.287041 R-Sq = 59.86% R-Sq(adj) = 48.72%					

* indicates significance at $p < 0.05$

Two-way nested ANOVA for seasonal diversity indices

Autumn

S					
Source	DF	SS	MS	F	P
Reef type	1	15.042	15.042	1.70	0.262
Site (Reef type)	4	35.333	8.833	2.33	0.095
Error	18	68.250	3.792		
Total	23	118.625			
S = 1.94722 R-Sq = 42.47% R-Sq(adj) = 26.48%					
H					
Reef type	1	0.00484	0.00484	0.02	0.888
Site (Reef type)	4	0.86305	0.21576	17.93	0.000 *
Error	18	0.21656	0.01203		
Total	23	1.08445			
S = 0.109687 R-Sq = 80.03% R-Sq(adj) = 74.48%					
N					
Reef type	1	366548	366548	0.88	0.402
Site (Reef type)	4	1673340	418335	11.77	0.000 *
Error	18	639704	35539		
Total	23	2679593			
S = 188.518 R-Sq = 76.13% R-Sq(adj) = 69.50%					

* indicates significance at $p < 0.05$

Winter

S					
Source	DF	SS	MS	F	P
Reef type	1	135.375	135.375	9.97	0.034 *
Site (Reef type)	4	54.333	13.583	9.31	0.000 *
Error	18	26.250	1.458		
Total	23	215.958			
S = 1.20761 R-Sq = 87.84% R-Sq(adj) = 84.47%					
H					
Reef type	1	0.10400	0.10400	0.26	0.638
Site (Reef type)	4	1.61017	0.40254	47.20	0.000 *
Error	18	0.15350	0.00853		
Total	23	1.86767			
S = 0.0923463 R-Sq = 91.78% R-Sq(adj) = 89.50%					
N					
Reef type	1	237805	237805	1.36	0.308
Site (Reef type)	4	698087	174522	65.77	0.000 *
Error	18	47763	2654		
Total	23	983655			
S = 51.5123 R-Sq = 95.14% R-Sq(adj) = 93.80%					

* indicates significance at $p < 0.05$

Spring

S					
Source	DF	SS	MS	F	P
Reef type	1	8.167	8.167	1.12	0.350
Site (Reef type)	4	29.167	7.292	4.69	0.009 *
Error	18	28.000	1.556		
Total	23	65.333			
S = 1.24722 R-Sq = 57.14% R-Sq(adj) = 45.24%					
H					
Reef type	1	0.00258	0.00258	0.01	0.928
Site (Reef type)	4	1.12884	0.28221	13.71	0.000 *
Error	18	0.37040	0.02058		
Total	23	1.50181			
S = 0.143449 R-Sq = 75.34% R-Sq(adj) = 68.49%					
N					
Reef type	1	1.38701	1.38701	2.77	0.171
Site (Reef type)	4	2.00220	0.50055	77.34	0.000 *
Error	18	0.11649	0.00647		
Total	23	3.50570			
S = 0.0804472 R-Sq = 96.68% R-Sq(adj) = 95.75%					

* indicates significance at $p < 0.05$

Summer

S					
Source	DF	SS	MS	F	P
Reef type	1	40.042	40.042	0.63	0.472
Site (Reef type)	4	254.167	63.542	22.99	0.000 *
Error	18	49.750	2.764		
Total	23	343.958			
S = 1.66249 R-Sq = 85.54% R-Sq(adj) = 81.52%					
H					
Reef type	1	0.48258	0.48258	2.66	0.178
Site (Reef type)	4	0.72555	0.18139	16.38	0.000 *
Error	18	0.19928	0.01107		
Total	23	1.40741			
S = 0.105219 R-Sq = 85.84% R-Sq(adj) = 81.91%					
N					
Reef type	1	156655	156655	0.18	0.693
Site (Reef type)	4	3482369	870592	14.16	0.000 *
Error	18	1106460	61470		
Total	23	4745485			
S = 247.931 R-Sq = 76.68% R-Sq(adj) = 70.21%					

* indicates significance at $p < 0.05$

Seasonal SIMPER results (caged data)

Autumn caged

Artificial (Av similiarity = 84.52)		Natural (Av similarity = 73.58)	
Taxa	% Contr.	Taxa	% Contr.
Anomiidae	15.89	Anomiidae	16.34
Sinistral spirorbid	13.22	*Pomatoceros* sp.	12.55
Pomatoceros sp.	10.76	Sinistral spirorbid	12.53
Hydroides elegans	9.14	*Hydroides elegans*	9.88
Tubulipora	8.54	*Bugula* sp.	7.73
Bugula sp.	7.79	Bryozoan ancestrulae	6.77
Porifera spp.	7.57	Tubulipora	4.74
Lichenopora	5.77	Lichenopora	4.57
Bryozoan ancestrulae	4.63	Porifera spp.	3.87
Microporella ciliata	3.91	*Microporella ciliata*	3.27
Unidentified bryozoan	2.48	Unidentified bryozoan	2.74
Haplopoma sciaphilum	2.18	*Modiolarka tumida*	2.26
		Callopora craticula	2.17
		Callopora dumerilii	2.16

Taxa causing dissimilarity between artificial and natural (average dissimilarity 24.85)
Microporella ciliata, Tubulipora, Sinistral spirorbid, *Bugula* sp. , *Ascidiella aspersa*, Porifera spp., *Haplopoma sciaphilum*, *Fenestrulina malusii*, Bryozoan ancestrulae, *Callopora craticula*, Unidentified bryozoan, *Callopora dumerilii*, Lichenopora, Small solitary ascidian, *Electra pilosa*, *Modiolarka tumida*, *Escharoides coccinea*, Worm in sand tube, Anomiidae, Newly settled barnacle, *Hydroides elegans*, *Escharella immersa*.

Winter caged

Artificial (Av similiarity = 81.00)		Natural (Av similarity = 67.42)	
Taxa	% Contr.	Taxa	% Contr.
Sinistral spirorbid	22.45	Sinistral spirorbid	33.66
Hydroides elegans	11.50	*Hydroides elegans*	21.37
Dextral spirorbid	10.36	Dextral spirorbid	11.87
Tubulipora	10.24	Tubulipora	11.14
Microporella ciliata	9.41	*Pomatoceros* sp.	4.69
Pomatoceros sp.	7.76	Anomiidae	4.55
Anomiidae	5.69	*Haplopoma sciaphilum*	4.20
Bryozoan ancestrulae	5.64		
Fenestrulina malusii	4.61		
Haplopoma sciaphilum	4.19		

Taxa causing dissimilarity between artificial and natural (average dissimilarity 34.26) *Microporella ciliata*, Anomiidae, *Fenestrulina malusii*, *Pomatoceros* sp., *Haplopoma sciaphilum*, Dextral spirorbid, Sinistral spirorbid, Tubulipora, *Callopora dumerilii*, Bryozoan ancestrulae, Porifera spp., Newly settled barnacle, Unidentified bryozoan, Small solitary ascidian, *Escharoides coccinea*

Spring caged

Artificial (Av similiarity = 72.92)		Natural (Av similarity = 53.38)	
Taxa	% Contr.	Taxa	% Contr.
Sinistral spirorbid	48.01	Sinistral spirorbid	43.80
Tubulipora	29.51	Small solitary ascidian	19.11
Electra pilosa	11.79	*Hydroides elegans*	11.28
Small solitary ascidian	3.42	*Electra pilosa*	8.87
		Tubulipora	8.67

Taxa causing dissimilarity between artificial and natural (average dissimilarity 44.99): Tubulipora, Sinistral spirorbid, Small solitary ascidian, *Electra pilosa*, Newly settled barnacle, *Hydroides elegans*, Dextral spirorbid, *Haplopoma sciaphilum*, Bryozoan ancestrulae, *Microporella ciliata*.

Summer caged

Artificial (Av similiarity = 76.78)		Natural (Av similarity = 72.12)	
Taxa	% Contr.	Taxa	% Contr.
Pomatoceros sp.	14.76	*Pomatoceros* sp.	16.49
Sinistral spirorbid	13.10	*Hydroides elegans*	14.73
Hydroides elegans	12.10	Anomiidae	11.17
Anomiidae	9.58	Sinistral spirorbid	8.91
Lichenopora	7.66	*Ascidiella aspersa*	8.88
Electra pilosa	7.55	Anthozoa juv	6.66
Tubulipora	6.42	*Corella paralelogramma*	5.85
Bryozoan ancestrulae	3.68	Tubulipora	3.69
Callopora dumerilii	2.64	*Balanus crenatus*	3.53
Dextral spirorbid	2.52	Lichenopora	3.12
Balanus crenatus	2.30	*Electra pilosa*	2.97
Bugula sp.	2.24	Porifera spp.	2.71
Anthozoa juv	2.10	Bryozoan ancestrulae	2.49
Microporella ciliata	2.01		

Escharoides coccinea	1.60

Taxa causing dissimilarity between artificial and natural (average dissimilarity 33.06) *Ascidiella aspersa*, Sinistral spirorbid, Lichenopora, Anthozoa juv, *Electra pilosa*, *Corella paralelogramma*, Tubulipora, Porifera spp., *Microporella ciliata*, Worm in sand tube, small solitary ascidian, dextral spirorbid, *Ascidiella scabra*, *Balanus crenatus*, *Botryllus schlosseri*, *Pomatoceros* sp., *Callopora dumerilii*, *Escharoides coccinea*, Anomiidae, *Bugula* sp., *Ciona intestinalis*, Bryozoan ancestrulae, *Haplopoma sciaphilum*, *Escharella immersa*, *Fenestrulina malusii*, Didemnid/tridemnid

Seasonal taxonomic two-way nested AVOVA results

Autumn

ANOVA: log abundance *Pomatoceros triqueter*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.109880	0.109880	1.29	0.320
Site (reef type)	4	0.341836	0.095459	19.39	0.000 *
Error	18	0.079352	0.004408		
Total	23	0.531069			

S = 0.0663963 R-Sq = 85.06% R-Sq(adj) = 80.91%

ANOVA: log abundance *Hydroides elegans*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.03855	0.03855	0.22	0.663
Site (reef type)	4	0.69757	017439	25.24	0.00 *
Error	18	0.12435	0.00691		
Total	23	0.86048			

S = 0.0831162 R-Sq = 85.55% R-Sq(adj) = 81.53%

ANOVA: Sinistral spirorbid abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	438210	438210	0.73	0.440
Site (reef type)	4	2385273	596318	18.97	0.000 *
Error	18	565814	31434		
Total	23	3389297			

S = 177.297 R-Sq = 83.31% R-Sq(adj) = 78.67%

ANOVA: Dextral spirorbid abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	1.0417	1.0417	1.09	0.356
Site (reef type)	4	3.8333	0.9583	1.35	0.289
Error	18	12.7500	0.7083		
Total	23	17.6250			

S = 0.841625 R-Sq = 27.66% R-Sq(adj) = 7.57%

ANOVA: log abundance Anomiidae

Source	Df	SS	Adj MS	F	P
Reef type	1	0.18055	0.18005	1.48	0.291
Site (reef type)	4	0.48675	0.12169	24.38	0.000 *
Error	18	0.08983	0.00499		
Total	23	0.75662			

S = 0.0706432 R-Sq = 88.13% R-Sq(adj) = 84.83%

ANOVA: log abundance Porifera spp.

Source	Df	SS	Adj MS	F	P
Reef type	1	1.55692	1.55692	2.43	0.194
Site (reef type)	4	2.55893	0.63973	20.25	0.000 *
Error	18	0.56875	0.03160		

Total	23	4.68459			
S = 0.177755 R-Sq = 87.86% R-Sq(adj) = 84.49%					

ANOVA: *Ascidiella aspersa* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	108.38	108.38	4.42	0.103
Site (reef type)	4	98.00	24.50	2.32	0.096
Error	18	190.25	10.57		
Total	23	396.63			
S = 3.25107 R-Sq = 52.03% R-Sq(adj) = 38.71%					

ANOVA: *Corella paralelogramma* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	1.0417	1.0417	1.32	0.315
Site (reef type)	4	3.1667	0.7917	1.21	0.340
Error	18	11.7500	0.6528		
Total	23	15.9583			
S = 0.807947 R-Sq = 26.37% R-Sq(adj) = 5.92%					

ANOVA: Solitary ascidian (small) abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	30.375	30.375	1.83	0.248
Site (reef type)	4	66.500	16.625	12.60	0.000 *
Error	18	23.750	1.319		
Total	23	120.625			
S = 1.14867 R-Sq = 80.31% R-Sq(adj) = 74.84%					

ANOVA: *Bugula* sp. abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	7597	7594	0.25	0.646
Site (reef type)	4	123748	30937	107.65	0.000 *
Error	18	5173	287		
Total	23	136518			
S = 16.9521 R-Sq = 96.21% R-Sq(adj) = 95.16%					

ANOVA: log abundance Tubiliopra

Source	Df	SS	Adj MS	F	P
Reef type	1	0.5055	0.5055	0.33	0.595
Site (reef type)	4	6.0667	1.5167	73.24	0.000 *
Error	18	0.3727	0.0207		
Total	23	0.69449			
S = 0.143904 R-Sq = 94.63% R-Sq(adj) = 93.14%					

ANOVA: Lichenopora abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	40.04	40.04	0.13	0.732
Site (reef type)	4	1189.83	297.46	8.97	0.000 *
Error	18	596.75	33.15		
Total	23	1826.63			
S = 5.75784 R-Sq = 67.33% R-Sq(adj) = 58.26%					

ANOVA: *Callopora craticula* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	80.667	80.667	3.01	0.158
Site (reef type)	4	107.333	26.833	8.94	0.000 *
Error	18	54.000	3.000		
Total	23	242.000			
S = 1.73205 R-Sq = 77.69% R-Sq(adj) = 71.49%					

ANOVA: log abundance *Callopora dumerilii*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.33501	0.33501	0.59	0.487
Site (reef type)	4	2.28930	0.57232	21.46	0.000 *
Error	18	0.47995	0.02666		
Total	23	3.10426			

S = 0.163290 R-Sq = 84.54% R-Sq(adj) = 80.24%

ANOVA: *Haplopoma sciaphilum* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	5.042	5.042	0.05	0.839
Site (reef type)	4	431.167	107.792	15.07	0.000 *
Error	18	128.750	7.153		
Total	23	564.958			

S = 2.67447 R-Sq = 77.21% R-Sq(adj) = 70.88%

ANOVA: log abundance *Microporella ciliata*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.0896	0.0896	0.04	0.856
Site (reef type)	4	9.6316	2.4079	101.85	0.000 *
Error	18	0.4256	0.0236		
Total	23	10.1468			

S = 0.153760 R-Sq = 95.81% R-Sq(adj) = 94.64%

ANOVA: log abundance *Fenestrulina malusii*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.73942	0.73942	1.21	0.333
Site (reef type)	4	2.44420	0.61105	17.11	0.000 *
Error	18	0.64271	0.03571		
Total	23	3.82633			

S = 0.188961 R-Sq = 83.20% R-Sq(adj) = 78.54%

ANOVA: *Escharoides coccinea* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.167	0.167	0.02	0.890
Site (reef type)	4	30.667	7.667	5.21	0.006 *
Error	18	26.500	1.492		
Total	23	57.333			

S = 1.21335 R-Sq = 53.78% R-Sq(adj) = 40.94%

ANOVA: *Electra pilosa* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	13.500	13.500	0.72	0.445
Site (reef type)	4	75.500	18.875	14.77	0.000 *
Error	18	23.000	1.278		
Total	23	112.000			

S = 1.13039 R-Sq = 79.46% R-Sq(adj) = 73.76%

ANOVA: *Modiolarca tumida* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	1.500	1.500	0.31	0.607
Site (reef type)	4	19.333	4.833	1.02	0.422
Error	18	85.000	4.722		
Total	23	105.833			

S = 2.17307 R-Sq = 19.69% R-Sq(adj) = 0.00%

* indicates significance at $p < 0.05$

Winter

ANOVA: *Pomatoceros triqueter* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	352.67	352.67	6.96	0.058
Site (reef type)	4	202.67	50.67	7.86	0.001 *
Error	18	116.00	6.44		
Total	23	671.33			

S = 2.53859 R-Sq = 82.72% R-Sq(adj) = 77.92%

ANOVA: log abundance *Hydroides elegans*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.01818	0.01818	0.20	0.678
Site (reef type)	4	0.36486	0.09121	8.63	0.000 *
Error	18	0.19033	0.01057		
Total	23	0.57337			

S = 0.102830 R-Sq = 66.80% R-Sq(adj) = 57.58%

ANOVA: Sinistral spirorbid abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	114402	114402	0.74	0.438
Site (reef type)	4	646789	154197	97.52	0.000 *
Error	18	28460	1581		
Total	23	759651			

S = 39.7634 R-Sq = 96.25% R-Sq(adj) = 95.21%

ANOVA: Dextral spirorbid abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	1162.04	1162.04	3.28	0.144
Site (reef type)	4	1417.33	354.33	14.10	0.000 *
Error	18	452.25	25.13		
Total	23	3031.63			

S = 5.01248 R-Sq = 85.08% R-Sq(adj) = 80.94%

ANOVA: Anomiidae abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	260.04	260.14	0.86	0.407
Site (reef type)	4	1215.83	303.96	25.13	0.000 *
Error	18	217.75	12.10		
Total	23	1693.63			

S = 3.47811 R-Sq = 87.14% R-Sq(adj) = 83.57%

ANOVA: Porifera spp. abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	18.375	18.375	1.87	0.243
Site (reef type)	4	39.333	9.833	3.04	0.045 *
Error	18	58.250	3.236		
Total	23	115.958			

S = 1.79892 R-Sq = 49.77% R-Sq(adj) = 35.81%

ANOVA: Solitary ascidian (small) abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	3.3750	3.3750	1.09	0.355
Site (reef type)	4	12.3333	3.0833	4.53	0.010 *
Error	18	12.2500	0.6806		
Total	23	27.9583			

S = 0.824958 R-Sq = 56.18% R-Sq(adj) = 44.01%

ANOVA: *Bugula* sp. abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.1667	0.1667	1.00	0.374
Site (reef type)	4	0.6667	0.1667	1.20	0.345
Error	18	2.5000	0.1389		
Total	23	3.3333			

S = 0.372678 R-Sq = 25.00% R-Sq(adj) = 4.17%

ANOVA: Tubulipora abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	400.17	400.17	0.72	0.443
Site (reef type)	4	2211.67	552.92	47.39	0.000 *
Error	18	210.00	11.67		
Total	23	2821.83			

S = 3.41565 R-Sq = 92.56% R-Sq(adj) = 90.49%

ANOVA: log abundance *Callopora dumerilii*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.99445	0.99445	24.70	0.008 *
Site (reef type)	4	0.16102	0.04025	1.02	0.425
Error	18	0.71304	0.03961		
Total	23	1.86850			

S = 0.199031 R-Sq = 61.84% R-Sq(adj) = 51.24%

ANOVA: log abundance *Haplopoma sciaphilum*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.10389	0.10389	0.11	0.761
Site (reef type)	4	3.92923	0.98231	14.71	0.000 *
Error	18	1.20218	0.06679		
Total	23	5.23529			

S = 0.258433 R-Sq = 77.04% R-Sq(adj) = 70.66%

ANOVA: *Microporella ciliata* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	816.67	816.67	16.87	0.015 *
Site (reef type)	4	193.67	48.42	8.14	0.001 *
Error	18	107.00	5.94		
Total	23	1117.33			

S = 2.43812 R-Sq = 90.42% R-Sq(adj) = 87.76%

ANOVA: *Fenestrulina malusii* log abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	2.05083	2.05083	31.18	0.005 *
Site (reef type)	4	0.26311	0.06578	3.04	0.045 *
Error	18	0.38973	0.02165		
Total	23	2.70367			

S = 1.147146 R-Sq = 85.59% R-Sq(adj) = 81.58%

ANOVA: *Escharoides coccinea* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	2.6667	2.6667	1.88	0.242
Site (reef type)	4	5.6667	1.4167	3.40	0.031 *
Error	18	7.5000	0.4167		
Total	23	15.8333			

S = 0.645497 R-Sq = 52.63% R-Sq(adj) = 39.47%

ANOVA: *Electra pilosa* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.1667	0.1667	1.00	0.374

Site (reef type)	4	0.6667	0.1667	1.20	0.345
Error	18	2.5000	0.1389		
Total	23	3.3333			
S = 0.372678 R-Sq = 25.00% R-Sq(adj) = 4.17%					

ANOVA: *Modiolarca tumida* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.37500	0.37500	3.00	0.158
Site (reef type)	4	0.50000	0.12500	1.27	0.312
Error	18	1.75000	0.09722		
Total	23	2.62500			
S = 0.311805 R-Sq = 33.33% R-Sq(adj) = 14.81%					

* indicates significance at $p < 0.05$

Spring

ANOVA: *Hydroides elegans* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.3750	0.3750	0.06	0.813
Site (reef type)	4	23.5000	5.8750	7.69	0.001 *
Error	18	13.7500	0.7639		
Total	23	37.6250			
S = 0.0874007 R-Sq = 63.46% R-Sq(adj) = 53.30%					

ANOVA: log abundance Sinistral spirrobid

Source	Df	SS	Adj MS	F	P
Reef type	1	2.2271	2.2271	1.57	0.279
Site (reef type)	4	5.6862	1.4215	57.31	0.000 *
Error	18	0.4465	0.0248		
Total	23	8.3598			
S = 0.157493 R-Sq = 94.66% R-Sq(adj) = 93.18%					

ANOVA: Dextral spirorbid abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.375	0.375	0.08	0.786
Site (reef type)	4	17.833	4.458	4.28	0.013 *
Error	18	18.750	1.042		
Total	23	36.958			
S = 1.02062 R-Sq = 49.27% R-Sq(adj) = 35.17%					

ANOVA: Solitary ascidian (small) abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	2.667	2.667	0.05	0.837
Site (reef type)	4	220.333	55.083	11.95	0.000 *
Error	18	83.000	4.611		
Total	23	306.000			
S = 2.14735 R-Sq = 72.88% R-Sq(adj) = 65.34%					

ANOVA: sqrt abundance Tubulipora

Source	Df	SS	Adj MS	F	P
Reef type	1	62.896	62.896	9.43	0.037 *
Site (reef type)	4	26.672	6.668	20.95	0.000 *
Error	18	5.729	0.318		
Total	23	95.297			
S = 0.564143 R-Sq = 93.99% R-Sq(adj) = 92.32%					

ANOVA: *Haplopoma sciaphilum* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.6667	0.6667	2.29	0.205

Site (reef type)	4	1.1667	0.2917	1.50	0.244
Error	18	3.5000	0.1944		
Total	23	5.3333			
S = 0.440959 R-Sq = 34.38% R-Sq(adj) = 16.15%					

ANOVA: *Microporella ciliata* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.1667	0.1667	1.00	0.374
Site (reef type)	4	0.6667	0.1667	0.67	0.623
Error	18	4.5000	0.2500		
Total	23	5.3333			
S = 0.5 R-Sq = 15.63% R-Sq(adj) = 0.00%					

ANOVA: *Escharoides coccinea* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.04167	0.04167	0.20	0.678
Site (reef type)	4	0.83333	0.20833	2.14	0.117
Error	18	1.75000	0.09722		
Total	23	2.62500			
S = 0.311805 R-Sq = 33.33% R-Sq(adj) = 14.81%					

ANOVA: *Electra pilosa* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	16.667	16.667	2.11	0.220
Site (reef type)	4	31.667	7.917	4.91	0.007 *
Error	18	29.000	1.611		
Total	23	77.333			
S = 1.26930 R-Sq = 62.50% R-Sq(adj) = 52.08%					

* indicates significance at $p < 0.05$

Summer

ANOVA: log abundance *Pomatoceros triqueter*

Source	Df	SS	Adj MS	F	P
Reef type	1	0.09219	0.09219	0.22	0.664
Site (reef type)	4	1.68474	0.42118	39.30	0.000 *
Error	18	0.19291	0.01072		
Total	23	1.96984			
S = 0.103525 R-Sq = 90.21% R-Sq(adj) = 87.49%					

ANOVA: log abundance *Hydroides elegans*

Source	Df	SS	Adj MS	F	P
Reef type	1	9963	9963	1.03	0.368
Site (reef type)	4	38732	9683	4.27	0.013 *
Error	18	40772	2265		
Total	23	89467			
S = 47.5930 R-Sq = 54.43% R-Sq(adj) = 41.77%					

ANOVA: log abundance Sinistral spirorbid

Source	Df	SS	Adj MS	F	P
Reef type	1	2.8452	2.8452	1.12	0.349
Site (reef type)	4	10.1535	2.5384	96.24	0.000 *
Error	18	0.4748	0.0264		
Total	23	13.4735			
S = 0.162405 R-Sq = 96.48% R-Sq(adj) = 95.50%					

ANOVA: log abundance dextral spirorbid

Source	Df	SS	Adj MS	F	P
Reef type	1	0.88242	0.88242	3.37	0.140

Site (reef type)	4	1.04846	0.26212	8.20	0.001 *
Error	18	0.57503	0.03195		
Total	23	2.50591			
S = 0.178735 R-Sq = 77.05% R-Sq(adj) = 70.68%					

ANOVA: Anomiidae abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	4648	4648	0.19	0.686
Site (reef type)	4	98259	24565	58.70	0.000 *
Error	18	7532	418		
Total	23	110440			
S = 20.4566 R-Sq = 93.18% R-Sq(adj) = 91.28%					

ANOVA: Porifera spp. abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	6.00	6.00	0.04	0.860
Site (reef type)	4	676.33	169.08	11.82	0.000 *
Error	18	257.50	14.31		
Total	23	939.83			
S = 3.78227 R-Sq = 72.60% R-Sq(adj) = 64.99%					

ANOVA: *Balanus crenatus* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	63.38	63.38	0.77	0.430
Site (reef type)	4	329.33	82.33	8.04	0.001 *
Error	18	184.25	10.24		
Total	23	576.96			
S = 3.19939 R-Sq = 68.07% R-Sq(adj) = 59.19%					

ANOVA: log abundance *Ascidiella aspersa*

Source	Df	SS	Adj MS	F	P
Reef type	1	4.5826	4.5826	2.81	0.169
Site (reef type)	4	6.5156	1.6289	40.04	0.000 *
Error	18	0.7323	0.0407		
Total	23	11.8305			
S = 0.201698 R-Sq = 93.81% R-Sq(adj) = 92.09%					

ANOVA: *Corella paralelogramma* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	222.04	222.04	2.41	0.196
Site (reef type)	4	369.17	92.29	4.58	0.010 *
Error	18	362.75	20.15		
Total	23	953.96			
S = 4.48918 R-Sq = 61.97% R-Sq(adj) = 51.41%					

ANOVA: 4th root abundance Solitary ascidian (small)

Source	Df	SS	Adj MS	F	P
Reef type	1	0.2123	0.2123	0.06	0.813
Site (reef type)	4	13.3727	3.3432	19.13	0.000 *
Error	18	3.1461	0.1748		
Total	23	16.7311			
S = 0.418069 R-Sq = 81.20% R-Sq(adj) = 75.97%					

ANOVA: *Bugula* sp. abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	26.042	26.042	3.91	0.119
Site (reef type)	4	26.667	6.667	2.91	0.051
Error	18	41.250	2.292		
Total	23	93.958			

S = 1.51383 R-Sq = 56.10% R-Sq(adj) = 43.90%

ANOVA: Tubulipora abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	1350.00	1350.00	9.51	0.037 *
Site (reef type)	4	568.00	142.00	4.42	0.012 *
Error	18	578.00	32.11		
Total	23	2496.00			

S = 5.66667 R-Sq = 76.84% R-Sq(adj) = 70.41%

ANOVA: log abundance Lichenopora

Source	Df	SS	Adj MS	F	P
Reef type	1	3.3989	3.3989	3.29	0.144
Site (reef type)	4	4.1362	1.0341	30.43	0.000 *
Error	18	0.6075	0.0337		
Total	23	8.1426			

S = 0.183706 R-Sq = 92.54% R-Sq(adj) = 90.47%

ANOVA: *Callopora craticula* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	0.6667	0.6667	0.62	0.477
Site (reef type)	4	4.3333	1.0833	13.00	0.000 *
Error	18	1.5000	0.0833		
Total	23	6.5000			

S = 0.288675 R-Sq = 76.92% R-Sq(adj) = 70.51%

ANOVA: *Callopora dumerilii* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	57.042	57.042	1.91	0.239
Site (reef type)	4	119.667	29.917	43.96	0.000 *
Error	18	12.250	0.681		
Total	23	188.958			

S = 0.824958 R-Sq = 93.52% R-Sq(adj) = 91.72%

ANOVA: *Haplopoma sciaphilum* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	10.667	10.667	3.32	0.142
Site (reef type)	4	12.833	3.208	3.12	0.041 *
Error	18	18.500	1.028		
Total	23	42.000			

S = 1.01379 R-Sq = 55.95% R-Sq(adj) = 43.72%

ANOVA: log abundance *Microporella ciliata*

Source	Df	SS	Adj MS	F	P
Reef type	1	1.50689	1.50689	6.39	0.065
Site (reef type)	4	0.94285	0.23571	6.80	0.002 *
Error	18	0.62409	0.03467		
Total	23	3.07382			

S = 0.186203 R-Sq = 79.70% R-Sq(adj) = 74.06%

ANOVA: *Fenestrulina malusii* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	2.667	2.667	0.20	0.677
Site (reef type)	4	53.167	13.292	3.44	0.029 *
Error	18	69.500	3.861		
Total	23	125.333			

S = 1.96497 R-Sq = 44.55% R-Sq(adj) = 29.14%

ANOVA: *Escharoides coccinea* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	20.167	20.167	48.40	0.002 *
Site (reef type)	4	1.667	0.417	0.25	0.906
Error	18	30.000	1.667		
Total	23	51.833			
S = 1.29099 R-Sq = 42.12% R-Sq(adj) = 26.15%					

ANOVA: *Electra pilosa* abundance

Source	Df	SS	Adj MS	F	P
Reef type	1	3825.38	3825.38	31.32	0.005 *
Site (reef type)	4	488.50	122.13	1.47	0.253
Error	18	1497.75	83.21		
Total	23	5811.63			
S = 9.12186 R-Sq = 74.23% R-Sq(adj) = 67.07%					

* indicates significance at $p < 0.05$

Epifaunal recruitment to artificial and natural sites (15 month open data)

Taxa causing dissimilarity between reef types determined using the SIMPER routine in PRIMER (Clarke & Warwick 2001)

Taxa	Average Abundance Natural	Average Abundance Artificial
Balanus crenatus scar	2.67	3.69
Ascidiella aspersa	1.98	0.53
Balanus crenatus	3.06	2.06
Filograna implexa	0.15	1.90
Modiolarca tumida	1.72	0.66
Fenestrulina malusii	2.61	3.17
Porifera spp.	0.36	1.85
Electra pilosa	0.36	1.69
Tubulipora	1.24	2.37
Bryozoan ancestrulae	1.22	1.93
Anomiidae	4.11	5.24
Sinistral spirorbid	3.03	3.51
Microporella ciliata	1.78	2.37
Terebellid	1.10	0.00
Escharoides coccinea	0.06	1.12
Callopora dumerilii	1.20	2.03
Lichenopora	0.12	1.07
Serpula vermicularis	2.42	3.15
Bugula sp.	1.72	2.26
Haplopoma sciaphilum	0.06	0.85
Escharella ventricosa	0.00	0.77
Dextral spirorbid	0.76	1.06
Didemnid/tridemnid	0.32	0.65
Pomatoceros triqueter	4.75	5.12
Botryllus schlosseri	0.32	0.51
Callopora craticula	0.06	0.59
Escharella immerse	0.15	0.56
Smittoidea reticulate	0.00	0.53
Hydroides elegans	3.96	4.19
Callopora aurita	0.00	0.46
Polychaete in sand tube	0.06	0.38
Elminius modestus	0.26	0.12

Two-way nested ANOVA results for taxonomic data

ANOVA: log abundance *Pomatoceros triqueter*

Source	Df	Seq SS	Adj MS	F	P
Reef type	1	0.15995	0.15995	0.81	0.420
Site (reef type)	4	0.79397	0.19849	9.79	0.000 *
Error	18	0.36506	0.02028		
Total	23	1.31898			

S = 0.142412 R-Sq = 72.32% R-Sq(adj) = 64.63%

ANOVA: log abundance *Hydroides elegans*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	0.06122	0.06122	0.43	0.549
Site (reef type)	4	0.59197	0.16349	19.85	0.000 *
Error	18	0.13013	0.00723		
Total	23				

S = 0.0850269 R-Sq = 83.00% R-Sq(adj) = 78.27%

ANOVA: log abundance *Balanus crenatus* scar

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	1.1902	1.1902	0.49	0.523
Site (reef type)	4	9.7555	2.4389	29.89	0.000 *
Error	18	1.4689	0.0816		
Total	23				

S = 0.285666 R-Sq = 88.17% R-Sq(adj) = 84.88%

ANOVA: log abundance *Ascidiella aspersa*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	2.3941	2.3941	1.83	0.248
Site (reef type)	4	5.2400	1.3100	43.81	0.000 *
Error	18	0.5382	0.0299		
Total	23				

S = 0.172912 R-Sq = 93.41% R-Sq(adj) = 91.59%

ANOVA: log abundance *Balanus crenatus*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	1.1217	1.1217	0.83	0.413
Site (reef type)	4	5.3888	1.3472	7.01	0.001 *
Error	18	3.4610	0.1923		
Total	23				

S = 0.438494 R-Sq = 65.29% R-Sq(adj) = 55.65%

ANOVA: log abundance *Filograna implexa*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	3.4526	3.4526	2.88	0.165
Site (reef type)	4	4.7898	1.1975	7.15	0.001 *
Error	18	3.0003	0.1667		
Total	23				

S = 0.408266 R-Sq = 73.31% R-Sq(adj) = 65.90%

ANOVA: log abundance *Modiolarca tumida*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	1.2850	1.2850	0.93	0.390
Site (reef type)	4	5.5299	1.3925	22.99	0.000 *
Error	18	1.0826	0.0601		
Total	23				

S = 0.245244 R-Sq = 86.29% R-Sq(adj) = 82.48%

ANOVA: log abundance *Fenestrulina malusii*

Source	Df	Adj SS	Adj MS	F	P

Reef type	1	0.3490	0.3490	0.20	0.677
Site (reef type)	4	6.9483	1.7371	75.39	0.000 *
Error	18	0.4147	0.0230		
Total	23				
S = 0.151789 R-Sq = 94.62% R-Sq(adj) = 93.13%					

ANOVA: log abundance Porifera spp.

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	2.53360	2.53360	14.47	0.019 *
Site (reef type)	4	0.70049	0.17512	5.32	0.005 *
Error	18	0.59296	0.03294		
Total	23				
S = 0.181499 R-Sq = 84.51% R-Sq(adj) = 80.20%					

ANOVA: log abundance *Electra pilosa*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	2.01660	2.01660	12.53	0.024 *
Site (reef type)	4	0.64357	0.16089	2.34	0.095
Error	18	1.24013	0.06890		
Total	23				
S = 0.262481 R-Sq = 68.20% R-Sq(adj) = 59.37%					

ANOVA: log abundance Tubulipora

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	1.44145	1.44145	2.35	0.200
Site (reef type)	4	2.44862	0.61216	16.72	0.000 *
Error	18	0.65918	0.03662		
Total	23				
S = 0.191367 R-Sq = 85.51% R-Sq(adj) = 81.49%					

ANOVA: Anomiidae abundance

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	101660	101660	8.49	0.044 *
Site (reef type)	4	47921	11980	2.45	0.083
Error	18	87959	4887		
Total	23				
S = 69.9043 R-Sq = 62.97% R-Sq(adj) = 52.68%					

ANOVA: log abundance Sinistral spirorbid

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	0.26111	0.26111	0.24	0.650
Site (reef type)	4	4.34344	1.08586	19.21	0.000
Error	18	1.01749	0.05653		
Total	23				
S = 0.237754 R-Sq = 81.90% R-Sq(adj) = 76.87%					

ANOVA: log abundance *Microporella ciliata*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	0.38887	0.38887	0.44	0.542
Site (reef type)	4	3.50983	0.87746	33.17	0.000 *
Error	18	0.47609	0.02645		
Total	23				
S = 0.162633 R-Sq = 89.12% R-Sq(adj) = 86.09%					

ANOVA: log abundance *Escharoides coccinea*

Source	Df	Adj SS	Adj MS	F	P
Reef type	1	1.27500	1.27500	275.73	0.000 *
Site (reef type)	4	0.01850	0.00462	0.14	0.966
Error	18	0.60272	0.03348		

Total	23				
S = 0.182988 R-Sq = 68.21% R-Sq(adj) = 59.39%					
ANOVA: log abundance *Callopora dumerilii*					
Source	Df	Adj SS	Adj MS	F	P
Reef type	1	112.667	112.667	3.40	0.139
Site (reef type)	4	132.667	33.167	4.25	0.014 *
Error	18	140.500	7.806		
Total	23				
S = 2.79384 R-Sq = 63.59% R-Sq(adj) = 53.47%					
ANOVA: log abundance *Serpula vermicularis*					
Source	Df	Adj SS	Adj MS	F	P
Reef type	1	0.61364	0.61364	5.30	0.083
Site (reef type)	4	0.46274	0.11568	2.62	0.069
Error	18	0.79431	0.04413		
Total	23				
S = 0.210068 R-Sq = 57.54% R-Sq(adj) = 45.74%					
ANOVA: log abundance *Bugula* sp.					
Source	Df	Adj SS	Adj MS	F	P
Reef type	1	0.3928	0.32928	1.22	0.332
Site (reef type)	4	1.08177	0.27044	5.03	0.007 *
Error	18	0.96835	0.05380		
Total	23				
S = 0.231942 R-Sq = 59.30% R-Sq(adj) = 48.00%					

* shows significance at $p < 0.05$

Two-way nested ANOVA results for epifaunal biomass data

ANOVA: Log dry weight					
Source	Df	Seq SS	Adj MS	F	P
Reef type	1	3.9703	3.9703	5.95	0.075
Site (reef type)	4	2.7617	0.6904	58.80	0.000 *
Error	18	0.2114	0.0117		
Total	23	6.9434			
S = 0.108365 R-Sq = 96.96 % R-Sq(adj) = 96.11%					
ANOVA: Log ash free dry weight					
Source	Df	Seq SS	Adj MS	F	P
Reef type	1	2.0493	2.0493	2.46	0.192
Site (reef type)	4	3.3297	0.8324	118.04	0.000
Error	18	0.1269	0.0071		
Total	23	5.5060			
S = 0.0839761 R-Sq = 97.69% R-Sq(adj) = 97.05%					

* shows significance at $p < 0.05$

Two-way nested ANOVA results for diversity indices

ANOVA: N (log)					
Source	Df	Seq SS	Adj MS	F	P
Reef type	1	0.17427	0.17427	1.55	0.280
Site (reef type)	4	0.44841	0.11210	26.20	0.000 *
Error	18	0.07701	0.00428		
Total	23				
S = 0.0654108 R-Sq = 88.99 % R-Sq(adj) = 85.94%					

ANOVA: S (log)

Source	Df	SS	MS	F	P
Reef type	1	0.171388	0.171388	8.33	0.045 *
Site (reef type)	4	0.082268	0.020567	12.03	0.000 *
Error	18	0.030786	0.001710		
Total	23				

S = 0.0413561 R-Sq = 89.18% R-Sq(adj) = 86.17%

ANOVA: H'

Source	Df	SS	MS	F	P
Reef type	1	0.00563	0.00563	0.06	0.823
Site (reef type)	4	0.39288	0.09822	6.18	0.003 *
Error	18	0.28602	0.01589		
Total	23				

S = 0.126055 R-Sq = 58.22% R-Sq(adj) = 46.61%

* shows significance at $p < 0.05$

SIMPER (by site)

N1 (average similiarity 83.87%)		N2 (average similiarity 80.57%)	
Taxon	% contr.	Taxon	% contr.
Pomatoceros triqueter	11.20	*Pomatoceros triqueter*	16.77
Anomiidae	11.13	*Hydroides elegans*	16.67
Sinistral spirorbid	10.75	*Modiolarca tumida*	14.50
Fenestrulina malusii	10.21	*Ascidiella aspersa*	14.16
Hydroides elegans	8.68	Anomiidae	11.58
Balanus crenatus	8.49	Terebellidae	9.05
Serpula vermicularis	7.40	*Serpula vermicularis*	5.04
Balanus crenatus scar	7.09	*Bugula* sp.	4.95
Bryozoan ancestrulae	6.91		
Microporella ciliata	6.20		
Callopora dumerilii	4.31		

N3 (average similiarity 83.95%)	
Taxon	% contr.
Pomatoceros triqueter	11.63
Balanus crenatus scar	10.44
Anomiidae	9.98
Balanus crenatus	9.62
Hydroides elegans	8.86
Fenestrulina malusii	8.15
Sinistral spirorbid	8.12
Microporella ciliata	5.45
Tubulipora	5.15
Bugula sp.	5.03
Serpula vermicularis	4.86
Ascidiella aspersa	3.89

A1(average similiarity 81.73%)		A2 (average similiarity 83.53%)	
Taxon	% contr.	Taxon	% contr.
Anomiidae	12.72	Anomiidae	9.59
Pomatoceros triqueter	11.96	*Pomatoceros triqueter*	8.97
Hydroides elegans	10.74	*Hydroides elegans*	7.49
Fenestrulina malusii	8.11	Sinistral spirorbid	6.56
Balanus crenatus scar	8.06	Balanus crenatus scar	6.52
Serpula vermicularis	7.59	*Filograna implexa*	6.37
Sinistral spirorbid	6.19	*Serpula vermicularis*	5.89
Bryozoan ancestrulae	5.63	*Fenestrulina malusii*	5.18
Porifera spp.	4.29	*Bugula sp.*	4.93
Microporella ciliata	4.00	*Callopora dumerilii*	4.48
Callopora dumerilii	3.54	Tubulipora	4.39
Tubulipora	3.37	Porifera spp.	4.31
Bugula sp.	2.94	*Balanus crenatus*	3.98
Balanus crenatus	2.51	*Microporella ciliata*	3.82
		Bryozoan ancestrulae	2.76
		Lichenpora	2.06
		Electra pilosa	1.84
		Modiolarca tumida	1.83

A3(average similiarity 81.05%)	
Taxon	% contr.
Pomatoceros triqueter	10.54
Anomiidae	9.28
Hydroides elegans	7.89
Sinistral spirorbid	7.30
Balanus crenatus scar	6.09
Microporella ciliata	5.64
Fenestrulina malusii	5.41
Serpula vermicularis	5.35
Tubulipora	5.12
Bugula sp.	4.40
Electra pilosa	4.00
Haplopoma sciaphilum	3.55
Byrozoan ancestrulae	3.33
Callopora dumerilii	3.20
Dextral spirorbid	2.89
Lichenopora	2.21
Porifera spp.	2.00
Balanus crenatus	1.97

Appendix IV Results tables for chapter 5

ANOVA tables

Abundance of main characterising infauna in sediments

Turitella communis

Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	1.3	0.650	3.34	0.096
Error	7	1.363	0.195		
Total	9	2.662			

S = 0.4412 R-Sq = 48.82% R-Sq (adj) = 34.20%

Nucula nucleus

Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	0.0361	0.0180	0.50	0.622
Error	10	0.3622	0.0362		
Total	12	0.3983			

S = 0.1903 R-Sq = 9.06% R-Sq(adj) = 0.00%

Corbula gibba

Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	0.0686	0.0343	2.82	0.152
Error	5	0.0609	0.0122		
Total	7	0.1294			

S = 0.1103 R-Sq = 52.97% R-Sq(adj) = 34.16%

Maldanidae

Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	1	1.80	1.80	1.08	0.375
Error	3	5.00	1.67		
Total	4	6.80			

S = 1.291 R-Sq = 26.47% R-Sq(adj) = 1.96%

Eunicidae I

Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	0.68	0.34	0.32	0.737
Error	5	5.20	1.04		
Total	7	5.88			

S = 1.020 R-Sq = 11.49% R-Sq(adj) = 0.00%

Amparetidae – data not testable using ANOVA as only one treatment had any individuals in it

Terebellidae

Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	0.700	0.350	1.40	0.417
Error	2	0.500	0.250		
Total	4	1.200			

S = 0.5 R-Sq = 58.33% R-Sq(adj) = 16.67%

One-way ANOVA: Diversity (H') of infauna in sediments from different treatments (control, complex, simple).

Source	Df	SS	MS	F	P
Infauna treatment	2	1.035	0.518	2.90	0.084
Error	16	2.851	0.178		
Total	18	3.886			
S = 0.4222 R-Sq = 26.63% R-Sq(adj) = 17.46%					

* shows significance at $p < 0.05$

One-way ANOVA: Diversity (H') of epifauna on simple and complex reef blocks.

Source	Df	SS	MS	F	P
Epifauna treatment	1	0.000	0.000	0.00	0.994
Error	10	2.258	0.226		
Total	11	2.258			
S = 0.4752 R-Sq = 0.00% R-Sq(adj) = 0.00%					

* shows significance at $p < 0.05$

One-way ANOVA: dry weight and ash free dry weight of infaunal biomass in sediments

Dry weight of infauna in sediments Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	60.96	30.48	4.86	0.022*
Error	16	100.34	6.27		
Total	18	161.30			
S = 2.504 R-Sq = 37.79% R-Sq(adj) = 30.02%					
Log ash free dry weight of infauna in sediments Source	Df	SS	MS	F	P
Infaunal treatment (control, complex, simple)	2	9.534	4.767	7.19	0.006*
Error	16	10.602	0.663		
Total	18	20.135			
S = 0.8140 R-Sq = 47.35% R-Sq(adj) = 40.77%					

* shows significance at $p < 0.05$

One-way ANOVA: dry weight and ash free dry weight of epibiotic biomass on different orientations

Dry weight of epibiota on different orientations					
Source	Df	SS	MS	F	P
Orientation (horizontal up, horizontal down, vertical)	2	732.9	336.4	7.29	0.013*
Error	9	452.4	50.3		
Total	11	1185.3			
S = 7.090 R-Sq = 61.83% R-Sq(adj) = 53.35%					
Log ash free dry weight of infauna in sediments					
Source	Df	SS	MS	F	P
Orientation (horizontal up, horizontal down, vertical)	2	4.50	2.25	1.31	0.315
Error	9	15.37	1.71		
Total	11	19.88			
S = 1.307 R-Sq = 22.67% R-Sq(adj) = 5.48%					

* shows significance at $p < 0.05$

One way ANOVA: comparisons between the size of footprint, the height and the surface area of complex and simple reef modules

One-way ANOVA: Footprint of complex and simple reef modules					
Source	Df	SS	MS	F	P
Reef type	1	79238	79238	42.49	0.000*
Error	12	22378	1865		
Total	13	101616			
S = 43.18 R-Sq = 77.98% R-Sq(adj) = 76.14%					
One-way ANOVA: Height of complex and simple reef modules					
Source	Df	SS	MS	F	P
Reef type	1	4.986	4.986	6.57	0.025*
Error	12	9.112	0.759		
Total	13	14.098			
S = 0.8714 R-Sq = 35.37% R-Sq(adj) = 29.98%					
One-way ANOVA: Surface area of cone of complex and simple reef modules					
Source	Df	SS	MS	F	P
Reef type	1	68824	68824	52.01	0.000*
Error	12	15878	1323		
Total	13	84702			
S = 36.38 R-Sq = 81.25% R-Sq(adj) = 79.69%					

* shows significance at $p < 0.05$

Appendix V Results tables for chapter 6

Two-way nested ANOVA results

∂^{15}N Plankton

Source	DF	SS	MS	F	P
Reef type	1	1.3357	1.3357	2.09	0.244
Reef site (reef type)	3	1.9210	0.6403	1.18	0.343
Error	20	10.8569	0.5428		
Total	24	14.1136			

S = 0.736779 R-Sq = 23.07% R-sq(adj) = 7.69%

∂^{13}C Plankton

Source	DF	SS	MS	F	P
Reef type	1	10.8661	10.8661	9.30	0.055
Reef site (reef type)	3	3.5057	1.1686	16.26	0.000 *
Error	20	1.4372	0.0719		
Total	24	15.8090			

S = 0.268070 R-Sq = 90.91% R-Sq(adj) = 89.09%

∂^{15}N *Laminaria* sp.

Source	DF	SS	MS	F	P
Reef type	1	2.2815	1.0901	0.42	0.600
Reef site (reef type)	2	3.9517	1.9759	2.91	0.106
Error	9	6.1078	0.6786		
Total	12	12.3410			

S = 0.823799 R-Sq = 50.51% R-Sq(adj) = 34.01%

∂^{13}C *Laminaria* sp.

Source	DF	SS	MS	F	P
Reef type	1	31.380	24.197	12.43	0.182
Reef site (reef type)	2	3.706	1.853	1.11	0.370
Error	9	14.972	1.664		
Total	12	50.058			

S = 1.28979 R-Sq = 70.09% R-Sq(adj) = 60.12%

∂^{15}N Filamentous red algae.

Source	DF	SS	MS	F	P
Reef type	1	11.1093	3.9600	0.83	0.544
Reef site (reef type)	1	2.8013	2.8013	7.78	0.024 *
Error	8	2.8792	0.3599		
Total	10	16.7897			

S = 0.599914 R-Sq = 82.85% R-Sq(adj) = 78.56%

∂^{13}C Filamentous red algae.

Source	DF	SS	MS	F	P
Reef type	1	0.9030	0.0359	0.02	0.925
Reef site (reef type)	1	1.4615	1.4615	1.92	0.203
Error	8	6.0960	0.7620		
Total	10	8.4604			

S = 0.872925 R-Sq = 27.95% R-Sq(adj) = 9.93%

∂^{15}N *Gibbula cineraria* <1cm

Source	DF	SS	MS	F	P
Reef type	1	0.00449	0.12331	0.19	0.704
Reef site (reef type)	2	1.29856	0.64928	6.55	0.010 *
Error	14	1.38798	0.09914		
Total	17	2.69103			

S = 0.314867 R-Sq = 48.42% R-Sq(adj) = 37.37%

$\partial^{13}C$ *Gibbula cineraria* <1cm

Source	DF	SS	MS	F	P
Reef type	1	3.2710	3.4383	0.60	0.518
Reef site (reef type)	2	11.5678	5.7839	21.62	0.000 *
Error	14	3.7460	3.7460	0.2676	
Total	17	18.5848			

S = 0.517275 R-Sq = 79.84% R-Sq(adj) = 75.52%

$\partial^{15}N$ *Gibbula cineraria* >1cm

Source	DF	SS	MS	F	P
Reef type	1	0.0237	0.0237	1.02	0.336
Reef site (reef type)	2	0.0021	0.0010	0.01	0.993
Error	9	1.3936	0.1548		
Total	12	1.4194			

S = 0.393500 R-Sq = 1.82% R-Sq(adj) = 0.00%

$\partial^{13}C$ *Gibbula cineraria* >1cm

Source	DF	SS	MS	F	P
Reef type	1	0.3746	0.6910	0.11	0.773
Reef site (reef type)	2	14.7680	7.3840	23.96	0.000 *
Error	14	2.7731	0.3081		
Total	17				

S = 0.555084 R-Sq = 84.52% R-Sq(adj) = 79.36%

$\partial^{15}N$ *Balanus crenatus*

Source	DF	SS	MS	F	P
Reef type	1	4.0310	4.0310	1.52	0.305
Reef site (reef type)	3	7.9510	2.6503	90.53	0.000 *
Error	10	0.2928	0.0293		
Total	14	12.2748			

S = 0.171103 R-Sq = 97.61% R-Sq(adj) = 96.66%

$\partial^{13}C$ *Balanus crenatus*

Source	DF	SS	MS	F	P
Reef type	1	0.70545	0.70545	3.29	0.167
Reef site (reef type)	3	0.64264	0.21421	7.73	0.006 *
Error	10	0.27714	0.02771		
Total	14	1.62522			

S = 0.166474 R-Sq = 82.95% R-Sq(adj) = 76.13%

$\partial^{15}N$ *Echinus esculentus*

Source	DF	SS	MS	F	P
Reef type	1	0.0080	0.2871	0.07	0.805
Reef site (reef type)	3	11.9496	3.9832	19.46	0.000 *
Error	25	5.1167	0.2047		
Total	29	17.0742			

S = 0.452401 R-Sq = 70.03% R-Sq(adj) = 65.24%

$\partial^{13}C$ *Echinus esculentus*

Source	DF	SS	MS	F	P
Reef type	1	2.4501	2.6079	8.67	0.059
Reef site (reef type)	3	0.9021	0.3007	1.02	0.400
Error	25	7.3618	0.2945		
Total	29	10.7140			

S = 0.542651 R-Sq = 31.29% R-Sq(adj) = 20.29%

$\partial^{15}N$ *Asterias rubens*

Source	DF	SS	MS	F	P
Reef type	1	12.029	12.029	10.49	0.048 *
Reef site (reef type)	3	3.441	1.147	1.03	0.402

Error	20	22.375	1.119		
Total	24	37.845			
S = 1.05771 R-Sq = 40.88% R-Sq(adj) = 29.05%					

$\partial^{13}C$ *Asterias rubens*

Source	DF	SS	MS	F	P
Reef type	1	4.0824	4.0824	3.18	0.172
Reef site (reef type)	3	3.8462	1.2821	6.50	0.003 *
Error	20	3.9434	0.1972		
Total	24	11.8720			
S = 0.444037 R-Sq = 66.78% R-Sq(adj) = 60.14%					

$\partial^{15}N$ *Necora puber*

Source	DF	SS	MS	F	P
Reef type	1	0.9131	0.9131		
Reef site (reef type)	3	0.1092	0.0364	25.08	0.015 *
Error	20	2.9983	0.1499	0.24	0.865
Total	24	4.0207			
S = 0.387189 R-Sq = 25.43% R-Sq(adj) = 10.51%					

$\partial^{13}C$ *Necora puber*

Source	DF	SS	MS	F	P
Reef type	1	0.0015	0.0015	0.04	0.853
Reef site (reef type)	3	0.1122	0.0374	0.24	0.867
Error	20	3.1031	0.1552		
Total	24	3.2169			
S = 0.393899 R-Sq = 3.54% R-Sq(adj) = 0.00%					

$\partial^{15}N$ *Centrolabrus exoletus* >10cm

Source	DF	SS	MS	F	P
Reef type	1	0.0644	0.0702	0.93	0.343
Reef site (reef type)	2	0.0406	0.0203	0.10	0.902
Error	43	8.4882	0.1974		
Total	46	8.5932			
S = 0.444296 R-Sq = 1.22% R-Sq(adj) = 0.00%					

$\partial^{13}C$ *Centrolabrus exoletus* >10cm

Source	DF	SS	MS	F	P
Reef type	1	0.08842	0.08878	2.00	0.176
Reef site (reef type)	2	0.04018	0.02009	0.20	0.816
Error	43	4.21600	0.09805		
Total	46	4.34460			
S = 0.313124 R-Sq = 2.96% R-Sq(adj) = 0.00%					

* shows significance at $p < 0.05$

Mean values of $\delta^{15}N$ and $\delta^{13}C$ at artificial and natural reef types

Taxa	Artificial Site	$\delta^{15}N \pm SD$	$\delta^{13}C \pm SD$	Natural Site	$\delta^{15}N \pm SD$	$\delta^{13}C \pm SD$
G. cineraria <1cm	M1c	8.67 ± 0.29	-17.39 ± 0.42	Rubha Garbh-aird	9.03 ± 0.10	-18.52 ± 0.60
	B1c	-	-	Eilean Mor	8.28 ± 0.59	-16.60 ± 0.34
	B3c	8.75	-15.16	Natural ALL	8.78 ± 0.48	-17.88 ± 1.08
	Artificial ALL	8.68 ± 0.27	-17.11 ± 0.88			
G. cineraria >1cm	M1c	9.06 ± 0.19	-17.19 ± 0.38	Rubha Garbh-aird	9.13 ± 0.52	-18.16 ± 0.38
	B1c	-	-	Eilean Mor	9.23 ± 0.27	-15.61 ± 0.57
	B3c	9.28	-16.33	Natural ALL	9.18 ± 0.38	-16.88 ± 1.44
	Artificial ALL	9.13 ± 0.18	-16.90 ± 0.57			
E. esculentus	M1c	9.16 ± 0.43	-17.04 ± 0.63	Rubha Garbh-aird	9.87 ± 0.23	-16.78 ± 0.40
	B1c	9.04 ± 0.74	-17.50 ± 0.62	Eilean Mor	7.85 ± 0.44	-16.50 ± 0.58
	B3c	9.00 ± 0.29	-17.18 ± 0.49	Natural ALL	8.94 ± 1.09	-16.65 ± 0.46
	Artificial ALL	9.06 ± 0.49	-17.24 ± 0.58			
B. crenatus	M1c	8.09 ± 0.09	-16.92 ± 0.03	Rubha Garbh-aird	10.41 ± 0.14	-16.64 ± 0.03
	B1c	10.0 ± 0.20	-16.71 ± 0.01	Eilean Mor	10.53 ± 0.12	-16.45 ± 0.04
	B3c	10.15 ± 0.25	-17.33 ± 0.37	Natural ALL	10.47 ± 0.14	-16.54 ± 0.11
	Artificial ALL	9.41 ± 1.01	-16.99 ± 0.33			
A. rubens	M1c	10.74 ± 1.10	-14.80 ± 0.58	Rubha Garbh-aird	12.76 ± 0.29	-13.05 ± 0.46
	B1c	10.61 ± 1.39	-14.00 ± 0.54	Eilean Mor	11.71 ± 0.41	-13.93 ± 0.20
	B3c	11.11 ± 1.49	-14.18 ± 0.33	Natural ALL	12.24 ± 0.65	-13.50 ± 0.57
	Artificial ALL	10.82 ± 1.26	-14.32 ± 0.59			
N. puber	M1c	12.33 ± 0.35	-15.61 ± 0.50	Rubha Garbh-aird	11.85 ± 0.19	-15.48 ± 0.42
	B1c	12.36 ± 0.39	-15.56 ± 0.30	Eilean Mor	12.05 ± 0.28	-15.68 ± 0.16
	B3c	12.34 ± 0.60	-15.62 ± 0.50	Natural ALL	11.95 ± 0.25	-15.58 ± 0.32
	Artificial ALL	12.34 ± 0.43	-15.60 ± 0.41			
C. exoletus <10cm	M1c	12.98 ± 0.38	-16.46 0.31	Rubha Garbh-aird	-	-
	B1c	12.88 0.21	-16.55 0.43	Eilean Mor	-	-
	B3c	-	-	Natural ALL	-	-
	Artificial ALL	-	-			
C. exoletus >10cm	M1c	12.92 ± 0.36	-16.62 ± 0.38	Rubha Garbh-aird	12.77 ± 0.29	-16.54 ± 0.33
	B1c	12.84 ± 0.60	-16.64 ± 0.29	Eilean Mor	-	-
	B3c	12.86 ± 0.33	-16.70 ± 0.25	Natural ALL	-	-
	Artificial ALL	12.87 ± 0.46	-16.65 ± 0.30			

ANOVA results for trophic position

Echinus esculentus

Source	DF	SS	MS	F	P
Reef type	1	0.00854	0.03894	0.09	0.789
Reef site (reef type)	2	0.83465	0.41733	39.97	0.000 *
Error	20	0.20884	0.01044		
Total	23	1.05203			

S = 0.102186 R-Sq = 80.15% R-sq(adj) = 77.17%

Balanus crenatus

Source	DF	SS	MS	F	P
Reef type	1	0.43232	0.43232	1.96	0.297
Reef site (reef type)	2	0.44186	0.22093	95.69	0.000 *
Error	8	0.01847	0.00231		
Total	11	0.89265			

S = 0.0480501 R-Sq = 97.93% R-Sq(adj) = 97.15%

Necora puber

Source	DF	SS	MS	F	P
Reef type	1	0.08456	0.08456	2.96	0.228
Reef site (reef type)	2	0.05717	0.02858	2.20	0.143
Error	16	0.20787	0.01299		
Total	19	0.34960			

S = 0.113982 R-Sq = 40.54% R-Sq(adj) = 29.39%

Asterias rubens

Source	DF	SS	MS	F	P
Reef type	1	0.67630	0.67630	9.42	0.092
Reef site (reef type)	2	0.14357	0.07178	0.90	0.425
Error	16	1.27079	0.07942		
Total	19	2.09066			

S = 0.281823 R-Sq = 39.22% R-Sq(adj) = 27.82%

Centrolabrus exoletus >10cm

Source	DF	SS	MS	F	P
Reef type	1	0.45240	0.047299	1.21	0.455
Reef site (reef type)	1	0.047886	0.047886	5.12	0.032 *
Error	28	0.261962	0.009356		
Total	30	0.355089			

S = 0.0967254 R-Sq = 26.23% R-Sq(adj) = 20.96%

* shows significance at $p < 0.05$