Ecological effects of the Lundy No-take Zone: The first five years (2003-2007)

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EXECUTIVE SUMMARY

Background

The establishment of the Lundy No-take Zone (NTZ) in 2003 required English Nature (now Natural England) to assess its effectiveness for achieving conservation goals, in particular the recovery of previously fished species and associated changes in biodiversity due to the cessation of fishing. In 2004, a programme of annual monitoring was established to evaluate these potential effects of the Lundy NTZ.

The general expectation was that compliance with the NTZ would remove or substantially reduce fishing-related disturbances, which would cause previously impacted populations within the NTZ to exhibit increased production (*e.g.* abundance, body size, etc.) relative to populations in similar places where fishing was ongoing.

The main forms of fishing that occur around Lundy are 'potting' (fishing with baited traps) for lobster and crab, diver-harvesting of lobster, crabs and scallops and angling for various types of fishes. Angling was not considered to be a major influence on the proposed NTZ, so effects related to this activity were not investigated. Monitoring was therefore designed to investigate potential effects of the NTZ on the following three components of Lundy's marine fauna:

i. populations of four species of commercially-fished crustacean; the lobster (*Homarus gammarus*), edible or brown crab (*Cancer pagurus*), velvet swimming crab (*Necora puber*) and spider crab (*Maja squinado*);

ii. populations of scallop (*Pecten maximus*) and

iii. an assemblage of sessile epifauna in circalittoral rocky habitats that are of interest for nature conservation, including pink sea-fan (*Eunicella verrucosa*), dead men's fingers (*Alcyonium digitatum*), ross coral (*Pentapora fascialis*) and axinellid sponges.

A total of 20 different taxa were monitored for potential effects of the Lundy NTZ.

Since the managerial decision to monitor potential effects of the NTZ was made after it was established (in January 2003), a 'post-impact' sampling design was the only option. Hypotheses about potential effects of the NTZ were therefore tested by comparing data from the NTZ with similar data from nearby control locations (within 1-5km of the NTZ). For lobster and crabs, there was also a large-scale comparison with reference locations that were several 10s of km away. Monitoring began 18 months after the designation of the NTZ.

Lobster and crabs were sampled using baited pots (as per commercial fishing) whilst and scallops and sessile epifauna were sampled *in situ* by scuba divers.

After four years of monitoring (to 2007), only three of the 20 species that were monitored showed evidence of an effect of the NTZ – all three were commercially-fished crustaceans; lobster, brown crab and velvet crab. There was no evidence for an effect of the NTZ on spider crabs, scallops, or sessile epifauna (either as an assemblage or as individual species).

Lobster and crabs

For lobster and brown crab, the apparent effects of the Lundy NTZ were manifested as increased abundance and/or increased size of individuals within the NTZ relative to fished areas. Lobster provided the most compelling evidence for a positive effect of the NTZ, both in terms of the multiplicity of evidence and the magnitude of changes. Distinct forms of evidence for an effect of the NTZ were obtained for landable-sized lobsters (carapace length (CL) ≥90mm) and undersized lobsters (CL <90mm).

When monitoring began in 2004 (18 months post-designation) the mean abundance of landable-sized lobsters in the NTZ was already 205% greater than the average for control and reference locations. When first consulted on the proposed NTZ, local fishermen gave no indication that the area concerned was especially productive for lobsters, so this initial difference could well have been an early response to the NTZ. In the course of subsequent monitoring, the mean abundance in the NTZ increased by 127% whilst abundances in control and reference locations remained relatively constant. By 2007, landable-sized lobsters were 427% more abundant in the NTZ compared to control and reference locations. Landable-sized lobsters in the NTZ also showed a small (~5%), but statistically significant increase in average size relative to control and reference locations during the study. These results indicate that even small NTZs (<5km^2) are capable of producing rapid and substantial increases in the local biomass of landable-sized lobsters.

From 2004 to 2007, the mean abundance of undersized lobsters increased significantly in the NTZ (up 97%) and also in adjacent control locations (up 124%), but showed no significant changes in the more-distant reference locations. There was no evidence for an effect of the NTZ on the average size of undersized lobsters. Abundance findings for undersized lobsters were interpreted as potential evidence of a 'spillover' effect of the NTZ; *i.e.* that the NTZ had caused a localised increase in abundance that had spread (via migration) to surrounding areas. We caution, however, that spillover has not been proved and that there is no obvious and straightforward mechanism by which the NTZ could have caused a localised increase in undersized lobsters.

Brown crabs showed no change in relative abundance within the NTZ, but they did exhibit a significant 25% increase in size relative to control and reference locations. Given the small sample size available (n=5), however, this increase in size may have been a statistical artefact due to sampling error, rather than an effect of the NTZ.

The abundances of velvet crabs exhibited a pattern of change that was almost the exact opposite of that seen in undersized lobsters. The abundance of velvet crabs declined significantly within the NTZ and adjacent control locations (by 65 and 75%, respectively), but increased 26% on average in the more-distant reference locations. It is believed that the decline in the abundance of velvet crabs around Lundy may have been caused by the increased competition and/or predation from large lobsters within the NTZ. This decline in velvet crabs may also have contributed to the general increase in undersized lobsters within the NTZ and control locations, as velvet crabs are believed to have negative effects on small lobsters (particularly newly-settled lobsters) via predation and competition.

Spider crab populations showed no detectable changes in response to the Lundy NTZ. This was thought to be because spider crabs are highly migratory throughout their lives, such that individuals only gained a small, transient benefit from the NTZ that was undetectable at the population level against background variations.

Since there is nothing to suggest that apparent effects of the Lundy NTZ on lobster and velvet crab (and potentially brown crab) are fully developed, we recommend continued monitoring to assess potential future changes. To test whether the NTZ has caused increased production and spillover of undersized lobsters we also recommend a programme of streamer tagging to determine rates of migration into and out of the different sampling locations. If spillover is occurring, net export of undersized lobsters from the NTZ should be significantly greater than from control and reference locations. For the reliable assessment of spillover, sampling for tagging and recapture should be implemented on the back of continued monitoring because this would provide for standardised (unbiased) sampling in all locations.

To assist the interpretation of potential future changes in lobster and crabs, we also recommend new work to assess types and levels of fishing for these species in each of the different monitoring locations. This should include improved surveillance of illegal fishing within the NTZ. Illegal potting has been observed in the NTZ and is probably under-detected. This may confound scientific efforts to assess the effectiveness of the NTZ for achieving conservation goals.

- **Scallops**

Scallops showed no changes in either abundance or size that indicated an effect of the Lundy NTZ. We believe the most likely explanation for this is that the structure of scallop populations in the NTZ and the control location currently provides little scope for differentiation. At present, scallop populations are at very low density in both locations and mostly comprise large, old individuals – there appears to have been no significant recruitment in either location for several years. If there was significant recruitment, increased abundance of scallops might lead to increased fishing in the control location and eventually a detectable difference in the density and/or size of scallops relative to the NTZ. Legally, scallops should only be taken by diving in the control locations as dredging is banned in this area.

Given the current situation of stasis in adult populations, we recommend that scallop monitoring should be temporarily suspended and that research effort should be directed towards surveillance of scallop recruitment using spat collection devices that provide an artificial substrate for spat settlement. This would be much less expensive than monitoring of adults since it would not require scientific divers. If a significant recruitment event was detected, we would recommend the resumption of monitoring two years later - this would allow new recruits time to grow to a size where they could be readily detected by divers. Suspending monitoring without implementing surveillance of recruitment would risk missing an opportunity to detect an effect of the NTZ on scallops.

To aid the interpretation of potential future changes in scallops, we also recommend new work to assess levels of scallop harvesting by divers (currently only recreational divers) in the different monitoring locations, including potential illegal scallop diving in the NTZ. There should also be improved surveillance for potential illegal scallop dredging within the Lundy MNR as there are some indications that this may occur. In terms of monitoring, this is most likely to impact scallops in the control location, which is adjacent to the MNR boundary.

- **Sessile epifauna**

Sessile epifauna in circalittoral rocky habitats failed to produce any evidence of an effect of the Lundy NTZ. Within the NTZ, sessile epifauna showed no changes indicating recovery from potential impacts of previous fishing activities. Nor were there signs of ongoing impacts of fishing in the control location. The main fishing activity that these fauna were previously exposed to the NTZ and which they are still exposed to in the control location is commercial potting for lobsters and crabs. Our monitoring results led us to conclude that at current levels of fishing effort, disturbances created by commercial potting have no direct impacts on sessile epifauna.

If sessile epifauna do eventually respond to the NTZ, we believe that this is now most likely to occur via indirect interactions with fished species, such as lobster, rather than as a direct effect of NTZ protection. Such effects on sessile benthos have been observed in several marine reserves elsewhere in the World, but they typically take much longer to emerge than direct effects on fished species. Generally speaking, the form, time-scale and mechanism of indirect reserve effects cannot be accurately predicted *a priori* and in most cases where they have been observed they were entirely unexpected.

Not only did sessile epifauna in circalittoral rocky habitats fail to show any changes indicating an effect of the NTZ, they typically showed no significant changes of any kind. This stasis was presumably either because there was negligible turnover of individuals within populations, or because ongoing mortality was matched by ongoing recruitment. Greater knowledge of turnover-rates within populations of sessile epifauna at Lundy would be useful for assessing the likely time-scale of potential indirect effects of the NTZ. If such effects are developing within the Lundy NTZ, we would expect that high turnover of individuals within epifaunal populations would hasten their appearance. To investigate turnover within epifaunal populations we recommend new research involving repeated monitoring of fixed quadrats to observe the recruitment, growth and mortality of individual animals.

Given the current unresponsiveness of sessile epifauna in the Lundy NTZ and uncertainty about mechanisms and time-scales of potential indirect effects in the future, we recommend a temporary cessation of the current monitoring programme. Based on studies elsewhere in the World where marine reserves have indirectly affected the sessile benthos, we suggest that monitoring of sessile epifauna at Lundy might be usefully resumed after an interval of 5-10 years.

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1 INTRODUCTION

This report describes a programme of monitoring and analyses to assess potential effects of the Lundy fisheries No-Take Zone (NTZ) – the United Kingdom's first statutory NTZ – during the first 5 years post-designation (2003 to 2008).

This section gives an introduction to Lundy's marine natural history and discussion of its national and international significance for nature conservation. There is then a brief review of the rationale for NTZs (and other forms of Highly Protected Marine Area – HMPA) and the available empirical evidence of their effects when implemented. This section concludes with a statement of the managerial goals for the Lundy NTZ and the hypotheses about potential effects of the NTZ that informed the monitoring programme.

1.1 Lundy

1.1.1 Natural history

Lundy is an island in the Bristol Channel (51° 10' N, 4° 40' W). The closest mainland coast is North Devon, which lies ~18km to the south. Lundy is about 5km long and about 1.25km wide and its long axis lies approximately north-south. The island is formed from single, flat-topped granite outcrop that rises abruptly from the sea to a height of around 130m above sea-level.

Lundy's significance for marine life is the fact that it is the only substantial rock outcrop in a region where the seabed is dominated by sedimentary habitats (mud, sand and gravel). As such, it provides essential habitat for many kinds of marine life that reside nowhere else in the vicinity. Best known of these are Lundy's diverse and prolific assemblages of filter-feeding animals, many of which are nationally rare or scarce; *e.g.* the branching sponges *Axinella dissimilis* and *Raspalia ramosa*, the trumpet anemone *Aiptasia mutablis*, and a variety of stony and soft corals. These mainly occur on rock surfaces below 15-20m; shallower rock surfaces are dominated by macroalgae.

Filter-feeding animals are particularly prolific around Lundy because it is situated in the midst of the productive, tide-swept waters of the Bristol Channel. The strong

currents that flow past Lundy provide a rich and steady supply of particulate food. The high diversity of Lundy's filter-feeding reef fauna arises from its situation at the boundary of the cold Boreal biogeographic province and warm temperate Lusitanean province, which means that both northern and southern species co-occur here. Lundy is one of very few marine sites around the UK where the ranges of northern and southern species of reef fauna are seen to overlap.

Further environmental complexity is provided by Lundy's shape and orientation. Lundy is very exposed to Atlantic weather-systems, which can send strong winds and powerful waves up the Bristol Channel from the west. The island is such an effective breakwater, however, that there is generally only negligible wave-action on the east coast in such conditions. The east coast is open to waves created by easterly winds, but these occur less frequently than waves from the west and owing to the shorter fetch they are typically less powerful. This difference in the degree of wave exposure between the east and west coast of Lundy produces differences in the assemblages of plants and animals inhabiting these coasts.

The same marine productivity that makes Lundy a favourable place for filter-feeding animals also supports a wealth of other marine life, from invertebrates like crabs (*e.g.* the brown or edible crab, *Cancer pagurus* and the spider crab, *Maja squinado*), lobster (*Homarus gammarus*) and scallop (*Pecten maximus*), to fishes like pollack (*Pollachius pollachius*), wrasses (*e.g.* ballan wrasse, *Labrus bergylta* and cuckoo wrasse, *L. bimaculatus*) and seasonal visitors such as the sun fish (*Mola mola*) and basking shark (*Cetorhinus maximus*). Lundy also provides rich feeding grounds and an important breeding site for grey seal (*Halichoerus grypus*) and a variety of seabirds, including razorbills (*Alca torda*), guillemots (*Uria aalge*), kittiwake (*Rissa tridactyla*), Manx shearwater (*Puffinus puffinus*) and puffin (*Fratercula arctica*).

Because of Lundy's importance for wildlife it has a number of conservation designations, national and international. Above the mean low water (MLW) mark, the majority of Lundy is designated as a Site of Special Scientific Interest (SSSI). In 1986, the shore and seas around Lundy were designated as Britain's first Marine Nature Reserve (MNR) (Figures 1 & 2). More recently in 2000, in

recognition of the international significance of its marine habitats and species, Lundy acquired the status of Special Area of Conservation (SAC) under the European Union's Habitats Directive. The key features of the Lundy SAC are its reefs and caves, subtidal sandbanks and the resident population of grey seals.

1.1.2 Rationale for the Lundy No-Take Zone (NTZ)

Despite Lundy's numerous conservation designations, English Nature (now 'Natural England'), the statutory conservation advisers for the site, considered that some of the island's important marine habitats and species were not adequately safeguarded from human disturbances. English Nature's principal concerns were potential impacts of commercial and/or recreational fishing. Prompted by this, English Nature proposed that some substantial proportion of Lundy's priority habitats should be protected from all forms of fishing and collecting of marine life via a statutory No-Take Zone (NTZ).

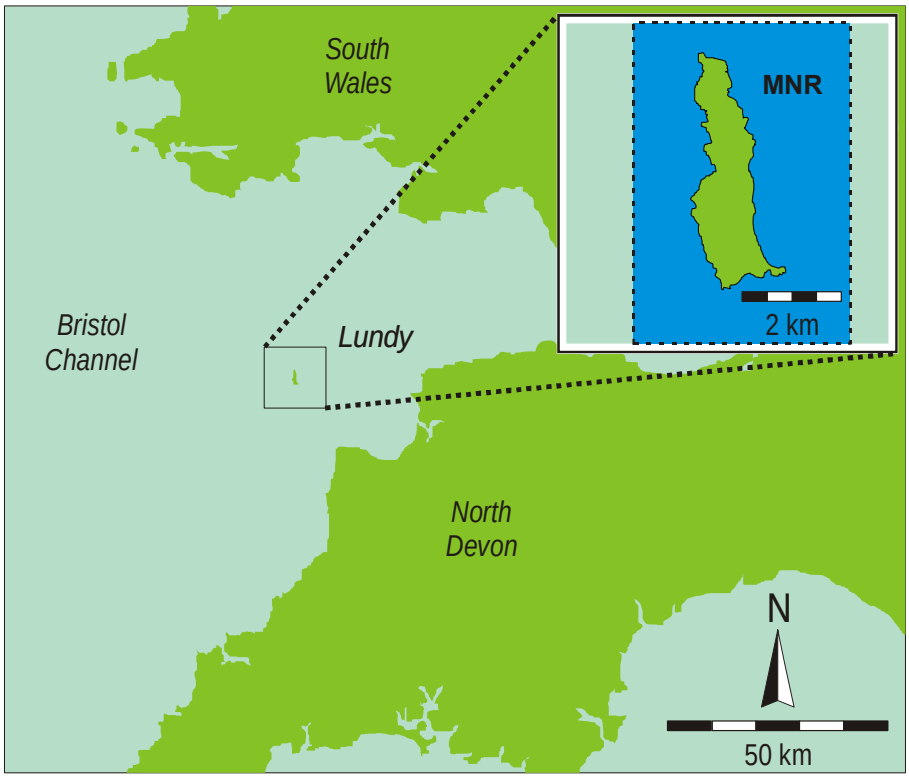

Figure 1. Location of Lundy in the Bristol Channel, between North Devon and South Wales. Inset shows the boundary of the Marine Nature Reserve (MNR) around Lundy.

1.1.3 Potential fisheries impacts around Lundy

When the Lundy NTZ was first proposed, the principal commercial fishery within the Lundy MNR was fishing with baited pots for lobsters and crabs. At this time, the MNR already provided a 'Refuge Zone' around Lundy (the yellow area in the schematic of the zoning scheme; Figure 2) in which fishing with mobile gear (*i.e.* trawls, dredges, etc.) and static gill-nets were banned via a Devon Sea Fisheries byelaw. The MNR's Refuge Zone extends 0.1-1.5km offshore from Lundy (according to the approximate seaward distance of the 30m isobath). This zone was intended to protect circalittoral rocky habitats, but it also protects a number of archaeologically important shipwrecks that are also vulnerable to damage by some types of fishing gear. Despite the existence of the byelaw, it is generally acknowledged that there has been an ongoing low-level of non-compliance by commercial fishermen. Of greatest concern are boats fishing with mobile bottom gear that occasionally stray, perhaps inadvertently, into the refuge zone (Chris Davis, English Nature, pers. comm.). This is mainly only an issue on the eastern side of Lundy and in the north-west corner of the MNR where the seabed is sedimentary. The likelihood of enforcement against such illegal activities is very low because a sea fisheries patrol vessel is only active on the north Devon coast for two weeks per year.

As well as allowing commercial fishing with static gears, the MNR byelaw also allowed various forms of recreational fishing and harvesting to occur around Lundy. Anglers fish from boats and from the shore and mainly catch species such as mackerel, pollack, bass, dogfish and rays. Scuba divers mainly target shellfish such as scallops, crabs and lobsters, but may also take flatfish (*e.g.* plaice) and rays opportunistically (Chris Davis, Natural England and Keith Hiscock, Marine Biological Association of the UK; personal communications). Because Lundy is an attractive location relatively accessible from several towns and villages on the north Devon coast, it is regularly frequented for these purposes. There are a number of diving clubs on the north Devon coast that visit Lundy often to collect shellfish. The east coast of Lundy is particularly amenable to diving and angling from small boats because it sheltered from the prevailing westerly wind and waves. Spear-fishing is the only form of recreational fishing that was banned

under the MNR byelaw. Whilst the general makeup of recreational fishing and harvesting activity at Lundy is reasonably well-known, there is no precise data on the spatial distribution of individual activities, their temporal trends or catches of particular species.

Despite initial measures to reduce and regulate fishing activity within the Lundy MNR, the forms of fishing that continued still presented a number of potential concerns for nature conservation. These include both direct and indirect potential impacts on marine habitats and species.

Fishing can cause several types of impact on marine ecosystems. First and most-obvious is the impact due to depredation of the target species. Most forms of commercial fishing gear used in UK waters also capture and often kill a range of by-catch species, including undersize commercial fishes, non-commercial fishes (*e.g.* wrasse, dragonets, rockling and even basking shark) and a diverse range of epibenthic invertebrates (*e.g.* starfish, sea urchins, hermit crabs, shrimps, erect sponges, ross coral, pink sea-fan, etc.). Towed fishing gears such as bottom trawls and dredges can also cause immense physical disturbance to benthic habitats, including the re-suspension and homogenization of sediments, fracturing of rocks and over-turning of boulders. Where these gears remove erect, sessile taxa such as sponges, soft corals and bryozoans, the loss of 'biological architecture' that they provide is a further important form of physical habitat disturbance. Whilst bottom trawling and dredging present the greatest threats to erect epifauna, they may also be detached from the seabed or damaged via entanglement in bottom-set gill nets (M. Hoskin; personal observation).

Since erect sessile species are typically slow-growing and long-lived their destruction by commercial fishing is considered to be one of its most negative consequences. As well as removing species that have long-recovery times and which may never recover if frequently disturbed, these erect sessile fauna are often an ecological resource (*e.g.* habitat, food, refuge, etc.) for a second, even more diverse suite of organisms (Hartnoll 1975, Hayward & Ryland 1979, Klitgaard 1995, Fish & Fish 1996, Koukouras *et al.* 1996, Cocito *et al.* 1998, Jackson & Hiscock 2000). Some of the species associated with erect sessile fauna occur on

an extremely limited number of hosts *e.g.* the nudibranch *Tritonia hombergi*, which is most commonly associated with *Alcyonium digitatum* (dead men's fingers) (Picton & Morrow, 1994) and the anemone *Amphianthus dohrnii*, ditto on *Eunicella verrucosa* (Hiscock, 2004). The biological architecture provided by erect macrofauna is also considered to be a critical resource for diverse demersal fishes (Sainsbury 1987, 1988, ICES 1994, Auster *et al.* 1996, Auster & Langton 1999, Kaiser *et al.* 1999).

Prior to the designation of the Lundy NTZ, however, the forms of commercial fishing that are considered to have the most negative environmental effects, specifically the various forms of trawling, dredging and gill netting (Hall 1999, Kaiser & de Groot 2000) were banned within the MNR in 1986. The main commercial fishery that remained, potting for lobsters and crabs, is relatively benign in terms of mortality of undersize and non-commercial species in the by-catch, since by-catch can usually be returned alive. Concerns have been expressed, however, about physical impacts of pots and pot-ropes on sessile epifauna within the Lundy MNR (Chris Davis, Natural England; personal communication).

Although potting and sea angling are relatively benign in terms of physical impacts on the seabed, they are not innocent of all impacts. Aside from the mortality of targeted species, potting and sea angling are associated with losses of gear capable of ghost fishing; *i.e.* gear that captures and kills marine life after it is lost. Pots are much worse than angling gear in this regard since they can continue ghost fishing until they are physically destroyed, which may take months or even years. Potting fisheries that are comparable to the Lundy lobster fishery lose approximately 10-30% of pots annually, either to storms or interaction with towed fishing gears (Smolowitz 1978, Breen 1987).

1.1.4 Designation of the Lundy NTZ

The purpose of the Lundy NTZ was to ensure that at least some part of the Lundy MNR was protected from all forms of fishing. It came into effect under a byelaw from the local Sea Fisheries Committee at the beginning of 2003. The NTZ spans ~3.6km (or ¾) of the east coast of Lundy between latitude 51° 12.04' N and 51°

10.07' N. It extends ~1km east from Lundy's shore out to longitude 4° 39.00' W and encompasses an area of ~4km^2 (Figure 2). Rocky and sedimentary habitats are present within the NTZ, with the latter occupying the greater portion. Apart from a small number of isolated outcrops, rock habitats only occur within ~100m of the shore.

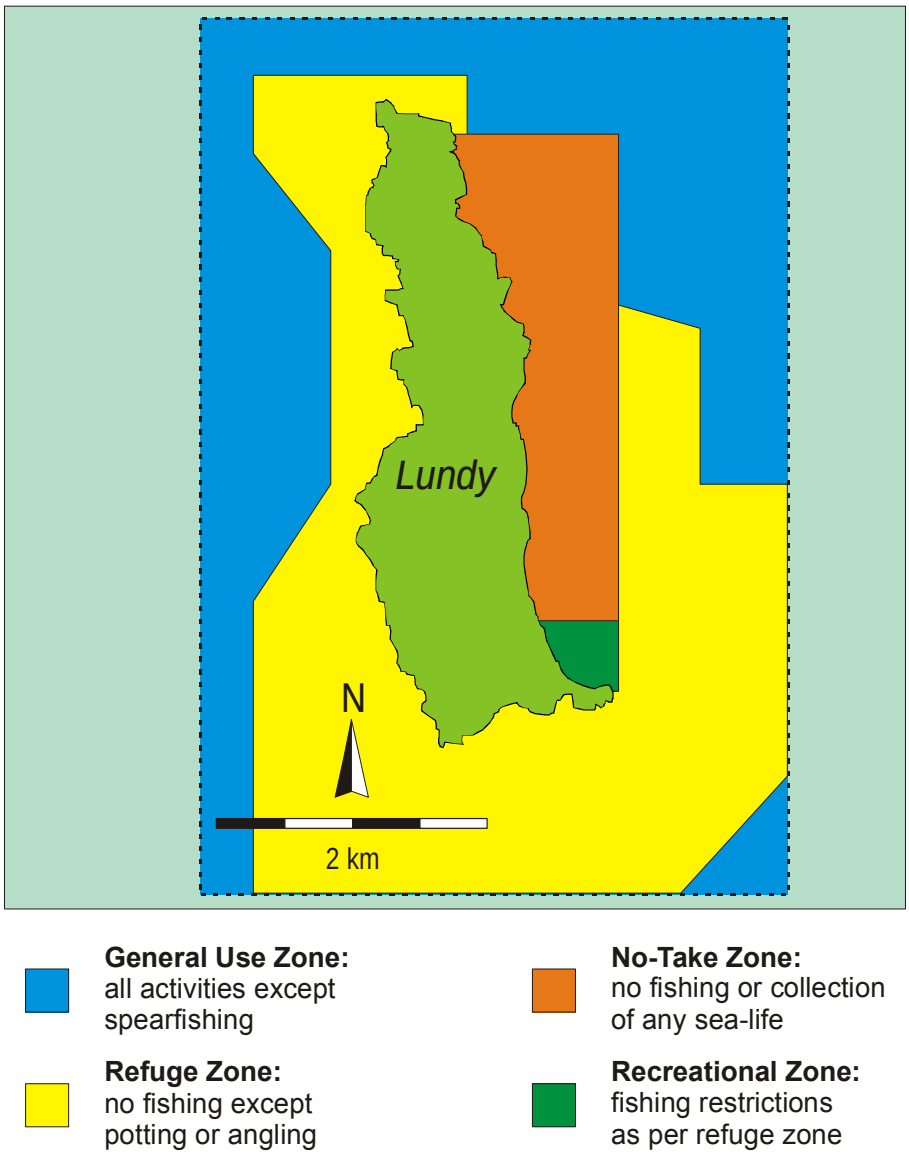

Figure 2. Zoning scheme for the Lundy MNR, which since 2003 includes the Lundy No-Take Zone (Natural England 2008).

1.2 NTZs for fisheries management and marine conservation

1.2.1 Failings of traditional managerial approaches

Beginning in the 1990s, many marine scientists and conservation biologists became increasingly concerned that traditional ways of managing fisheries and the wider marine environment were failing in their objectives – many commercial stocks were in persistent decline and there was a growing appreciation of the nature and scale of fisheries impacts on non-target species and ecologically important habitat features (Marine Conservation Biology Institute 1998). Arising from this perception was the idea that some fisheries and marine ecosystems would only survive in the long-term if there were some places where they were completely protected from all forms of fishing – so-called No-Take Zones. This view was forcibly represented in the statement '*Troubled Waters: A Call for Action'*, which was signed by 1,605 marine scientists and conservation biologists from 70 countries.

Prior to the 1990s, it was generally the case that fisheries were managed separately from other aspects of the marine environment and the focus in each case was generally the biology of individual species rather than structure and functioning of ecosystems. Fisheries science was principally concerned with modeling the dynamics of single-species stocks. Marine conservation biology was preoccupied with the effects of pollutants at organismal and sub-organismal levels in so-called 'indicator species'. The rising tide of support for NTZs has been stimulated by four main factors.

1. The perception that traditional approaches to fisheries management, informed by single-species models and implemented via complex, poorly enforced, politically manipulated systems of size-limits, quotas and other technical measures, were failing to prevent over-exploitation of stocks.
2. Increased awareness of complex, multidirectional interactions between fish stocks and their biotic and abiotic environments that were either ignored or grossly simplified in single-species models.

3. The increased involvement of ecologists in fisheries-related research gave rise to numerous studies revealing the often alarming environmental disturbances and ecological impacts caused by fishing.

4. Initial models and empirical trials of no-take zones indicated significant benefits for fish stocks, non-target species and the habitats that support them.

(Dugan & Davis 1993, Roberts & Polunin 1993, Tundi Agardy 1994, Ballantine 1996, Lauck *et al.* 1998, Pinnegar *et al.* 2000, Sumaila *et al.* 2000, Norse 2003).

1.2.2 Potential benefits of NTZs

Reviews of the now-extensive body of empirical evidence all conclude that NTZs (and other forms of HMPA) can trigger lasting, often rapid, increases in the abundance, diversity and productivity of marine organisms (Roberts & Polunin 1991, Dugan & Davies 1993, Sánchez Lizaso *et al.* 2000, Côté *et al.* 2001, Jennings 2001, Halpern & Warner 2002, Lubchenco *et al.* 2003). The potential for NTZs to promote local enhancement of natural populations is of interest for both biodiversity conservation and fisheries management. Of further and perhaps even-greater interest to fisheries managers is the theory that increased production within NTZs can 'spillover' into surrounding areas via adult migration and larval dispersal causing increased catches in these areas (Dugan & Davis 1993, Roberts & Polunin 1993, Rakitin & Kramer 1996, Guénette *et al.* 1998). Direct evidence of 'spillover' benefits to fisheries is much more limited, however, than evidence of enhanced production within NTZs (*e.g.* Yamasaki & Kuwahara 1990 (cited in Gell & Roberts 2002), Russ & Alcala 1996, McClanahan & Mangi 2000, Roberts *et al.* 2001, Goñi *et al.* 2006). If such effects were a commonplace effect of NTZs, this would be compelling argument for their widespread use as a tool for fisheries management.

Areas free from fishing disturbance can also serve as the essential controls in experiments to measure the effects of fishing (Ballantine 1996). At present there are very few such areas and it is often only by chance that they exist. Other favourable aspects of NTZs included their relative ease of enforcement and their

potential to stimulate 'spin-off' socio-economic benefits via eco-tourism/recreation, research and education (Ballantine 1996).

1.2.3 Potential failings of NTZs

Clearly, there are many potential benefits to NTZs, but it would be wrong to assume that they are always successful and universally desirable. Aside from objections from fishermen that NTZs deny their 'right to fish' (usually assumed, but not always) there are many reasons to caution against uncritical advocacy. Several fisheries scientists have questioned the need for NTZs by challenging the underlying premise that traditional fisheries management has failed. They argue that the over-exploitation of many of the world's fish stocks is the result of poor management many years ago and that current approaches are reversing those declines without needing no-take zones, (*e.g.* Grimes & Ralston 2003). This assumes, however, that the sole purpose of NTZs is fisheries management. Most advocates of NTZs would argue, however, that protection of the wider environment for its inherent value is just as important and often more so.

The less-easily countered criticisms of NTZs turn on *how* rather than *whether* they are implemented and concern issues of purpose, design, enforcement and the assessment of effects. These criticisms present the caution that some NTZs may fail to provide any benefits to fisheries or the wider marine environment and that in the absence of proper assessment, failures may go unnoticed.

Experience shows that the most effective no-take zones are generally those that begin with specific biological objectives in mind (fisheries and/or conservation) and are then designed for that purpose on scientific principles (Roberts *et al.* 2003a & b, Bernstein *et al.* 2004).

The foremost design-criterion for a NTZ is its location. Clearly, a NTZ can only benefit a particular species or habitat if it is located in an area that supports that species or habitat and, ideally, somewhere that it is well represented. To benefit a mobile or migratory species, a NTZ should contain resources that are critical for at least some part of its life-history; *e.g.* food, refugia from predators, habitats or

other features associated with mating or spawning aggregations, migration bottlenecks, etc.

After location, the next most important design criterion is the size of the NTZ. For restoration and conservation goals the benefits of a NTZ generally increase with size (*e.g.* Margules *et al.* 1998, Edgar & Barret 1999, Dayton *et al.* 2000, Roberts & Hawkins 2000), however, even small NTZs (<1km^2) can yield detectable benefits (Halpern 2003) for some species.

When NTZs are intended to provide benefits to fisheries, their size is a much more important consideration than when restoration or conservation is the goal (Hilborn 2003, Roberts *et al.* 2003b). In this regard, it is not size *per se* that is the critical issue, but size relative to the scale of dispersal in the species of interest. When the NTZ is very large relative to the scale of dispersal, benefits that accrue within the NTZ are not exported to outside areas. When the NTZ is very small compared to the scale of dispersal, the boost to protected stocks is generally less and any benefit that's exported is spread so thinly as to be insignificant. Another aspect of area that has consequences for the effectiveness of a NTZ is its relationship to edge effects. It is a rule of geometry applicable to any given shape that as area decreases the ratio of perimeter to area increases. The more perimeter a NTZ has relative to its area, the more effective it is at exporting individuals to outside areas (Roberts *et al.* 2003b). Where fishing is concentrated around the edge of a NTZ (which often occurs; see examples cited in Gell & Roberts 2002), a small NTZ may be so efficient at exporting individuals to the fishery that it provides little or no protection. This is one of the reasons why the local enhancement effect of NTZs generally increases with area.

Compliance and enforcement are critical determinants of the success of a NTZ. There is little point in calling an area a NTZ if it is not respected and enforced. Almost all of the well-known, successful NTZs around the World have been statutory NTZs subject to robust policing and the threat of legal enforcement.

1.3 Monitoring the effectiveness of NTZs

Since there are several reasons why NTZs could fail in their objectives it is sensible that any that are implemented are subject to rigorous monitoring to evaluate their performance. There are three important reasons for doing so.

The first reason for monitoring is that it provides an important mechanism for auditing the effectiveness of management. Where a government agency is tasked with maintaining or enhancing the well-being of specific living marine natural resources, be they commercial stocks or features of conservation interest, it is important that both the agency and society at large know whether that responsibility is being fulfilled.

Second, designation of a NTZ requires that people who are accustomed to using the area for commercial fishing and/or recreational harvesting must cease doing so. These people may feel entitled to robust proof that significant environmental benefits are actually accrued from their perceived socio-economic disbenefits. Should the come to the opinion that their loss achieved no compensatory environmental gain it would undermine their confidence in the fairness and competence of resource managers. Such occurrences would make it harder for resource managers to implement other, perhaps better-conceived, NTZs elsewhere in the future.

Third, by monitoring the consequences of their actions, natural resource managers can learn from their successes and failures and, over time, improve their overall effectiveness in the design and implementation of NTZs.

1.3.1 Effective monitoring of NTZs

The first requirement for effective monitoring of any managerial action with respect to the environment is an *a priori* decision as to what outcome would constitute (and demonstrate) success. Once a 'success goal' has been set, it must be translated into a precise, testable hypothesis to inform the design of a programme of sampling and statistical analyses that will test that hypothesis reliably (Underwood 1995, 1998). Without a testable *a priori* hypothesis, monitoring yields results that are ambiguous and sometimes impossible to interpret with respect to

the broad objectives of the study. Hypotheses are implicit in managerial decision-making, but this fact may be overlooked if managers believe that the decision to act (or not to act) is the end-point of management.

Implicit in the decision to implement a NTZ is the general hypothesis that a population or populations inside the NTZ will experience positive changes (*e.g.* increased abundance, size, fecundity of individuals, etc.) that are significantly greater than those experienced by similar populations in areas that continue to be fished. Testing this hypothesis requires that time-series data from the NTZ is compared with contemporaneous data from similar places that are not NTZs.

1.4 Monitoring the Lundy NTZ

1.4.1 Subjects of investigations

In view of the main fishing activities that were excluded from the Lundy NTZ, its features of conservation interest and an assessment of what was logistically feasible (within the set budget), it was decided that the evaluation of the NTZ would focus on the following three components of Lundy's marine fauna:

1. populations of four species of commercially-fished crustacean - the lobster (*Homarus gammarus* (Linnaeus 1758)), brown crab (*Cancer pagurus* (Linnaeus 1758)), velvet crab (*Necora puber* (Linnaeus 1767)) and spider crab (*Maja squinado* (Herbst 1788));
2. populations of the scallop, *Pecten maximus* (Linnaeus 1758); and
3. an assemblage of species of sessile epifauna in circalittoral rocky habitats. This assemblage includes *inter alia* several species that are priorities for nature conservation; *e.g.* pink sea fan (*Eunicella verrucosa*), erect branching sponges (*e.g. Axinella dissimilis, Homaxinella subdola, Raspalia ramosa*), soft corals (*e.g. Alcyonium digitatum* and *A. glomeratum*) and ross coral (the bryozoan *Pentapora fascialis*) (Taxonomic authorities for these and the other species in the assemblage of interest are provided in Table 3, Section 2.3.1).

1.4.2 Testable hypotheses for evaluating the Lundy NTZ

The three monitoring programmes for evaluating the Lundy NTZ were each designed to provide tests of a number of hypotheses. With one exception these were all univariate hypotheses premised on the general model that the NTZ would remove or reduce fishing-related disturbances, which would cause previously impacted populations of marine species within the NTZ to increase in number, and in some cases size, relative to those in similar places where fishing was ongoing. The only exception was the hypothesis (Hypothesis 6, below), which was a multivariate hypothesis that only applied to sessile epifauna. This hypothesis was designed to test the model that ecological effects of the NTZ would indirectly benefit some species of epifauna and/or disadvantage other species, causing a change in the overall composition of this assemblage.

Monitoring programmes for scallops and epifauna provided tests of hypotheses about potential changes within the NTZ *versus* nearby control areas also at Lundy. Monitoring of lobsters and crabs was more complex in that it provided an additional test for changes within controls areas at Lundy *versus* reference areas 10's of km away; this allowed for an investigation of potential changes that might indicate spillover effects.

The specific hypotheses that were tested were as follow:

For lobster and crabs:

- **Hypothesis-1:** The mean abundances of commercially-fished crustaceans will increase in the NTZ relative to mean abundances in areas that continue to be fished.
- **Hypothesis-2:** The mean abundances of commercially-fished crustaceans will increase within the NTZ and adjacent areas relative to mean abundances in more-distant areas that continue to be fished. Acceptance of this hypothesis would only indicate that spillover may have occurred (there may be other explanations for these changes). Rejection of this hypothesis, however, would prove that spillover had not occurred.

- **Hypothesis-3:** The mean sizes of commercially-fished crustaceans will increase in the NTZ relative to mean sizes in areas that continue to be fished.

For scallops:

- **Hypothesis-4:** The mean abundance of scallops (*Pecten maximus*) within the NTZ will increase relative to mean abundances in areas where scallops continue to be harvested.
- **Hypothesis-5:** The mean size of scallops (*Pecten maximus*) within the NTZ will increase relative to mean sizes in areas where scallops continue to be harvested.
- **Hypothesis-6:** The size-structure of the scallop population within the NTZ will change relative to that in areas where scallops continue to be harvested.

For sessile epifauna in circalittoral rocky habitats:

- **Hypothesis-7:-** The assemblage composition of sessile epifauna in circalittoral rocky habitats inside the NTZ will change relative to the composition of assemblages in similar habitats where fishing continues.
- **Hypothesis-8:** Abundances of individual species of sessile epifauna in circalittoral rocky habitats inside the NTZ will increase relative to their abundances in similar habitats where fishing continues.

1.4.3 General scientific approach to monitoring the Lundy NTZ

If circumstances had allowed it, it would have been best to have used a Before-After/Control-Impact (BACI) monitoring design to test hypotheses about potential effects of the Lundy NTZ (*e.g.* Underwood 1992a & b, 1993, 1994, 1996) (the word 'impact' reflects the fact that these designs were developed for assessing the environmental effects of anthropogenic disturbances). BACI monitoring is generally recognised as being the most powerful and reliable form of monitoring for determining causal processes in ecology, including the potential effects of human interventions such as the implementation of NTZs (*e.g.* Guidetti 2002). BACI monitoring involves collecting data that is appropriate to the ecological

hypothesis of interest in 'impact' and 'control' sites, both before and after the commencement of the environmental change (anthropogenic or natural) whose potential effects are under investigation. If the hypothesised effect occurs, it will be manifested as a change in the relationship between control and impact sites, from before to after (*i.e.* a spatio-temporal interaction).

Unfortunately, the managerial decision to monitor potential effects of the Lundy NTZ was made after it was established, so the only option was a 'post-impact' sampling design (*i.e.* one comparing NTZ and control locations after designation of the NTZ). The present monitoring programme began in the summer of 2004, which was 18 months after the NTZ was designated. The consequence of post impact monitoring is reduced certainty in the interpretation of results. The absence of before data increases the risk that natural variations are mistaken for effects of the NTZ; this might occur if fauna within the NTZ underwent some unique natural change that was unrelated to the NTZ.

2 MATERIALS AND METHODS

2.1 Lobsters and crabs

2.1.1 Sampled species and variables

Potential effects of the Lundy NTZ were assessed for four species of commercially-fished crustaceans. These were *(i)* lobster (*Homarus gammarus*); *(ii)* brown crab (*Cancer pagurus*); *(iii)* spider crab (*Maja squinado*) and *(iv)* velvet crab (*Necora puber*).

The purpose of monitoring was to test the hypotheses that mean abundances and body-sizes of these species would increase within the NTZ relative to locations where normal commercial potting continued.

2.1.2 Sampling lobster and crabs

Lobsters and crabs were sampled using standard commercial shellfish pots deployed and retrieved from a suitably equipped boat. The pots were 71cm-length 'parlour pots' with 25cm entrances (Figure 3). This type of pot catches both lobster and crabs (Lovewell *et al.* 1988). The alternative 'ink well' pot is less suited to catching lobsters as they can readily escape from them. For sampling, pots were baited with salted whole mackerel, which attracts both lobster and crabs.

Figure 3. *(i)* A parlour pot; *(ii)* pot bait, salted mackerel (© M. Hoskin).

2.1.3 *Spatial aspects of the sampling design*

The programme of monitoring for lobster and crabs was designed to assess potential effects of the Lundy NTZ on abundances and body-sizes via comparisons at smaller (<1km) and larger (10-100km) spatial scales. At the smallest scale, there was a comparison between the NTZ and two adjacent control locations ('Near Controls'). At the larger scale, there was an additional comparison between the NTZ and two 'Far Reference' locations. One of these Far

Reference locations was ~20km from Lundy on the North Devon coast, near Hartland Point. The other Far Reference location was ~90km from Lundy on the coast of Pembrokeshire, South Wales, near the fishing village of Solva (Figure 4). Near Control and Far Reference locations were approximately the same size as the Lundy NTZ (areas ~3 to 4km in length, parallel to shore, and ~100m wide). The only major environmental difference among locations was that the NTZ and the North Devon Far Reference location were generally slightly shallower and more protected from prevailing westerly wave conditions compared to the other locations (10-20m depth of water *versus* 15-30m). It was assumed, however, that these natural environmental differences would not have any significant net effect on the relative favourability of these areas to lobsters and crabs. This assumption was supported by two factors. First, our prior experiences and advice from several shellfishermen all indicated that whilst lobsters and crabs generally disfavour wave-exposed locations, this becomes less apparent as the depth of water increases. Consistent with this, all sampling locations were (or in the case of the NTZ, were once) important areas for commercial lobster and crab fishing. Problems for the study would only have been expected if one or more sampling location had been exceptionally shallow and wave-exposed.

The advantage of comparing abundance data from the NTZ with data from Near Control and Far Reference locations is that it increased the capacity of the study to differentiate between potential effects of the NTZ and small-scale natural variations that might have resembled such effects. A further advantage of this sampling design is that it provided some capacity to detect potential 'spillover' effects arising from any increase in abundance within the NTZ. It was expected that spillover should cause abundances to increase within Near Control locations (becoming more like that within the NTZ) whilst abundances in Far Reference locations remain more-or-less unchanged. It was assumed that Far Reference locations were far enough away from Lundy to be unaffected by any spillover from the NTZ. It is important to note, however, that raised abundances within the NTZ and Near Control locations would not prove that spillover had occurred as a natural increase local to Lundy might produce the same result. Nevertheless, the absence of such changes would prove that spillover had not occurred.

For monitoring purposes, each location (NTZ, Near Control and Far Reference) was divided into two replicate sites, each ~1 to 1.5km in length parallel to the shore.

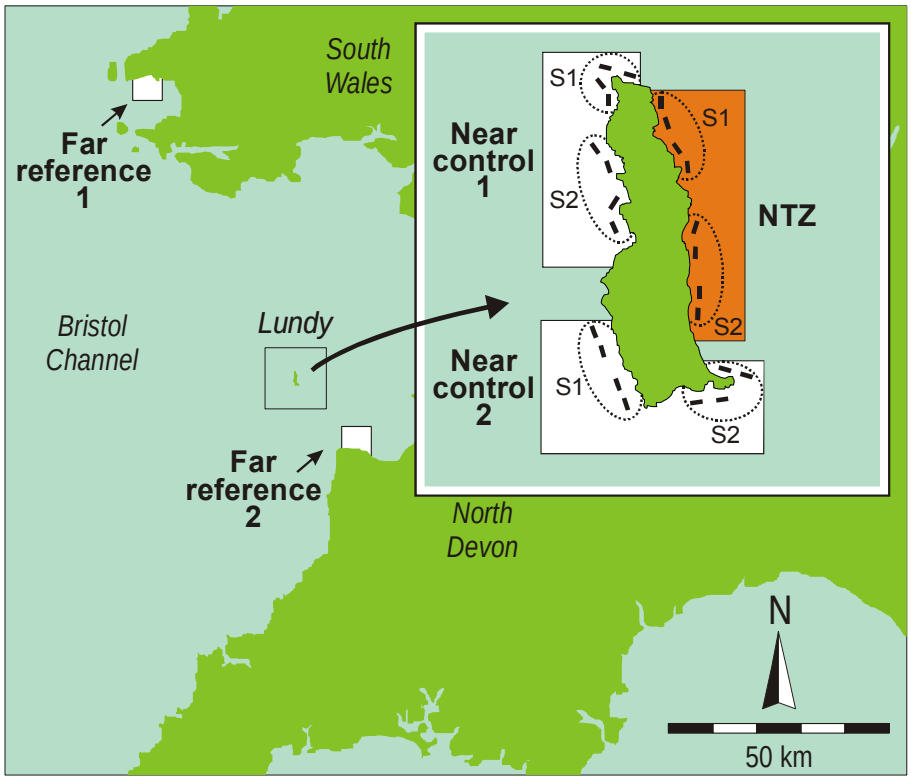

Figure 4. Sites of sampling for the potting study to assess effects of the Lundy NTZ on lobster and crabs.

Pots were deployed in 'strings' of 10, with approximately 15m between each pot. At both ends of each string of pots there was a heavy metal weight (~20 kg) serving as an anchor and a rope attached to a surface marker-buoy or 'dahn'. Each string of pots was recovered or 'hauled' by first retrieving one or other of its dahn-lines. Whilst hauling pots, care was taken to ensure they were lifted vertically and not dragged laterally across the seabed, which could disturb the benthos.

Adjacent pots on a string were sufficiently close to each other that they could not safely be considered as independent replicates (an important requirement for unbiased, independent sampling). To be a true 'replicate' in an experiment, samples must be obtained independently of one another; *i.e.* the sampling of one

datum must neither affect, nor be affected by, the sampling of other data (Underwood 1997). Here for instance, the presence of lobsters in one trap should neither deter nor attract lobsters encountering other pots (see Miller 1983 for a discussion of such interactions). Although there has been no detailed investigation of such interactions for the species sampled here, they are known for other crustacea that are harvested in baited traps (Miller 1983, Kennelly & Craig 1989). Hence, strings of pots rather than individual pots were the sampling unit for the study.

Monitoring involved sampling with four strings of 10 pots in each of the two sites per location (giving 80 pots per location). Within each site, strings were set in sequence along and parallel to the shoreline with 50-100m between adjacent strings. The same sites in each location were sampled in each year of monitoring.

2.1.4 Temporal aspects of the sampling design

Given the mobility of lobsters and crabs and the use of baited pots for sampling, it was expected that behavioural variability would mean a relatively great degree of day-to-day variation in catches. To increase the precision of annual population estimates of mean size and abundance it was decided that in each location in each year there would be five replicate days of sampling (which was the maximal possible under budgetary constraints). It was intended that sampling would be replicated over five consecutive days, with pots therefore having a ~24-hour 'soak' prior to each sampling event. To reduce potential problems with short-term temporal variation further, all sampling was done within the same period of year (June/July) each year.

On three occasions, weather conditions forced a situation where pots soaked for ~48 hours before sampling; this happened twice in the South Wales Reference location (in 2004 and 2005) and once in the NTZ (in 2007). Also, in 2007 whilst sampling at Lundy during 29th June to 4th July, poor weather meant that only one day of sampling could be completed in Near Control locations on the exposed west coast. Despite poor weather at this time, we were able to complete all five days of sampling within the NTZ. Completing the sampling of Near Control locations in 2007 required an additional two trips; three sets of samples were

obtained on the 14th, 15th and 16th July and the fifth and final set of samples was eventually obtained on 21st July. In total, 48-hour soaks and other instances of non-consecutive sampling occurred in 5% of sampling events.

Whilst it might be assumed that a longer soak-time would increase the catch proportionately, evidence suggests that when soak-time is five days or less, small-variations in soak-time have no consistent and significant effect on the catch rate of lobsters (Bennet & Lovewell 1977). Thus, whilst there was little cause for concern about systematic bias, it was expected that 48-hour soaks and the two other instances of non-consecutive sampling might introduce additional variance (or 'noise') to the data. This was expected to be only a negligible influence, however, and unlikely to complicate efforts to detect an effect of the NTZ.

Because of logistical constraints and the number of pots available to the study (240 in total), lobster and crabs could not be sampled simultaneously in all locations. The only locations sampled simultaneously were those at Lundy (*i.e.* the NTZ and the two Near Control locations). In each year, logistical necessity required that sampling was done first in North Devon, then in South Wales and finally at Lundy. The precise dates on which the different locations were sampled in each year are given in Table 1. Our inability to sample all locations simultaneously meant that some spatial differences were potentially confounded with an unknown amount of temporal (weekly) variation. It was considered unlikely, however, that sampling the different locations in the same order each year would cause any problems of bias, since there was no reason to expect any consistent tidal or weather trend during the sampling 'window' in each year.

Table 1. Beginning and end dates for periods of sampling for lobster and crabs in each location in each of the four years of the study (2004 to 2007).

	Start and finish dates of each sampling period:			
Sampling location	**2004**	**2005**	**2006**	**2007**
Lundy NTZ	26-30 July	21-25 June	29 June–3 July	29 June–4 July
Near Control 1 (Lundy)	26–30 July	21-25 June	29 June–3 July	29 June–21 July
Near Control 2 (Lundy)	26-30 July	21-25 June	29 June–3 July	29 June–21 July
Far Reference 1 (S Wales)	7-12 July	12-17 June	15-19 June	14-18 June
Far Reference 2 (N Devon)	19-23 July	6-10 June	9-16 June	7-11 June

2.1.5 Measurement of variables and other methodological details

For lobster and crabs, the measure of abundance used in the study was the number of individuals per string of ten pots. As each string was hauled, lobsters and crabs were removed from the pots and placed in separate fish boxes according to species. A potential problem with storing lobster and crabs, especially brown crabs, in this way is that they are apt to damage or even kill each other with their powerful claws. We found, however, that several individuals could be kept in close proximity to each other within a box if they were quickly covered with a piece of carpet dampened with seawater. Having covered several individuals thus, subsequent individuals were placed in layers above them until the

box was full. No attempt was made to identify which individuals came from which pot in the string.

Once each string had been hauled and cleared of its catch, pots were re-baited if needed and the string was immediately re-deployed in approximately the same position. The measuring of crabs and lobsters and their return to the sea proceeded whilst the string of pots was being re-deployed. This meant that the catch was evenly re-distributed in the area from which they had been caught.

For lobsters, the measure of size was carapace length – the distance from the rear of the eye-socket to the posterior edge of the carapace – measured to the nearest millimetre (Figure 5). Measurements of carapace length were made using a Vernier caliper. For crabs, the measure of size was carapace width, measured at the widest point using either the Vernier calliper, or a measuring board if the shell was wider than the maximum gape of the calliper (~15cm). Data were recorded on pre-prepared data sheets printed onto waterproof paper.

Figure 5. A lobster having its carapace length measured with a Vernier caliper (© M. Hoskin).

2.1.6 *Analysis of the abundances of lobster and crabs (Hypotheses-1 and 2)*

Hypotheses about potential effects of the NTZ on mean abundances of lobster and crabs were tested via analysis of variance (ANOVA). With the exception of lobster, hypotheses about changes in abundance were tested using data that comprised all sampled individuals, regardless of size. For lobster, however, data on the abundance of individuals larger than the minimum landing size (MLS) (carapace length (CL) = 90mm) were analysed separately from abundance data for individuals smaller than the MLS. This was because interim analyses of abundance data for lobster (Hoskin *et al.* 2006) had revealed difference responses to the NTZ in these two size-classes (referred to subsequently as 'landable-sized' and 'undersized', respectively).

For lobster and crabs, analyses to compare NTZ *versus* Near Control locations were done separately from comparisons with Far Reference locations. The required ANOVA in each case was an asymmetric model, in which the single NTZ location was compared to the two Near Control locations (or two Reference locations, as appropriate) (see Underwood 1992, 1994, 1997, 2000, Glasby 1997 for information on the theory and application of asymmetric ANOVA to ecological monitoring). It was necessary to use two separate ANOVAs because a single model encompassing all the data would have had such complex asymmetry that the likelihood of obtaining valid F-ratios for the important ANOVA tests would have been excessively small (A.J. Underwood, pers. comm.). Asymmetric ANOVAs for the different variables were constructed in Microsoft Excel using sums of squares calculated by the ANOVA software GMAV5 (EICC, University of Sydney).

The ANOVA models for small-scale 'NTZ *versus* Near Control' comparisons and large-scale 'NTZ *versus* Far Reference' comparisons were computationally identical. The following explanation of this statistical model is given in terms of the 'NTZ *versus* Near Control' comparison, but with appropriate substitution of terms, it also describes the ANOVA model for the 'NTZ *versus* Far Reference' comparison.

The asymmetric ANOVA for analyzing data on the abundances of lobster and crabs was a mixed model comprising four experimental factors. The first factor

was LOCATION, for which there were three levels, the NTZ (a fixed component) and two Control locations (random components). The second factor was YEAR, which was a fixed factor with four levels (the years 2004, 2005, 2006 and 2007). The third factor was the random factor SITE, which was nested in LOCATION and had two levels (Sites 1 and 2 in each location). Factor four was the random factor TIME, which was nested in YEAR and had five levels (the five replicate days of sampling in each year). The testable factors in the asymmetric ANOVA model based on this experimental design are listed and interpreted in Appendix 1, Table A1.1 (the equivalent factors for the 'NTZ *versus* Far Reference' ANOVA are listed and interpreted in Table A1.2).

For tests of Hypothesis-1, the critical ANOVA factors were YE x LO: NTZ *v* CON for the small-scale comparison and YE x LO: NTZ *v* FAR REF for the larger-scale comparison.

The test for potential spillover (Hypothesis-2) required the two ANOVAs described above and an additional ANOVA that was only needed for this purpose. This third, ancillary ANOVA used abundance data from Near Control and Far Reference locations only and is described in full in Appendix 1, Table A1.3. Each of these different ANOVA's provided one of three parts of the test for potential spillover. These were:

Part 1: A test for increased abundance in both NTZ and Near Control locations from 2004 to 2007.

Part 2: A test for increased abundance in the NTZ relative to Far Reference locations.

Part 3: A test for increased abundance in Near Control locations relative to Far Reference locations.

Part 1 was tested via the factor YEAR in the ANOVA of abundance data for NTZ and Near Control locations. Part 2 was tested via the factor YE x LO: NTZ *v* FAR REF. Part 3 was tested via the factor DISTANCE x YEAR (with 'distance' meaning distance from the Lundy NTZ) in the additional ANOVA applied to data from Near Control and Far Reference locations only. This third ANOVA was only done where

significant changes consistent with Parts 1 and 2 of test for potential spillover had already been confirmed.

Prior to ANOVA, abundances of lobster and crabs per string of pots were transformed to either L*n*(*X*+1)-data (if the species was generally abundant) abundant, or L*n*(*X*+0.1)-data (if the species was only present infrequently). With either transformation, the hypothesis tested is one of relative rather than absolute difference among treatments (Underwood 1997). This was considered appropriate because changes in relative abundance are more-informative than changes absolute abundance when assessing the performance of a NTZ. A logarithmic transformation also has the general effect of reducing heterogeneity of variances, which reduces the rate of Type-I error in ANOVA tests (*i.e.* false rejection of a true null-hypothesis). In an experiment such as this, however, with a relatively large number of treatments and balanced sampling, mild heterogeneity of variances should not be problematic (Underwood 1997). Nevertheless, heterogeneity of variance was tested for each ANOVA using Cochran's Test (Cochran 1951), which is the most useful such test in this context (Underwood 1997).

Where appropriate, *post hoc* pooling of non-significant factors ($P > 0.25$; Winer *et al.* 1991) was done to give more powerful tests for ANOVA factors. Where factors with more than two levels were statistically significant, Student-Newman-Keuls (SNK) multiple comparison tests were used to separate significantly different levels of such factors.

For the purpose of describing and plotting results, the abundance of each species was expressed as the untransformed mean abundance per string of pots ± 1 standard error (SE).

2.1.7 *Analysis of the sizes of lobster and crabs (Hypothesis-3)*

Hypotheses about potential effects of the NTZ on the mean sizes of lobster and crabs were tested using untransformed data. The asymmetric ANOVA model used in this case was very similar to that used for testing hypotheses about abundances and 'NTZ *versus* Near Control' comparisons for size data were likewise analysed separately from 'NTZ *versus* Far Reference' comparisons. The only difference was that the factors SITE and TIME were dispensed with in the experimental design. The reason for doing so was that, for all species, there were some sites and times in which abundance was ≤1, in which cases a mean could not be calculated.

For consistency with ANOVA tests on the abundances of lobster, data on the sizes of individuals larger than the MLS were analysed separately from data for individuals smaller than the MLS.

The testable factors in the asymmetric ANOVA model for analyzing size data were a subset of those in the ANOVA model for abundance data: specifically, all those factors not containing SITE and/or TIME. The factors in common have the same general interpretation in each case (see Appendix 1, Table A1.4).

ANOVA requires balanced sampling to provide reliable tests; *i.e.* the same number of samples for each level of each factor (Underwood 1997). Given that abundances of lobster and crabs varied amongst locations and years, it was necessary to randomly dispose of 'excess' data until balanced sample sizes were attained. Because the four species of crustacean differed in their patterns of abundance, the sample-sizes used in tests on size data (and hence the power of these tests) also varied amongst species (Table 2).

All other aspects of analyses of size data were as per analyses of abundance data. *Post hoc* pooling of non-significant factors ($P > 0.25$; Winer *et al.* 1991) was done wherever possible to give more powerful tests, SNK tests were used to separate significantly different levels of factors and all results were reported in the format mean ± 1 standard error (SE).

Table 2. Sample sizes (*n*) for ANOVA tests of hypotheses about potential effects of the NTZ on the mean sizes of lobster and crabs.

	Sample size (*n*)	
Subject of ANOVA test	**NTZ *vs* Near Control**	**NTZ *vs* Far Reference**
Lobster > MLS (CL = 90mm)	22	31
Lobster < MLS	78	75
Velvet crab	10	10
Brown crab	5	5
Spider crab	12	12

2.2 Scallops

2.2.1 Sampling design and methodology for scallops

Monitoring was designed to test the hypotheses that scallops will increase in both size and abundance within the NTZ relative to control locations where harvesting continues. As per monitoring of sessile epifauna, scallops were sampled by scuba divers and there were no Far Reference locations in the monitoring design because of the prohibitive cost of diver sampling.

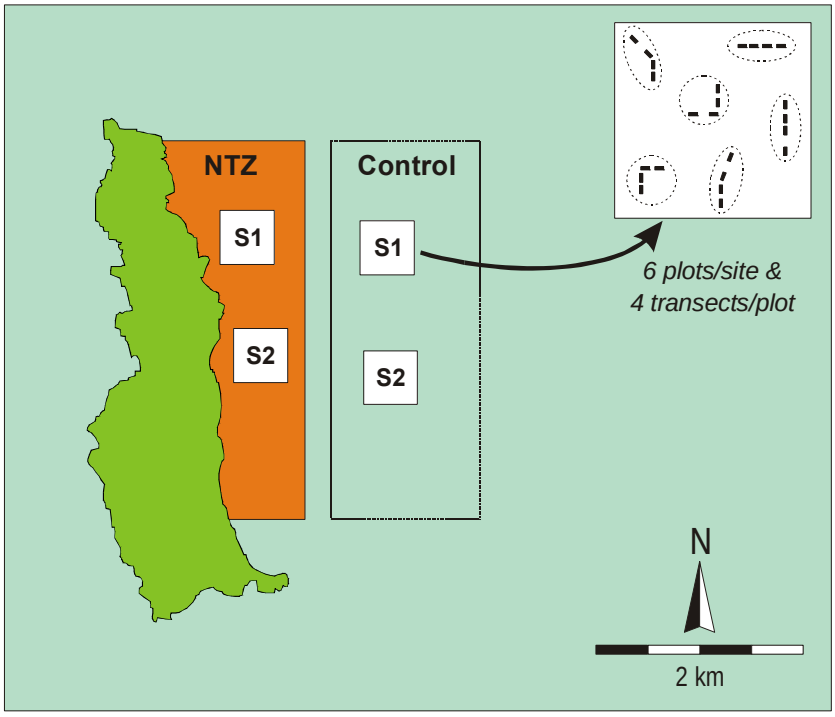

Figure 6. Sites of sampling for the diving survey of scallops.

The monitoring design for scallops compared two sites within the NTZ with two control sites to the east of the NTZ, but still within the Lundy MNR (Figure 6). The basic sampling unit for monitoring of scallops was a 10m x 3m transect, which was jointly sampled by a pair of divers. Within each site there were six plots with four transects per plot. It was intended that each plot would be completed by a pair of divers on a single dive. Power analyses of appropriate pilot data (Hoskin *et al.* 2004) indicated that with 24 transect-counts per site the monitoring programme for

scallops should have an 80% probability of detecting at least a 50% increase in scallop abundance due to the NTZ, if it occurred.

The area of each transect was delineated accurately on the seabed with the aid of a rigid 3m UPVC plastic pipe (10cm diameter), a 30m measuring-tape on a reel and a weighted shot-line to provide divers with a fixed reference point. The reel for the measuring-tape was fixed to the middle of the pipe and the free end to the bottom of the shot line.

In preparation for the first transect, the two divers positioned themselves at either end of the pipe, holding it perpendicular to the tape-measure and facing away from the shot-line on a predetermined, random compass heading. The divers then swam the pipe 10m along the seabed on this heading, with each diver counting and measuring the scallops in their half (*i.e.* 1.5m width) of the transect (Figure 7). All scallops thus encountered were measured for shell width (SW) to the nearest 5mm and immediately replaced. Having completed the first transect, divers swam a predetermined random distance (in the range of 1 to 20m) on the same heading at which point they began the second 10m transect. Having completed the second transect, they then returned to the shot line and did the third and fourth transects in the opposite direction to the first pair using a new random distance between transects.

Because of poor weather in 2004, it was only possible to sample four plots per site that year. Despite the problem of having unbalanced temporal sampling, it was nevertheless decided to continue with the plan for six plots per site in all subsequent years, which was accomplished.

Figure 7. A pair of divers carrying a modified 3m length of UPVC pipe for delineating the width of transects in quantitative surveys of scallops (© M. Hoskin).

2.2.2 *Analysis of the abundances of scallops (Hypothesis-4)*

The fact that data on the abundance scallops were available for only four plots per site in 2004, *versus* six plots per site in subsequent years, presented a problem of how to analyse these data. The problem arose from the requirement of ANOVA for balanced data (*i.e.* equal replication of levels of the same factor). Two possible solutions were apparent, but each had its disadvantages. One possible solution was to discard data for two randomly-selected plots per site for the years 2005, 2006 and 2007, giving four plots per site in every year. With this approach, statistical power would be less than initially planned, but the full time-series would be retained. The second possible solution was to exclude 2004-data from the analysis, in which case maximal power would be retained, but significant changes relative to 2004 might be missed. It was decided that retaining the 2004-baseline was the greatest priority, but that the analysis with six plots per site would be preferable if it could first be shown (via the analysis with four plots) that the difference in mean abundance between 2004 and 2005 was non-significant.

In both the four-plot and six-plot scenarios the ANOVA model had four factors. The first factor was the fixed factor LOCATION, which had two levels, the NTZ

location and the control location. The second factor was the fixed factor YEAR, which had either three or four levels according to whether 2004-data were included in the analysis. The third factor was the random factor SITE, which was nested in LOCATION and had two levels (Sites 1 and 2 in each location). The fourth factor was the random factor PLOTS, which was nested in the LOCATION x SITE interaction. PLOTS had four levels when 2004-data was included in the analysis and six levels when it was excluded. When six plots per site were available, but only four were needed for the analysis, data for two of the six plots were selected at random and discarded. The variance terms in the ANOVA model based on this design are listed and interpreted in Table A1.5, Appendix 1.

Prior to analyses, abundances of scallops were converted from numbers per transect ($30m^2$) to numbers per $10m^2$. Tests of hypotheses and spatial and temporal variations in the abundances of scallops were done using L*n*(*X*+0.1)-transformed data. All other methodological aspects of ANOVAs on scallop abundances and the presentation of results were as per the ANOVAs described in previous sections.

2.2.3 Analysis of the sizes of scallops (Hypothesis-5)

Within-location patchiness in the abundance of scallops meant that the set of data on the sizes of scallops was unbalanced (*i.e.* unequal replication amongst spatial units in the sampling design). As such, these data could not be analysed to test for an effect of the NTZ until the data-set had been balanced by discarding excess data. It was also necessary to combine size-data amongst replicate plots and sites within each combination of location and year in order to have a useful level of replication (having SITE as the smallest spatial unit allowed for a sample-size (*n*) of only two, whereas having LOCATION as the smallest unit allowed for a *n* of eight). Where there was size-data for more than eight scallops per location in any year, the data to be discarded was selected randomly. ANOVA tests were done using untransformed size-data.

Given the above, the ANOVA model for analysing the sizes of scallops was a symmetric model with only two factors, the fixed factors LOCATION and YEAR. The variance terms in the ANOVA model based on this design are listed and explained

in Table A1.6, Appendix 1. All other methodological aspects of this ANOVA and the presentation of results were as per the ANOVAs described in previous sections.

2.2.4 *Analysis of the size-structure of scallop populations (Hypothesis-6)*

The hypothesis that the NTZ has caused changes in the size-structure of scallop populations was tested via comparisons of the size-frequency distributions of scallops in NTZ *versus* Control locations in each of the four years of sampling. Comparisons of size-structure were done using two-sample Kolmogorov-Smirnov tests (Sokal & Rohlf 1995). Two forms of the Kolmogorov-Smirnov test were used: one form for small sample sizes (n_1 and n_2 both ≤25) and a second form for larger sample sizes (n_1 and/or n_2 >25).

2.3 Long-lived, sessile epifauna in circalittoral rocky habitats

2.3.1 Sampled species and variables

Monitoring was designed to test the general hypothesis that the assemblage of long-lived sessile epifauna within the NTZ would change relative to assemblages in nearby control locations where fishing continued. The set of sessile epifauna that were monitored were decided upon via a pilot study at Lundy during May 2004 (Hoskin *et al.* 2004) (Table 3, Figure 8).

Table 3. Species of long-lived sessile epifauna in circalittoral rocky habitats that were selected for monitoring potential effects of the Lundy NTZ

Phyla	Species	Common name (or description)
Porifera (Sponges)	*Axinella dissimilis* (Bowerbank 1866)	branching sponge
	Axinella infundibuliformis (*Linneaus 1758*)	funnel-shaped sponge
	Axinella damicornis (Esper 1794)	erect, non branching sponge
	Homaxinella subdola (Bowerbank 1866)	branching sponge
	Raspalia ramosa (Montagu 1818)	branching sponge
	Polymastia boletiformis (Lamarck 1815)	cushion sponge
	Polymastia mammilaris (Möller 1806)	cushion sponge
	Cliona celata (Grant 1826)	Boring sponge
Cnidaria	*Alcyonium digitatum* (Linneaus 1758)	Dead men's fingers
	Alcyonium glomeratum (Hassall 1843)	Red fingers
	Eunicella verrucosa (Pallas 1766)	Pink sea-fan
	Anemonia viridis (Forsskål 1775)	Snakelocks anemone
	Aiptasia mutablis (Gravenhorst 1831)	Trumpet anemone
Bryozoa	*Pentapora fascialis* (Pallas 1766)	Ross coral
Chordata (class Ascidacea)	*Stolonica socialis* (Hartmeyer 1903)	a colonial sea squirt

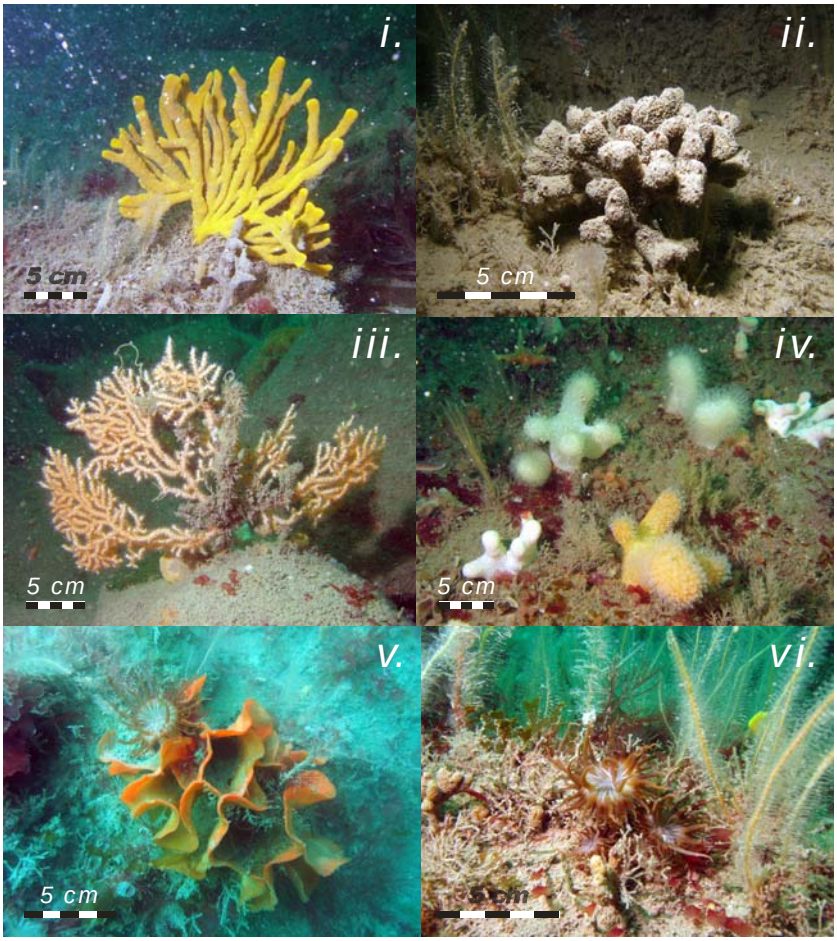

Figure 8. Examples of long-lived sessile epifauna in circalittoral rocky habitats at Lundy: (*i* & *ii*) the erect sponges *Axinella dissimilis* and *Raspalia ramosa*; (*iii*) the gorgonian sea fan *Eunicella verrucosa* (pink sea fan); (*iv*) the alcyonid soft-coral *Alcyonium digitatum* (dead men's fingers); (*v*) the bryozoan *Pentapora* fascialis (ross coral); and (*vi*) the anemone *Aiptasia mutablis* (trumpet anemone) (© *i-iv* and *vii*, K. Hiscock; *v*, M. Hoskin).

2.3.2 *Sampling design and methodology for epifauna*

Sessile epifauna were sampled underwater by scuba divers. The monitoring programme for epifauna did not include Far Reference locations, as for the monitoring of lobster and crabs, because they could not be afforded within the budget (due to the relatively greater cost per sample with diver sampling). The evaluation involved a comparison between epifaunal assemblages at two sites inside the NTZ and two control sites outside the NTZ, but also at Lundy.

Monitoring sites for epifauna were selected via a pilot study at Lundy in May 2004. The aim of this work was to identify a set of sites that were broadly comparable in terms of environmental conditions and the species of epifauna present (Hoskin *et al.* 2004). Since the NTZ occupies most of the east coast of Lundy, there was no alternative to having control sites on the west coast of the island (Figure 9). A problem presented by this arrangement was that there were at least three types of physical environmental difference between NTZ and control sites: *(i)* the west coast was more wave-exposed since it faced the prevailing weather; *(ii)* control sites on the west coast were ~5m deeper than NTZ sites within the NTZ (~20-25m *versus* 15-20m average depth respectively); and *(iii)* the seabed within west coast control sites was mainly bed-rock, whilst NTZ sites were boulder-dominated.

Whilst it was almost certain that differences in epifaunal assemblages between NTZ and control sites would be associated with these environmental differences, this was not expected to confound efforts to detect potential changes due to the NTZ. This is because the hypothesis of interest was that assemblage composition in the NTZ would change relative to that in the control sites (*i.e.* there would be a significant TIME X NTZ *VS* CONTROL interaction). This hypothesis allowed for either a potential increase or decrease in the magnitude of difference between NTZ and control sites.

Because of concerns about potential impacts of experimental potting for lobsters and crabs on sessile epifauna, experimental potting was excluded from all monitoring sites for epifauna.

Within each site, epifauna were sampled by scuba divers in six random plots using a 75cm x 75cm quadrat. This size of quadrat was selected in accordance with the recommendation of Andrew & Mapstone (1984) that the size of sampling unit should be approximately one order of magnitude larger than the organisms being counted. The species of epifauna of interest in this study ranged in typical body size from ~2cm width (*Aiptasia mutablis*) up to ~20cm width (*Eunicella verrucosa*), but most individuals were in the 5 to 10cm range. In each plot, divers recorded epifaunal abundances in each of 12 quadrats placed at predetermined random distances (1-6m apart) along a transect. This sampling scheme gave 72 quadrat counts per site. Only quadrats falling on 90-100% rock habitat were sampled. Where this condition was not met, the diver moved onto the next random position and so on. Each transect was orientated approximately parallel to the adjacent shoreline, which minimised variation in depth along it. All quadrat counts were converted to abundances per m^2 prior to statistical analyses.

Analyses of data from pilot work at Lundy (Hoskin *et al.* 2004) suggested that 72 samples per site was sufficient to maximise the precision of mean estimates of epifaunal abundances per quadrat (for a 75cm x 75cm quadrat). Power analyses of the same data (Hoskin *et al.* 2004) indicated that with this level of replication, univariate tests on epifaunal abundances should have an 80% probability of detecting a 100% change in abundance due to the NTZ, if it occurred.

Dates of epifauna sampling in each year of the study are given in Table 4. 2004 was the only year when it proved impossible to complete the sampling design for epifauna. Poor weather that year meant that data was collected from only one out of six plots in Control site-1 and five out of six plots in Control site-2.

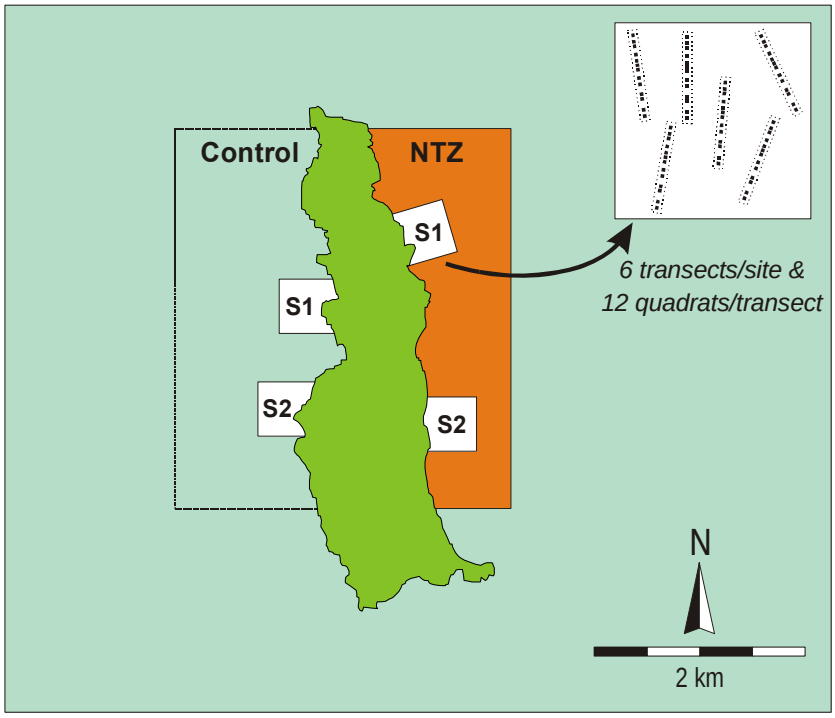

Figure 9. Sites of sampling for the diver surveys of sessile epifauna in circalittoral reefs**.**

Table 4. Beginning and end dates for periods of diver-sampling of epifauna and scallops at Lundy in each of the four years of the study (2004 to 2007).

Year	Dates of diving surveys at Lundy
2004	31st August to 15th September
2005	11th July to 31st July
2006	21st July to 13th August
2007	21st July to 10th August

2.3.3 Analysis of the composition of epifaunal assemblages (Hypothesis-7)

Multivariate analyses were used to test hypotheses about differences in the composition of epifaunal assemblages between years and locations. These analyses were done using the program PRIMER v5.2 (Clarke & Warwick 2001).

Multivariate variability among samples was quantified using the Bray-Curtis index of dissimilarity. This is a measure (on a scale of 0 to 100% dissimilarity) of the how different two samples are in terms of the types and numbers of animals in those samples. Dissimilarities were calculated using 4th-root transformed abundances of epifaunal species and one composite variable – total axinellid

sponges. A 4th-root transformation reduces the effect on Bray-Curtis dissimilarity values of differences in the overall abundances of different taxa. When data are untransformed, the most abundant taxa have the greatest influence on Bray-Curtis dissimilarity values (Clarke & Warwick 2001).

Bray-Curtis dissimilarity values were summarised and analysed in several ways to assess patterns of natural variation and potential effects of the NTZ. The first use was to construct a two-dimensional pictorial representation of the relative differences in epifaunal assemblages among locations. This was done using non-metric multidimensional scaling (nMDS). In an nMDS-plot, each sample is represented by a symbol and the distance between symbols is proportional to the degree to which assemblage composition differs between samples.

The interpretation of nMDS-plots was helped by looking at the actual values of the Bray-Curtis distances on which the plot was based. An nMDS-plot is a two-dimensional representation of a pattern of compositional differences that is actually multi-dimensional in nature (each species provides one dimension). Sometimes, the nMDS method is unable to make a good two-dimensional image of the true multi-dimensional pattern. When this happens, interpretation is difficult because the relative distances among different symbols on the nMDS plot do not accurately reflect the actual Bray-Curtis dissimilarities. The extent to which reality and its graphical representation by nMDS differ is expressed by the 'stress value'. An nMDS-plot with a stress-value of ≤ 0.15 is deemed to allow reliable interpretation of relative ecological differences among samples. When the stress-value for an nMDS-plot is >0.15, any ecological interpretation based wholly on that plot should be treated with caution.

Tests of the statistical significance of potential multivariate effects of the NTZ on epifaunal assemblages were done using ANOSIM. Unlike ANOVA, ANOSIM does not require balanced data, so tests of multivariate hypotheses about epifaunal assemblages were still possible, despite an incomplete set of data for 2004. Because ANOSIM cannot handle sampling designs with more than two factors, it was necessary to use two forms of ANOSIM and do multiple tests of each type to analyse the epifaunal data fully.

The first set of tests used one-way ANOSIM to test the multivariate difference in epifauna from one year to the next for each site in each location (requiring twelve ANOSIMs in total). Similar ANOSIM tests were also done to test for changes within individual sites over a two-year interval (eight separate ANOSIMs) and a three-year interval (four separate ANOSIMs). SIMPER-analyses were then used to investigate the contribution of each epifaunal variable to the overall dissimilarity for each of these different temporal comparisons.

The second set of tests used one-way ANOSIM to test for multivariate differences in epifauna among sites in each year (requiring two ANOSIMs in total).

Further interpretation of multivariate data was accomplished using the SIMPER procedure in PRIMER (Clarke & Warwick 1994). SIMPER calculates the contribution of each species contributes to the overall Bray-Curtis dissimilarity for a given comparison (a Bray-Curtis value, on its own, will not identify the species primarily responsible for any multivariate differences).

Here, SIMPER was used to investigate the contribution of each epifaunal variable to the overall dissimilarity between each pairwise combination of sites for which ANOSIM showed a significant difference. The results of these analyses were subsequently used to identify variables whose variations in abundance were of sufficient magnitude to warrant further univariate testing via ANOVA. The variables selected for ANOVA were those that contributed ≥15% to the multivariate difference for at least one temporal or spatial comparison.

2.3.4 Analysis of the abundances of individual of epifauna (Hypothesis-8)

The ANOVA for analysing data on the abundance of individual epifauna was a model with four factors. The first factor was the fixed factor LOCATION, which had two levels the NTZ location and the control location. The second factor was the random factor SITE, which was nested in LOCATION and had two levels (the two replicate sites in each location). The third factor was the fixed factor YEAR, which had three levels (2005, 2006 and 2007). Fourth was the random factor PLOTS, which was nested in the LOCATION x SITE interaction and had six levels. The variance terms in the ANOVA model based on this experimental design are

interpreted in Table A1.7, Appendix 1. The critical variance term for the test of Hypothesis-8 was the interaction term YEAR X LOCATION (abbreviated as LO X YE).

Abundances of epifauna were transformed to L*n*(*X*+0.001)-data prior to ANOVA (a small constant was used because abundances of epifauna were generally very low) Log transformation of the data made the hypothesis being tested one of relative difference in abundance rather than absolute difference, which was considered more appropriate for evaluating potential effects of the NTZ. All other methodological aspects of ANOVAs on epifaunal abundances and the presentation of results were as per the ANOVAs described in previous sections.

3 RESULTS

3.1 Lobsters and crabs

3.1.1 The abundance of lobsters and crabs (Hypotheses-1 and 2)

Before describing these results, it is first necessary to explain a slight modification to the planned ANOVA model that was applied to data on the abundances of lobster and velvet crab (as per Section 2.1.6 and Tables A1.1 and A1.2). Analyses of these data using the planned model revealed highly significant variation from time-to-time in some years. An unfortunate consequence of this variation was that valid *F*-ratios for testing the factors YE x LO: NTZ *v* CON and YE x LO: NTZ *v* REF - the critical factors of interest - were not available. The only way to test these factors for lobster and velvet crab was to negate the influence of this short-term variability by averaging abundance data across the five replicate times for each string of pots and analysing these average abundances instead. This modification was only possible because each string of pots in the sampling array was deployed in the same area each time. Unfortunately, averaging across times within years reduced the power of tests (by reducing *n* by $1/5_{th}$), but the important tests couldn't have been done otherwise. Apart from the absence of TIMES(YEAR), the modified ANOVA model was identical to the planned model and tests for the other factors are interpretable in exactly the same way (*i.e.* as per Tables A1.1 and A1.2).

Of the four species of commercially-fished crustaceans that were monitored for this study, only lobster and velvet crab showed significant changes in abundance that were potentially attributable to the NTZ.

- Abundance of landable-sized lobsters

For landable-sized lobsters, there was a significant interaction of YE x LO: NTZ *v* CON (Table 5) and YE x LO: NTZ *v* REF (Table 6). These results were due to a substantial increase in the abundance of landable-sized lobsters within the NTZ relative to abundances in both Near Control and Far Reference locations, neither of which changed significantly during the same period (Figure 10-*i.*).

In 2004, eighteen months after the NTZ was designated, the mean abundance of landable-sized lobsters within the NTZ was 2.95 (± 0.30) per string of 10 pots, *versus* 0.85 (± 0.09) in Near Control locations and 1.09 (± 0.14) in Far Reference locations. By 2007, mean abundance within the NTZ had increased by 127% to 6.70 (± 0.57) per string of pots, whilst abundances in Near Control and Far Reference locations had increased (non-significantly) by only 17% and 41%, respectively (Figure 10-*i.*). When monitoring began, landable-sized lobsters were more than twice as abundant, on average, within the NTZ compared to Near Control and Far Reference locations. By 2007, they were more than five times more-abundant in the NTZ compared to outside.

Table 5. Abundance of landable-sized lobsters – NTZ *vs* Near Control: ANOVA of L*n*(*X*+1)-transformed abundances of landable-sized lobsters (CL ≥90mm) per string of 10 pots for NTZ *versus* Near Control locations (*n*=4). The symbol '❶' indicates the factor used as the denominator for testing LO: NTZ *vs* CON. The symbol '❶' indicates the pooled factors used as the denominator for testing Ye x Lo: NTZ *vs* Ref. ns - *P* > 0.05.

				Pre-Pooling			Post-Pooling	
Source of Variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	20.48						
LO: NTZ *v* CON	1	20.37	20.375	LO: CON	200.73	*P* < 0.05		
LO: CON	1	0.10	0.102	SITES (CON)	1.30	ns		
SITES (LOCATIONS)	**3**	0.35						
SITES (NTZ)	1	0.20	0.195	RES: NTZ	1.35	ns		
SITES (CON)	2	0.16	0.078	RES: CON	1.41	ns		
YEAR	**3**	2.17	0.724	YE x LO: CON	**6.79**	**ns**		
YEAR x LOCATION	**6**	2.35						
YE x LO: NTZ *v* CON	3	2.03	0.676	YE x LO: CON	6.33	ns	7.96	*P* < 0.001
YE x LO: CON ❶	3	0.32	0.107	YE x SI (CON)	0.97	ns		
YEAR x SITE (LOCATION) ❶	**9**	0.68	0.076	**RESIDUAL**	**0.89**	ns		
YE x SI (NTZ)	3	0.02	0.007	RES: NTZ	0.05	ns		
YE x SI (CON)	6	0.66	0.110	RES: CON	1.98	ns		
RESIDUAL ❶	**72**	6.13	0.085					
RES: NTZ	24	3.47	0.145					
RES: CON	48	2.66	0.055					
TOTAL	**95**	32.16						

Cochran's Test C = 0.2055 (*P* < 0.05)

Largest variance = 0.4202, this occurred in the NTZ, Site 1 in 2005

Table 6. Abundance of landable-sized lobsters – NTZ *vs* Far Reference: ANOVA of L*n*(*X*+1)-transformed abundances of landable-sized lobsters (CL ≥90mm) per string of 10 pots for NTZ *versus* Far Reference locations (*n*=4). The symbol '❶' indicates the pooled factors used as the denominator for testing YE x LO: NTZ *vs* REF. ns - $P > 0.05$.

				Pre-Pooling			Post-Pooling	
Source of Variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	18.89						
LO: NTZ *v* REF	1	18.73	18.734	LO: REF	122.36	ns		
LO: REF	1	0.15	0.153	SITES (REF)	2.56	ns		
SITES (LOCATIONS)	**3**	0.31						
SITES (NTZ)	1	0.20	0.195	RES: NTZ	1.35	ns		
SITES (REF)	2	0.12	0.060	RES: REF	0.69	ns		
YEAR	**3**	2.13	0.709	YE x LO: REF	**9.55**	$P < 0.05$		
YEAR x LOCATION	**6**	2.27						
YE x LO: NTZ *v* REF	3	2.05	0.683	YE x LO: REF	9.20	ns	6.69	$P < 0.001$
YE x LO: REF ❶	3	0.22	0.074	YE x SI (REF)	0.62	ns		
YEAR x SITE (LOCATION) ❶	**9**	0.74	0.082	**RESIDUAL**	**0.77**	**ns**		
YE x SI (NTZ)	3	0.02	0.007	RES: NTZ	0.05	ns		
YE x SI (REF)	6	0.72	0.119	RES: REF	1.38	ns		
RESIDUAL ❶	**72**	7.62	0.106					
RES: NTZ	24	3.47	0.145					
RES: REF	48	4.15	0.086					
TOTAL	**95**	31.96						
Cochran's Test C = 0.1655 (Not Significant)								

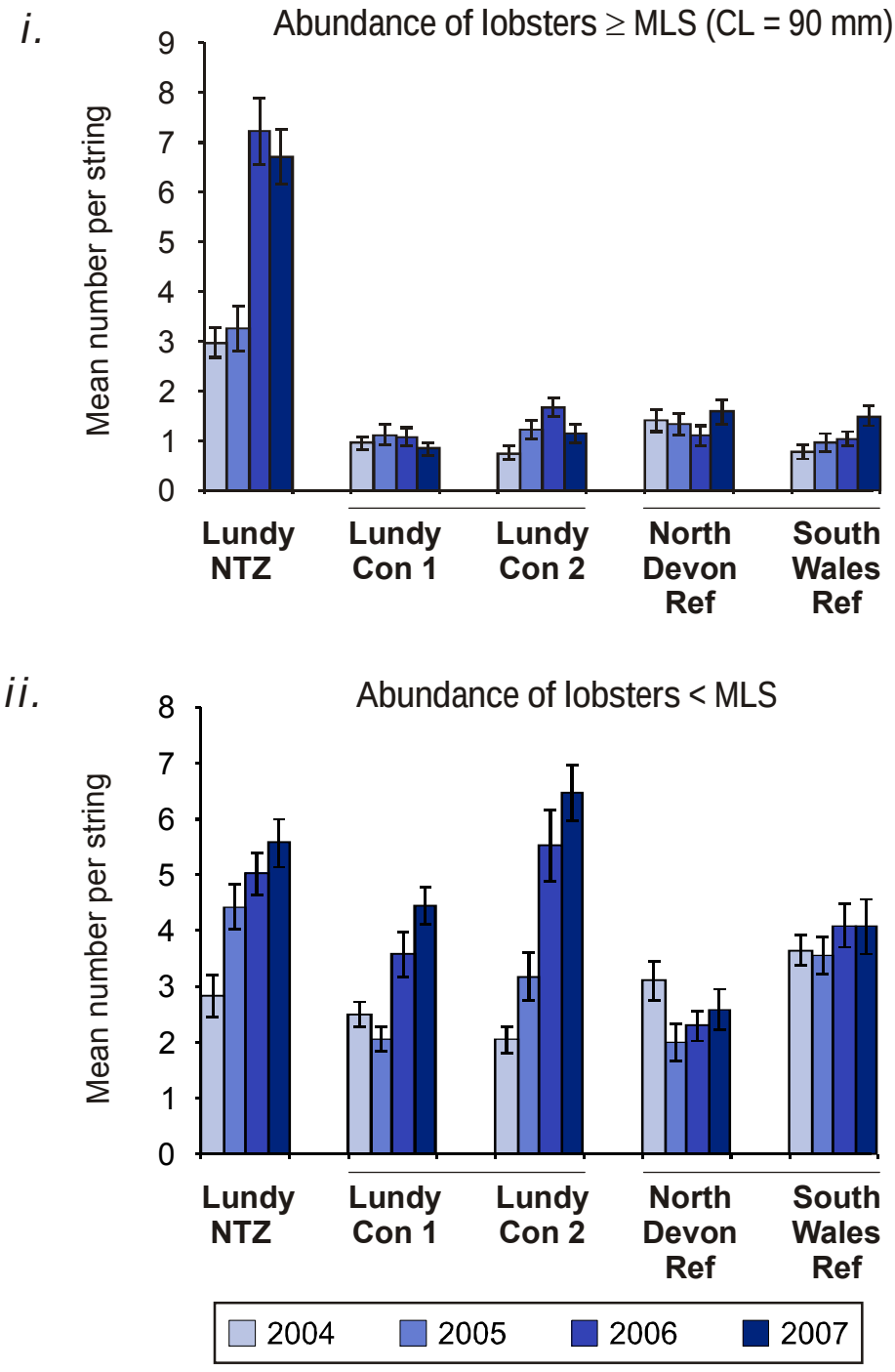

Figure 10. Abundance of lobsters: Variation in the mean abundances of *(i)* landable-sized lobsters (CL ≥90mm) and *(ii)* undersized lobsters (CL <90mm) among NTZ, Near Control and Far Reference locations year in the period 2004 to 2007. Each bar represents the mean abundance (±SE) per string of 10 pots over 5 days of sampling.

- Abundance of undersized lobsters

For undersized lobsters, there was a significant interaction of YE x LO: NTZ *v* REF (Table 7), but not for YE x LO: NTZ *v* CON (Table 8). These test results were due to large, progressive increases in the average abundance of undersized lobsters within the NTZ and Near Control locations, but relatively constant mean abundances in Far Reference locations (Figure 10-*il*.). From 2004 to 2007, the mean abundance of undersized lobsters within the NTZ increased by 97% from 2.83 ± 0.37 per string of pots to 5.58 ± 0.43 per string. In the same period, the mean abundance of undersized lobsters in Near Control locations increased 140% from 2.28 ± 0.17 per string to 5.46 ± 0.32 per string. The large simultaneous increases in abundance in the NTZ and Near Control locations caused a significant result for the factor YEAR in the ANOVA for these data (Table 7).

These outcomes affirmed Parts 1 and 2 of the three-part hypothesis designed to assess the theory that the NTZ would cause spillover into adjacent areas (see Section 2.1.6). As such, the criteria were met for analysing abundance data for undersized lobsters using the supplementary third ANOVA model (Table A1.3) to test Part 3 of this hypothesis - the hypothesis that mean abundance within Near Control locations had increased significantly relative to Far Reference locations. For consistency with ANOVAs already done for undersized lobsters, data were averaged across times within each year prior to analysis. The test of the critical factor, DISTANCE x YEAR (Table 9), showed that the increase in mean abundance within Near Control locations was statistically significant relative to the change in mean abundance within Far Reference locations.

Table 7. Abundance of undersized lobsters – NTZ *vs* Near Control: ANOVA of L*n*(*X*+1)-transformed abundances of landable-sized lobsters (CL <90mm) per string of 10 pots for NTZ *versus* Near Control locations (*n*=4). ns – *P* > 0.05.

				Pre-Pooling			Post-Pooling	
Source of Variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	1.27						
LO: NTZ *v* CON	1	0.87	0.866	LO: CON	2.16	ns		
LO: CON	1	0.40	0.401	SITES (CON)	0.61	ns		
SITES (LOCATIONS)	**3**	1.52						
SITES (NTZ)	1	0.20	0.201	RES: NTZ	3.75	ns		
SITES (CON)	2	1.32	0.658	RES: CON	5.13	*P* < 0.01		
YEAR	**3**	5.87	1.956	YE x LO: CON	**11.64**	*P* < 0.05		
YEAR x LOCATION	**6**	1.03						
YE x LO: NTZ *v* CON	3	0.53	0.177	YE x LO: CON	1.05	ns		NO TEST
YE x LO: CON	3	0.50	0.168	YE x SI (CON)	2.40	ns		
YEAR x SITE (LOCATION)	**9**	1.02	0.113	**RESIDUAL**	**1.09**	**ns**		
YE x SI (NTZ)	3	0.60	0.199	RES: NTZ	3.72	*P* < 0.05		
YE x SI (CON)	6	0.42	0.070	RES: CON	0.55	ns		
RESIDUAL	**72**	7.44	0.103					
RES: NTZ	24	1.28	0.053					
RES: CON	48	6.16	0.128					
TOTAL	**95**	18.15						

Cochran's Test C = 0.2680 (*P* < 0.01)

Largest variance = 0.6649, this occurred in Near Control location 2, Site 2 in 2006

Table 8. Abundance of undersized lobsters – NTZ *vs* Far Reference: ANOVA of L*n*(*X*+1)-transformed abundances of undersized lobsters (CL <90mm) for NTZ *versus* Far Reference locations per string of 10 pots (*n*=4). The symbol '❶' indicates the pooled factors used as the denominator for testing YE x LO: NTZ *vs* REF. ns - *P* > 0.05.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	4.09						
LO: NTZ *v* REF	1	2.00	2.005	LO: REF	0.96	ns		
LO: REF	1	2.09	2.086	SITES (REF)	2.12	ns		
SITES (LOCATIONS)	**3**	2.10						
SITES (NTZ)	1	0.20	0.201	RES: NTZ	3.75	ns		
SITES (REF)	2	1.90	0.950	RES: REF	9.70	*P* < 0.001		
YEAR	**3**	0.45	0.151	YE x LO: REF	**0.99**	ns		
YEAR x LOCATION	**6**	2.11						
YE x LO: NTZ *v* REF	3	1.65	0.550	YE x LO: REF	3.59	**ns**	1.682	ns
YE x LO: REF ❶	3	0.46	0.153	YE x SI (REF)	0.32	ns		
YEAR x SITE (LOCATION) ❶	**9**	3.46	0.385	**RESIDUAL**	**4.64**	*P* < 0.001		
YE x SI (NTZ)	3	0.60	0.199	RES: NTZ	3.72	*P* < 0.05		
YE x SI (REF)	6	2.87	0.478	RES: REF	4.88	*P* < 0.001		
RESIDUAL	**72**	5.98	0.083					
RES: NTZ	24	1.28	0.053					
RES: REF	48	4.70	0.098					
TOTAL	**95**	18.20						
Cochran's Test C = 0.1101 (Not Significant)								

Table 9. Abundances of undersized lobsters: ANOVA of L*n*(*X*+1)-transformed lobster abundances (CL <90mm) per string of 10 pots for Near Control locations *versus* Reference locations (*n*=4). The symbol '❶' indicates the pooled factors used as the denominator for testing DISTANCE and LOCATION (DI). The symbol ❷ indicates the pooled factors used as the denominator for testing YEAR, DISTANCE X YEAR and YEAR X LOCATION(DI). ns - *P* > 0.05.

Source	df	SS	MS	F	*P*	Denominator
DISTANCE	1	0.35	0.353	0.37	ns	❶-POOLED MS
LOCATION (DI) ❶	2	2.49	1.244	1.31	ns	❶-POOLED MS
SITE (DI X LO) ❶	4	3.21	0.804	7.11	*P* < 0.001	RES
YEAR	3	2.70	0.901	3.81	*P* < 0.05	❷-POOLED MS
DISTANCE X YEAR	3	2.45	0.818	3.46	*P* < 0.05	❷-POOLED MS
YEAR X LOCATION (DI) ❷	6	0.96	0.161	0.68	ns	❷-POOLED MS
YEAR X SITE (DI X LO) ❷	12	3.29	0.274	2.42	*P* < 0.01	RES
RESIDUAL	96	10.86	0.113			
TOTAL	127	26.32				
❶-POOLED MS	6	5.70	0.950			
❷-POOLED MS	18	4.25	0.236			

Cochran's Test C = 0.1837 (*P* < 0.05) Largest variance = 0.6649,
this occurred in Near Control location 2, Site 2 in 2006

- Abundance of velvet crab

Analyses of changes in velvet crab abundance from 2004 to 2007 revealed a significant interaction of both YE X LO: NTZ *v* CON and YE X LO: NTZ *v* REF (Tables 10 and 11). These results were attributable to a general trend of increasing mean abundance in Far Reference locations (26% increase from 3.20 ± 0.56 to 4.03 ± 0.44 per string) *versus* decreasing mean abundance in Near Control locations (75% decrease from 5.64 ± 0.44 to 1.43 ± 0.17 per string) and, to a lesser extent, in the NTZ (65% decrease from 2.45 ± 0.35 to 0.85 ± 0.17) (Figure 11). The overall conclusion to be drawn here is that the decline in velvet crab abundance within the NTZ was significant relative to changes in Far Reference locations, but non-significant in comparison with the greater decline in Near Control locations.

Analyses of data on the abundance of velvet crabs revealed only one notable result for a factor for which there was no *a priori* hypothesis; this was a significant result for the factor LO:REF (Table 11). This indicated an important difference in the overall mean abundance of velvet crab between the two Far Reference locations (Figure 11). On average, the abundance of velvet crabs in the South

Wales reference location (6.26 ± 0.36 per string) was 525% greater than in the North Devon reference location (1.00 ± 0.16).

Table 10. Abundances of velvet crabs – NTZ *vs* Near Control: ANOVA of L*n*(*X*+1)-transformed velvet crab abundances per string of 10 pots for NTZ *versus* Near Control locations (*n*=4). The symbol '❶' indicates the pooled factors used as the denominator for testing YE x LO: NTZ *vs* REF. ns - *P* > 0.05.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	15.64						
LO: NTZ *v* CON	1	15.12	15.122	LO: CON	29.32	ns		
LO: CON	1	0.52	0.516	SITES (CON)	0.395	ns		
SITES (LOCATIONS)	**3**	13.56						
SITES (NTZ)	1	10.95	10.949	RES: NTZ	22.16	*P* < 0.001		
SITES (CON)	2	2.61	1.307	RES: CON	5.17	*P* < 0.01		
YEAR	**3**	22.37	7.456	YE x LO: CON	**20.67**	*P* < 0.05		
YEAR x LOCATION	**6**	8.90						
YE x LO: NTZ *v* CON	3	7.82	2.607	YE x LO: CON	7.23	ns	6.034	*P* < 0.01
YE x LO: CON ❶	3	1.08	0.361	YE x SI (CON)	1.02	ns		
YEAR x SITE (LOCATION) ❶	**9**	4.10	0.456	**RESIDUAL**	**1.37**	ns		
YE x SI (NTZ)	3	1.99	0.662	RES: NTZ	1.34	ns		
YE x SI (CON)	6	2.12	0.353	RES: CON	1.40	ns		
RESIDUAL	**72**	23.98	0.333					
RES: NTZ	24	11.86	0.494					
RES: CON	48	12.12	0.253					
TOTAL	**95**	88.55						

Cochran's Test C = 0.1530 (Not Significant)

Table 11. Abundances of velvet crabs – NTZ *vs* Far Reference: ANOVA of L*n*(*X*+1)-transformed velvet crab abundances per string of 10 pots for NTZ *versus* Far Reference locations (*n*=4). The symbol '❶' indicates the pooled factors used as the denominator for testing YE x LO: NTZ *vs* REF. ns - *P* > 0.05.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	86.81						
LO: NTZ *v* REF	1	10.15	10.154	LO: REF	0.13	ns		
LO: REF	1	76.66	76.661	SITES (REF)	196.04	*P* < 0.05		
SITES (LOCATIONS)	**3**	11.73						
SITES (NTZ)	1	10.95	10.949	RES: NTZ	22.16	*P* < 0.001		
SITES (REF)	2	0.78	0.391	RES: REF	0.81	ns		
YEAR	**3**	1.88	0.627	YE x LO: REF	**1.02**	ns		
YEAR x LOCATION	**6**	14.30						
YE x LO: NTZ *v* REF	3	12.45	4.149	YE x LO: REF	6.73	**ns**	3.60	*P* < 0.05
YE x LO: REF ❶	3	1.85	0.617	YE x SI (REF)	0.37	ns		
YEAR x SITE (LOCATION) ❶	**9**	11.96	1.329	**RESIDUAL**	**2.73**	*P* < 0.01		
YE x SI (NTZ)	3	1.99	0.662	RES: NTZ	1.34	ns		
YE x SI (REF)	6	9.98	1.663	RES: REF	3.45	*P* < 0.01		
RESIDUAL	**72**	35.03	0.486					
RES: NTZ	24	11.86	0.494					
RES: REF	48	23.17	0.483					
TOTAL	**95**	**161.71**						

Cochran's Test C = 0.1380 (Not Significant)

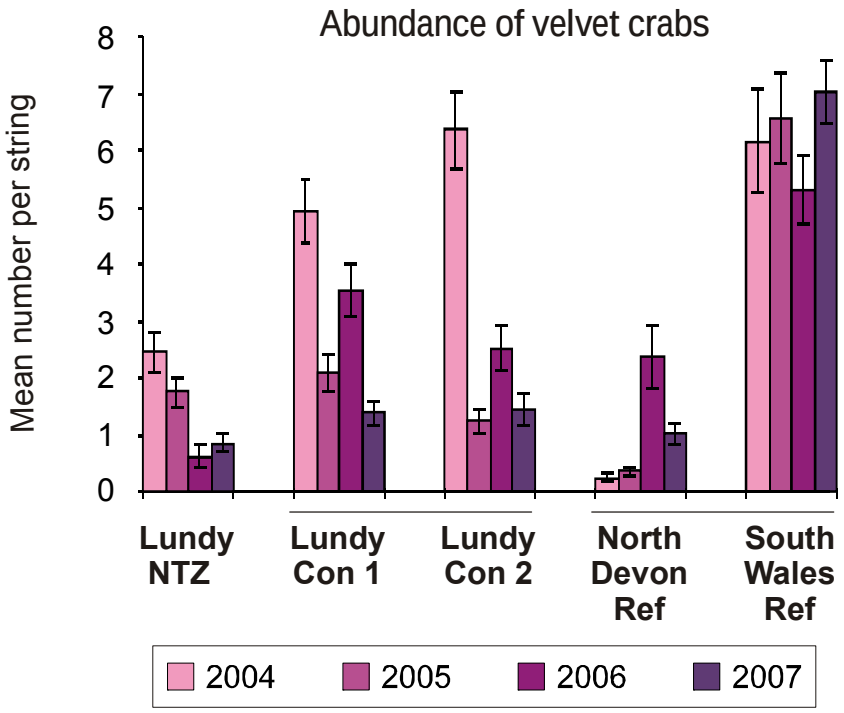

Figure 11. Abundance of velvet crabs: Variation in the mean abundances of velvet crab among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents the mean abundance (±SE) per string of 10 pots over 5 days of sampling.

- Abundance of brown crab

For brown crab, neither of the critical ANOVA factors for testing potential effects of the NTZ (*i.e.* YE x LO: NTZ *v* CON and YE x LO: NTZ *v* REF) were significant (Tables 12 and 13).

Analyses of data on the abundance of brown crabs revealed two notable results for factors for which there were no *a priori* hypotheses; these were significant results for the factors LO: NTZ *v* CON (Table 12) and LO: NTZ *v* REF (Table 13). These results were attributable to a relatively consistent pattern of differences in abundance among locations (Figure 12). The only major anomaly was a large 'spike' in the abundance of brown crab in the North Devon reference location in 2006. Brown crab were generally least abundant in the NTZ where there was an average of 0.21 ± 0.04 individuals per string. This was significantly fewer than in either Near Control locations (1.30 ± 0.08 individuals per string) or Far Reference locations (0.76 ± 0.08 per string).

Table 12. Abundances of brown crabs – NTZ *vs* Near Control: ANOVA of L*n*(*X*+1)-transformed brown crab abundances per string of 10 pots for NTZ *versus* Near Control locations (*n*=4). The symbol '❶' indicates the factors used as the denominator for testing LO: NTZ *vs* CON. The symbol '❷' indicates the factor used as the denominator for testing Lo: CON. The symbol '❸' indicates the factor used as the denominator for testing YEAR. The symbol '❹' indicates the factor used as the denominator for testing YE X LO: NTZ *vs* CON. The symbol '❺' indicates the factor used as the denominator for testing YE X LO: CON. ns – $P > 0.05$.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	236.73	118.363					
LO: NTZ *v* CON	1	236.59	236.589	NO TEST			31.03	*P* < 0.01
LO: CON ❶	1	0.14	0.137	NO TEST			0.01	ns
SITES (LOCATIONS) ❶❷	**3**	30.37	10.122	**TI (YE) x SI (LO)**	**5.33**	*P* < 0.01		
SITES (NTZ)	1	0.19	0.187	TI (YE) x SI (NTZ)	0.24	ns		
SITES (CON)	2	30.18	15.090	TI (YE) x SI (CON)	6.12	*P* < 0.01		
YEAR	**3**	9.21	3.069	**NO TEST**			**0.37**	**ns**
TIME (YE)	**16**	14.36	0.898	**TI(YE) x LO: CON**	0.40	**ns**		
YEAR x LOCATION	**6**	27.32	4.554					
YE x LO: NTZ *v* CON	3	2.46	0.821	NO TEST			0.10	ns
YE x LO: CON ❸❹	3	24.86	8.286	NO TEST			3.67	*P* < 0.05
LOCATION x TIME (YEAR)	**32**	52.57						
TI (YE) x LO: NTZ *v* CON	16	16.60	1.037	TI (YE) x LO: CON	0.46	ns		
TI (YE) x LO: CON ❺	16	35.97	2.248	TI (YE) x SI (CON)	0.91	ns		
YEAR x SITE (LOCATION)	**9**	10.03	1.114	**TI (YE) x SI (LO)**	**0.59**	**ns**		
YE x SI (NTZ)	3	3.08	1.028	TI (YE) x SI (NTZ)	1.34	ns		
YE x SI (CON) ❺	6	6.94	1.157	TI (YE) x SI (CON)	0,47	ns		
TIME (YEAR) x SITE (LOCATION)	**48**	91.12	1.898	**RES**	**1.24**	**ns**		
TI (YE) x SI (NTZ)	16	12.27	0.767	RES: NTZ	0.78	ns		
TI (YE) x SI (CON) ❺	32	78.86	2.464	RES: CON	1.36	ns		
RESIDUAL	**360**	551.90	1.533					
RES: NTZ	120	117.45	0.979					
RES: CON	240	434.46	1.810					
TOTAL	**479**	1023.61						
Cochran's Test C = 0.0291 (Not Significant)								

Table 13. Abundances of brown crabs – NTZ *vs* Far Reference: ANOVA of L*n*(*X*+1)-transformed brown crab abundances per string of 10 pots for NTZ *versus* Far Reference locations (*n*=4). The symbol '❶' indicates the factors used as the denominator for testing LO: NTZ *vs* REF. The symbol '❷' indicates the factor used as the denominator for testing Lo: REF. The symbol '❸' indicates the factor used as the denominator for testing YEAR. The symbol '❹' indicates the factor used as the denominator for testing YE x LO: NTZ *vs* REF. The symbol '❺' indicates the factor used as the denominator for testing YE x LO: REF. ns - *P* > 0.05.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	45.15	22.573					
LO: NTZ *v* REF	1	45.06	45.059	NO TEST			513.79	*P* < 0.05
LO: REF ❶	1	0.09	0.088	NO TEST			0.02	ns
SITES (LOCATIONS)	**3**	0.80	0.268	**TI (YE) x SI (LO)**	**0.25**	**ns**		
SITES (NTZ)	1	0.19	0.187	TI (YE) x SI (NTZ)	0.24	ns		
SITES (REF)	2	0.62	0.309	TI (YE) x SI (REF)	0.25	ns		
YEAR	**3**	18.44	6.146	**NO TEST**			**0.26**	**ns**
TIME (YE)	**16**	61.93	3.871	**TI(YE) x LO: REF**	0.79	**ns**		
YEAR x LOCATION	**6**	93.11	15.518					
YE x LO: NTZ *v* REF	3	20.98	6.992	NO TEST			0.29	ns
YE x LO: REF ❸❹	3	72.13	24.043	NO TEST			4.94	*P* < 0.05
LOCATION x TIME (YEAR)	**32**	110.91						
TI (YE) x LO: NTZ *v* REF	16	32.99	2.062	TI (YE) x LO: REF	0.42	ns		
TI (YE) x LO: REF ❷❺	16	77.92	4.870	TI (YE) x SI (REF)	3.93	*P* < 0.001		
YEAR x SITE (LOCATION)	**9**	9.68	1.076	**TI (YE) x SI (LO)**	**0.99**	**ns**		
YE x SI (NTZ)	3	3.08	1.028	TI (YE) x SI (NTZ)	1.34	ns		
YE x SI (REF)	6	6.60	1.100	TI (YE) x SI (REF)	0.89	ns		
TIME (YEAR) x SITE (LOCATION)	**48**	51.96	1.083	**RES**	**0.86**	**ns**		
TI (YE) x SI (NTZ)	16	12.27	0.767	RES: NTZ	0.78	ns		
TI (YE) x SI (REF)	32	39.69	1.240	RES: REF	0.89	ns		
RESIDUAL	**360**	451.47	1.254					
RES: NTZ	120	117.45	0.979					
RES: REF	240	334.02	1.392					
TOTAL	**479**	843.45						

Cochran's Test C = 0.0261 (Not Significant)

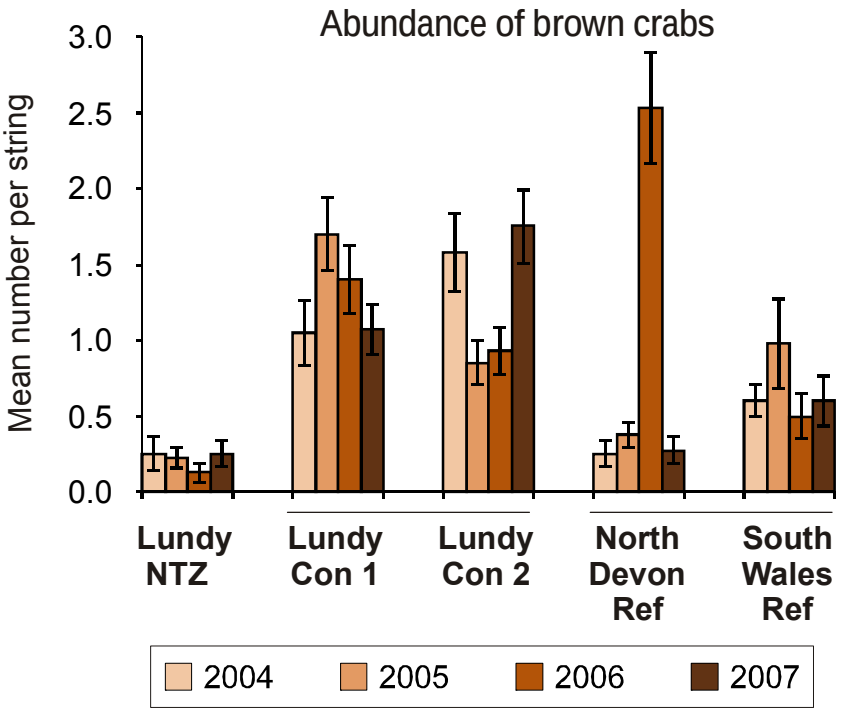

Figure 12. Abundance of brown crabs: Variation in the mean abundances of velvet crab among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents the mean abundance (±SE) per string of 10 pots over 5 days of sampling.

- Abundance of spider crab

Analyses of changes in spider crab abundance from 2004 to 2007 revealed a significant interaction of YE x LO: NTZ *v* CON (Table 14), but not of YE x LO: NTZ *v* REF (Table 15). The significant result for YE x LO: NTZ *v* CON was mainly attributable to a large difference in mean abundance between the NTZ and Near Control locations in one year (2006) (Figure 13). In 2006, the mean abundance of spider crab in Near Control locations (4.96 ± 0.38 individuals per string) was 261% greater than in the NTZ (1.38 ± 0.57 per string). In 2004, 2005 and 2007 mean abundances in the NTZ and the two Near Control locations ranged from 0.3 ± 0.11 to 2.35 ± 0.48 per string.

There was also a large spike in spider crab abundance in the North Devon reference location in 2006 (Figure 13), but this was not replicated in the South Wales reference location so it did not affect the outcome of the test of YE x LO: NTZ *v* REF.

Table 14. Abundance of spider crabs – NTZ *vs* Near Control: ANOVA of L*n*(*X*+1)-transformed spider crab abundances per string of 10 pots for NTZ *versus* Near Control locations (*n*=4). The symbol '❶' indicates the factors used as the denominator for testing LO: NTZ *vs* CON. The symbol '❷' indicates the factor used as the denominator for testing LO: CON. The symbol '❸' indicates the factor used as the denominator for testing YE x LO: NTZ *vs* CON. The symbol '❹' indicates the factor used as the denominator for testing YE x LO: CON. ns – $P > 0.05$.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	22.29	11.144					
LO: NTZ *v* CON	1	15.29	15.287	NO TEST			1.56	0.330 ns
LO: CON ❶	1	7.00	7.001	NO TEST			0.65	0.478 ns
SITES (LOCATIONS) ❶❷	**3**	32.18	10.726	**TI (YE) x SI (LO)**	**34.53**	$P < 0.001$		
SITES (NTZ)	1	1.54	1.542	TI (YE) x SI (NTZ)	5.47	$P < 0.05$		
SITES (CON)	2	30.64	15.318	TI (YE) x SI (CON)	47.14	$P < 0.001$		
YEAR	**3**	44.89	14.962	**NO TEST**				**NO TEST**
TIME (YE)	**16**	15.12	0.945	**TI(YE) x LO: CON**	3.28	$P < 0.05$		
YEAR x LOCATION	**6**	16.01	2.669					
YE x LO: NTZ *v* CON	3	14.99	4.998	NO TEST			11.13	$P < 0.01$
YE x LO: CON ❸	3	1.02	0.340	NO TEST			0.59	ns
LOCATION x TIME (YEAR)	**32**	9.77						
TI (YE) x LO: NTZ *v* CON	16	5.17	0.323	TI (YE) x LO: CON	1.12	ns		
TI (YE) x LO: CON	16	4.61	0.288	TI (YE) x SI (CON)	0.89	ns		
YEAR x SITE (LOCATION) ❸	**9**	4.37	0.485	**TI (YE) x SI (LO)**	**1.56**	**ns**		
YE x SI (NTZ)	3	0.89	0.296	TI (YE) x SI (NTZ)	1.05	ns		
YE x SI (CON) ❹	6	3.48	0.580	TI (YE) x SI (CON)	1.79	ns		
TIME (YEAR) x SITE (LOCATION)	**48**	14.91	0.311	**RES**	**0.89**	**ns**		
TI (YE) x SI (NTZ)	16	4.51	0.282	RES: NTZ	1.00	ns		
TI (YE) x SI (CON)	32	10.40	0.325	RES: CON	0.36	ns		
RESIDUAL	**360**	125.01	0.347					
RES: NTZ	120	33.92	0.283					
RES: CON	240	91.09	0.380					
TOTAL	**479**	284.54						

Cochran's Test C = 0.0362 (Not Significant)

Table 15. Abundance of spider crabs – NTZ *vs* Far Reference: ANOVA of L*n*(*X*+1)-transformed spider crab abundances per string of 10 pots for NTZ *versus* Far Reference locations (*n*=4). The symbol '❶' indicates the factors used as the denominator for testing LO: NTZ *vs* REF. The symbol '❷' indicates the factor used as the denominator for testing LO: REF. The symbol '❸' indicates the factor used as the denominator for testing YE x LO: NTZ *vs* REF. The symbol '❹' indicates the factor used as the denominator for testing YE x LO: REF. ns – $P > 0.05$.

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	57.86	28.928					
LO: NTZ *v* REF	1	56.31	56.307	NO TEST			9.50	$P < 0.05$
LO: REF ❶	1	1.55	1.549	NO TEST			0.21	ns
SITES (LOCATIONS) ❶❷	**3**	22.15	7.383	**TI (YE) x SI (LO)**	**22.37**	$P < 0.001$		
SITES (NTZ)	1	1.54	1.542	TI (YE) x SI (NTZ)	5.47	$P < 0.05$		
SITES (REF)	2	20.61	10.303	TI (YE) x SI (REF)	29.08	$P < 0.001$		
YEAR	**3**	37.72	12.573	**NO TEST**				**NO TEST**
TIME (YE)	**16**	13.68	0.855	**TI(YE) x LO: REF**	1.88	ns		
YEAR x LOCATION	**6**	38.37	6.395					
YE x LO: NTZ *v* REF	3	14.68	4.893	NO TEST			0.62	ns
YE x LO: REF ❸	3	23.69	7.897	NO TEST			4.47	ns
LOCATION x TIME (YEAR)	**32**	14.16						
TI (YE) x LO: NTZ *v* REF	16	6.89	0.431	TI (YE) x LO: REF	0.95	ns		
TI (YE) x LO: REF	16	7.27	0.454	TI (YE) x SI (REF)	1.28	ns		
YEAR x SITE (LOCATION)	**9**	11.49	1.277	**TI (YE) x SI (LO)**	**3.87**	$P < 0.01$		
YE x SI (NTZ)	3	0.89	0.296	TI (YE) x SI (NTZ)	1.05	ns		
YE x SI (REF) ❹	6	10.60	1.767	TI (YE) x SI (REF)	4.99	$P < 0.01$		
TIME (YEAR) x SITE (LOCATION)	**48**	15.85	0.330	**RES**	**0.92**	**ns**		
TI (YE) x SI (NTZ)	16	4.51	0.282	RES: NTZ	1.00	ns		
TI (YE) x SI (REF)	32	11.34	0.354	RES: REF	0.90	ns		
RESIDUAL	**360**	128.49	0.357					
RES: NTZ	120	33.92	0.283					
RES: REF	240	94.58	0.394					
TOTAL	**479**	339.76						

Cochran's Test C = 0.0381 (Not Significant)

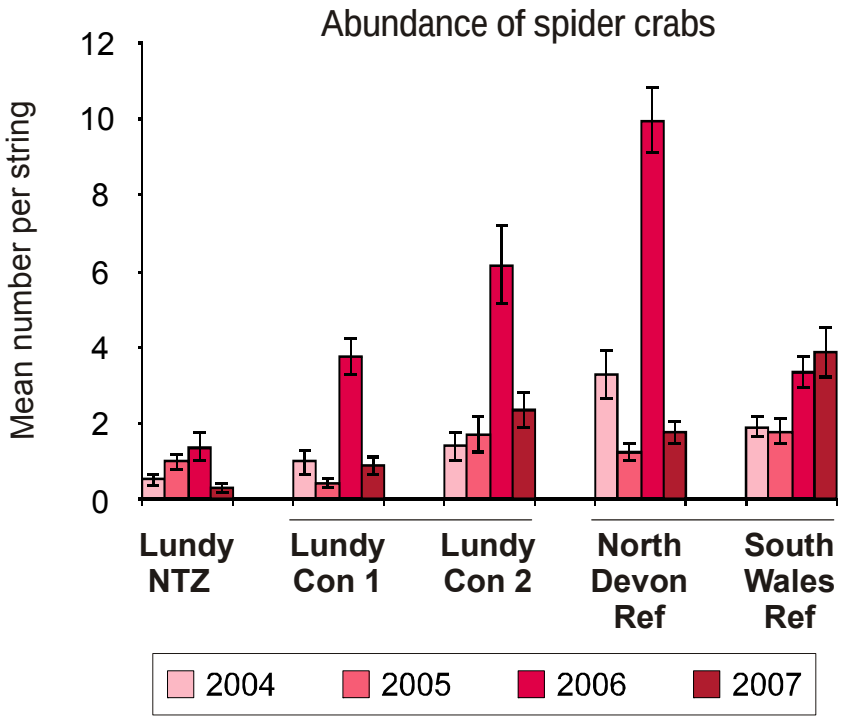

Figure 13. Abundance of spider crabs: Variation in the mean abundances of spider crab among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents the mean abundance (±SE) per string of 10 pots over 5 days of sampling.

3.1.2 The sizes of lobster and crabs (Hypothesis-3)

Of the four species of commercially-fished crustaceans that were monitored for this study, only lobster and brown crab showed significant changes in size that indicated a potential effect of the NTZ. In lobsters, this potential effect was seen only in the size-class of individuals with carapace lengths ≥90mm (*i.e.* landable-sized lobsters).

- Sizes of landable-sized lobsters

Analyses of data on the sizes (carapace length in mm) of landable-sized lobsters from 2004 to 2007 showed significant interactions of YE x LO: NTZ *v* CON (Table 16-*i*.) and YE x LO: NTZ *v* REF (Table 16-*ii.*).

These results were due to a progressive increase in the mean size of landable-sized lobsters in the NTZ and declining mean sizes in Near Control and Far Reference locations (Figure 14-*i.*). From 2004 to 2007, the mean size of landable-sized lobsters in the NTZ increased by 5.2% from 98.2 ± 1.2mm CL to 103.3 ± 2.1mm CL. In the same period, the mean size of landable-sized lobsters declined by 2.8% in Near Control locations (from 97.3 ± 0.7mm CL to 94.6 ± 0.7) and by 2.1% in Far Reference locations (from 96.9 ±0.8mm CL to 94.8 ± 0.7). By 2007, landable-sized lobsters in the NTZ were on average 9.1% larger than those in Near Control locations and 9.0% larger than those in Far Reference locations.

- Sizes of undersized lobsters

In analyses of data on the sizes of undersized lobsters neither of the critical factors for testing potential effects of the NTZ (*i.e.* YE x LO: NTZ *v* CON and YE x LO: NTZ *v* REF) were significant (Tables 17-*i.* and 17-*ii.*).

Analyses of size-data for undersized lobsters revealed two notable results for factors for which there were no *a priori* hypotheses. The first of these was a significant result for the factor YEAR in ANOVAs for both NTZ *versus* Near Control and NTZ *versus* Far Reference comparisons (Table 17). In each case, SNK tests showed that the significant result for YEAR was attributable to undersized lobsters being significantly smaller on average in 2004 than in subsequent years (Figure

14-*ii.*). In 2006 the mean size of undersized lobsters averaged across all locations was 75.3 ± 0.45mm CL. The mean size of undersized lobsters in the period 2005 to 2007 was larger by 3.7% (78.0 ± 0.23mm CL).

The significant result for the factor LO: NTZ V CON was due to undersized lobsters in the NTZ being 1.6% larger on average than those in Near Control locations (78.2 ± 0.5mm CL *versus* 77.0 ± 0.3mm CL, respectively) (Figure 14-*ii.*).

Table 16. Size of landable-sized lobsters: ANOVA of the mean sizes of landable-sized lobsters (CL ≥90mm) for *(i)* NTZ *versus* Near Control locations (*n*=22) and *(ii)* NTZ *versus* Far Reference locations (*n*=31). The symbol '❶' denotes the pooled factors used as the denominator for Lo: NTZ *vs* Con. The symbol '❷' denotes the pooled factors used as the denominator for Ye x Lo: NTZ *vs* Con/Ref. ns - *P* > 0.05.

***i.* NTZ *versus* Near Control locations**

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**1507.30**	753.652					
LO: NTZ *v* CON	1	1506.94	1506.939	LO: CON	4144.50	*P* < 0.05	43.77	*P* < 0.001
LO: CON ❶	1	0.36	0.364	RES: CON	0.01	**ns**		
YEAR	**3**	**107.33**	35.778	**YE x LO: CON**	**1.73**	ns		
YEAR x LOCATION	6	537.94	89.657					
YE x LO: NTZ *v* CON	3	475.98	158.662	YE x LO: CON	7.68	ns	4.58	*P* < 0.01
YE x LO: CON ❶❷	3	61.95	20.652	RES: CON	0.59	ns		
RESIDUAL	**252**	**14217.18**	56.417					
RES: NTZ	77	8116.82	105.413					
RES: CON ❶❷	175	6100.36	34.859					
TOTAL	**263**	**16369.76**						

Cochran's Test C = 0.2119 (P < 0.01) Largest variance = 143.4892, this occurred in NTZ 2006

***ii.* NTZ *versus* Far Reference locations**

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**3106.18**	1553.089					
LO: NTZ *v* REF	1	2916.30	2916.302	LO: REF	15.36	ns		NO TEST
LO: REF	1	189.88	189.875	RES: REF	6.72	*P* < 0.05		
YEAR	**3**	**8.74**	2.913	**YE x LO: REF**	**0.15**	**ns**		
YEAR x LOCATION	6	713.80	118.967					
YE x LO: NTZ *v* REF	3	655.72	218.575	YE x LO: REF	11.29	*P* < 0.05	7.76	*P* < 0.001
YE x LO: REF ❷	3	58.08	19.359	RES: REF	0.68	ns		
RESIDUAL	**360**	**18587.10**	51.631					
RES: NTZ	113	11603.68	102.687					
RES: REF ❷	247	6983.42	28.273					
TOTAL	**371**	**22415.81**						

Cochran's Test C = 0.2281 (P < 0.01) Largest variance = 141.3462, this occurred in NTZ 2007

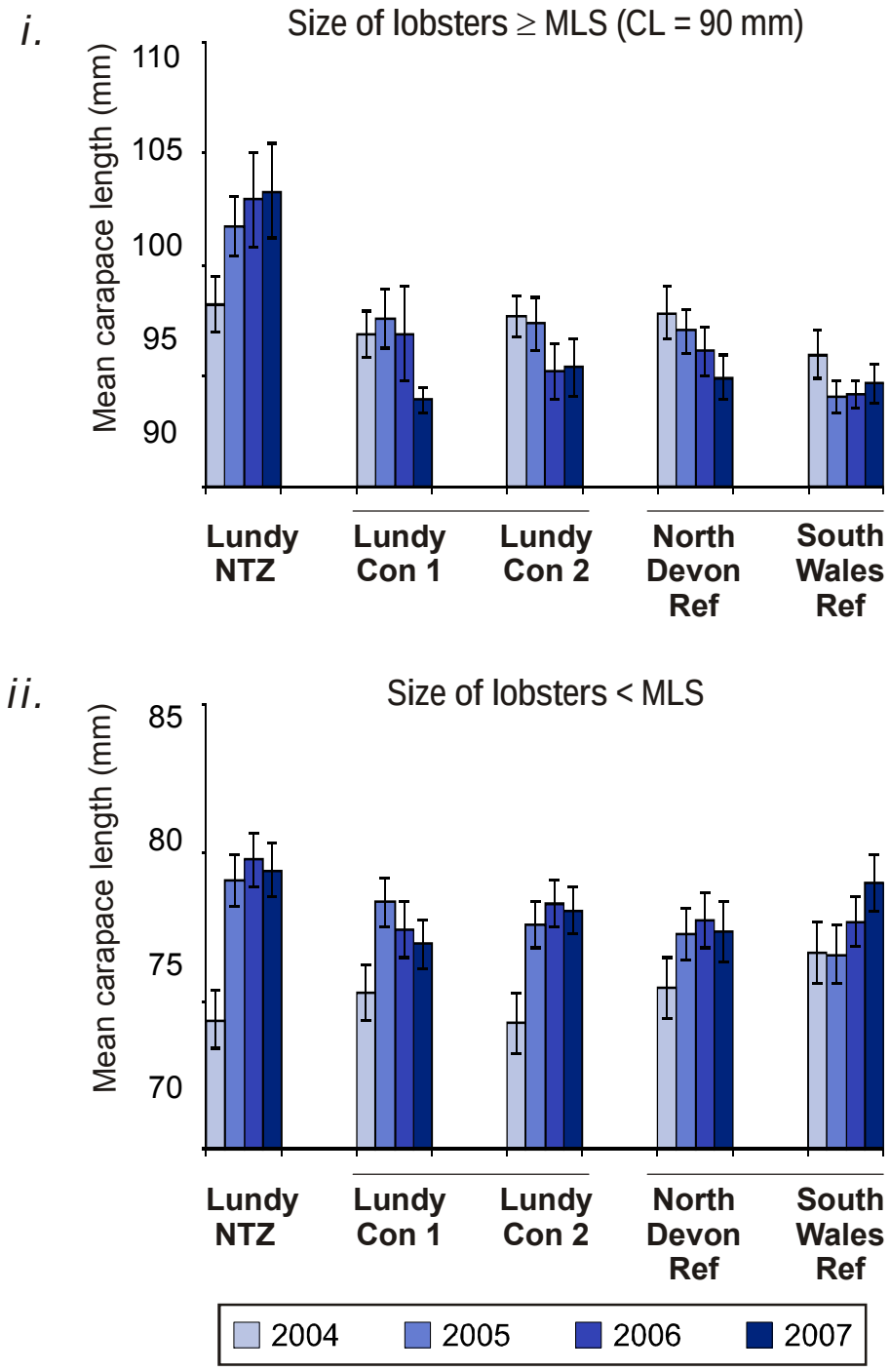

Figure 14. Size of lobsters: Variation in the mean size of *(i)* landable-sized lobsters (CL ≥90mm) and *(ii)* undersized lobsters (CL <90mm) among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents mean size (±SE) over 5 days of sampling per year. For landable-sized lobsters, plotted means were calculated from sample sizes of *n* = 31 for NTZ and Far Reference locations and *n* = 22 for Near Control locations. For undersized lobsters, plotted means were calculated from sample sizes of *n* = 78 for NTZ and Near Control locations and *n* = 75 for Far Reference locations.

Table 17. Sizes of undersized lobsters: ANOVA of the means sizes of undersized lobsters (CL <90mm) for *(i)* NTZ *versus* near control locations (*n*=78) and *(ii)* NTZ *versus* Far Reference locations (*n*=75). The symbol '❶' denotes the pooled factors used as the denominator for Lo: NTZ *vs* Con/Ref. The symbol '❷' denotes the pooled factors used as the denominator for Ye x Lo: NTZ *vs* Con/Ref. ns - $P > 0.05$.

i. NTZ *versus* Near Control locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**338.02**	169.010					
LO: NTZ *v* CON	1	327.50	327.505	LO: CON	31.15	ns	5.66	$P < 0.05$
LO: CON ❶	1	10.51	10.514	RES: CON	0.18	**ns**		
YEAR	**3**	**2181.30**	727.101	**YE x LO: CON**	**13.84**	$P < 0.05$		
YEAR x LOCATION	6	309.33	51.555					
YE x LO: NTZ *v* CON	3	151.71	50.570	YE x LO: CON	0.96	ns	0.87	ns
YE x LO: CON ❶❷	3	157.62	52.540	RES: CON	0.91	ns		
RESIDUAL	**924**	**56468.23**	61.113					
RES: NTZ	301	20344.04	67.588					
RES: CON ❶❷	623	36124.19	57.984					
TOTAL	**935**	**59296.88**						

Cochran's Test C = 0.1167 (Not Significant)

ii. NTZ *versus* Far Reference locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**219.58**	109.791					
LO: NTZ *v* REF	1	177.98	177.976	LO: REF	4.28	ns	2.62	ns
LO: REF	1	41.61	41.607	RES: REF	0.61	ns		
YEAR	**3**	**1378.86**	459.619	**YE x LO: REF**	**10.29**	$P < 0.05$		
YEAR x LOCATION	6	609.28	101.548					
YE x LO: NTZ *v* REF	3	475.30	158.432	YE x LO: REF	3.55	ns	2.33	ns
YE x LO: REF ❷	3	133.99	44.664	RES: REF	0.66	ns		
RESIDUAL	**888**	**60146.40**	67.732					
RES: NTZ	289	19375.76	67.044					
RES: REF ❷	599	40770.64	68.065					
TOTAL	**899**	**62354.13**						

Cochran's Test C = 0.0967 (Not Significant)

- Size of velvet crabs

In analyses of data on the sizes of velvet crabs (carapace width (CW) in mm) neither of the critical factors for testing potential effects of the NTZ (*i.e.* YE x LO: NTZ *v* CON and YE x LO: NTZ *v* REF) were significant (Tables 18-*i.* and 18-*ii.*).

Analyses of size-data for velvet crabs revealed only one notable result for a factor for which there was no *a priori* hypothesis; this was a significant result for the factor LO:REF (Table 18-*ii.*). This result was due to the mean size of velvet crabs in the South Wales reference location (67.5 ± 0.8mm CW) being 4.9% greater on average than that in the North Devon reference location (64.4 ± 1.1mm CW) (Figure 15).

Table 18. Sizes of velvet crabs: ANOVA of velvet crab sizes for *(i)* NTZ *versus* Near Control locations (*n*=10) and *(ii)* NTZ *versus* Far Reference locations (*n*=10). The symbol '❶' denotes the pooled factors used as the denominator for Ye x Lo: NTZ *vs* Con. ns - *P* > 0.05.

i. NTZ *versus* Near Control locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**224.72**	112.358					
LO: NTZ *v* CON	1	175.10	175.104	LO: CON	3.53	ns		NO TEST
LO: CON	1	49.61	49.613	RES: CON	2.00	**ns**		
YEAR	**3**	**0.47**	0.156	**YE x LO: CON**	**0.03**	ns		
YEAR x LOCATION	6	41.48	6.914					
YE x LO: NTZ *v* CON	3	26.75	8.915	YE x LO: CON	1.81	ns	0.37	ns
YE x LO: CON ❶	3	14.74	4.913	RES: CON	0.20	ns		
RESIDUAL	**108**	**3776.00**	34.963					
RES: NTZ	29	1815.90	62.617					
RES: CON ❶	79	1960.10	24.811					
TOTAL	**119**	**4042.67**						

Cochran's Test C = 0.2994 (P < 0.01) Largest variance = 125.6111, this occurred in NTZ 2004

ii. NTZ *versus* Far Reference locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**411.27**	205.633					
LO: NTZ *v* REF	1	212.82	212.817	LO: REF	1.07	ns		NO TEST
LO: REF	1	198.45	198.450	RES: REF	5.56	*P* < 0.05		
YEAR	**3**	**103.03**	34.342	**YE x LO: REF**	**0.62**	**ns**		
YEAR x LOCATION	6	181.40	30.233					
YE x LO: NTZ *v* REF	3	16.15	5.383	YE x LO: REF	0.10	ns		NO TEST
YE x LO: REF	3	165.25	55.083	RES: REF	1.54	ns		
RESIDUAL	**108**	**4633.30**	42.901					
RES: NTZ	29	1815.90	62.617					
RES: REF	79	2817.40	35.663					
TOTAL	**119**	**5328.99**						

Cochran's Test C = 0.2440 (P < 0.01) Largest variance = 125.6111, this occurred in NTZ 2004

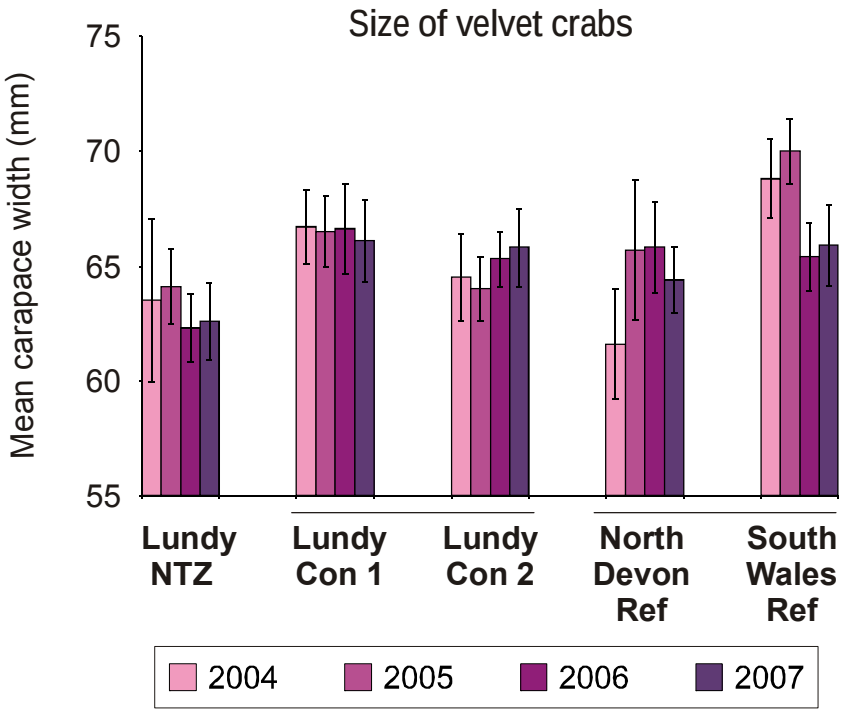

Figure 15. Size of velvet crabs: Variation in the mean size of velvet crabs among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents mean size over 5 days of sampling per year. Plotted means were calculated from sample sizes of *n* = 10 for all locations.

- Size of brown crabs

Analyses of data on the sizes of brown crabs (carapace width (CW) in mm) from 2004 to 2007 showed a significant interaction of YE x LO: NTZ *v* CON (Table 19-*i.*), but not of YE x LO: NTZ *v* REF (Table 19-*ii.*).

From 2004 to 2007, the mean size of brown crabs within the NTZ increased progressively from 114.6 ± 10.3mm CW to 143.4 ± 6.7mm CW; an overall increase in size of 25%. Mean size in the Near Control locations increased from 126.0 ± 6.2mm CW in 2004 to 139.9 ± 5.5mm CW in 2006 and then declined to 130.3 ± 7.4mm CW in 2007 (Figure 16).

Analyses of size-data for brown crabs revealed only one notable result for a factor for which there was no *a priori* hypothesis; this was a significant result for the factor LO:REF (Table 19-*ii.*). This result was due to the mean size of brown crabs in the North Devon reference location (137.3 ± 3.3mm CW) being 13.2% greater on average than that in the South Wales reference location (121.3 ± 3.3mm CW) (Figure 16).

Table 19. Size of brown crabs: ANOVA of untransformed brown crab sizes for *(i)* NTZ *versus* Near Control locations (*n*=5) and *(ii)* NTZ *versus* Far Reference locations (*n*=5). The symbol '❶' denotes the pooled factors used as the denominator for Lo: NTZ *vs* Con. The symbol '❷' denotes the pooled factors used as the denominator for Ye x Lo: NTZ *vs* Con/Ref. ns - $P > 0.05$.

i. NTZ *versus* Near Control locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**373.90**	186.950					
LO: NTZ *v* CON	1	54.68	54.675	LO: CON	0.17	ns	0.17	ns
LO: CON ❶	1	319.23	319.225	RES: CON	0.94	**ns**		
YEAR	**3**	**2310.98**	770.328	**YE x LO: CON**	**63.71**	*P* < 0.01		
YEAR x LOCATION	6	1191.97	198.661					
YE x LO: NTZ *v* CON	3	1155.69	385.231	YE x LO: CON	31.86	*P* < 0.01		
YE x LO: CON ❶❷	3	36.28	12.092	RES: CON	0.04	ns		
RESIDUAL	**48**	**22856.00**	476.167					
RES: NTZ	9	9586.40	1065.156					
RES: CON ❶❷	39	13269.60	340.246					
TOTAL	**59**	**26732.85**						

Cochran's Test C = 0.1631 (Not Significant)

ii. NTZ *versus* Far Reference locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**2584.30**	1292.150					
LO: NTZ *v* REF	1	24.30	24.300	LO: REF	0.01	ns		NO TEST
LO: REF	1	2560.00	2560.000	RES: REF	5.59	***P* < 0.05**		
YEAR	**3**	**1653.00**	551.000	**YE x LO: REF**	**2.44**	ns		
YEAR x LOCATION	6	1839.30	306.550					
YE x LO: NTZ *v* REF	3	1160.70	386.900	YE x LO: REF	1.71	ns	0.88	ns
YE x LO: REF ❷	3	678.60	226.200	RES: REF	0.49	ns		
RESIDUAL	**48**	**27444.00**	571.750					
RES: NTZ	9	9586.40	1065.156					
RES: REF ❷	39	17857.60	457.887					
TOTAL	**59**	**33520.60**						

Cochran's Test C = 0.2308 (Not Significant)

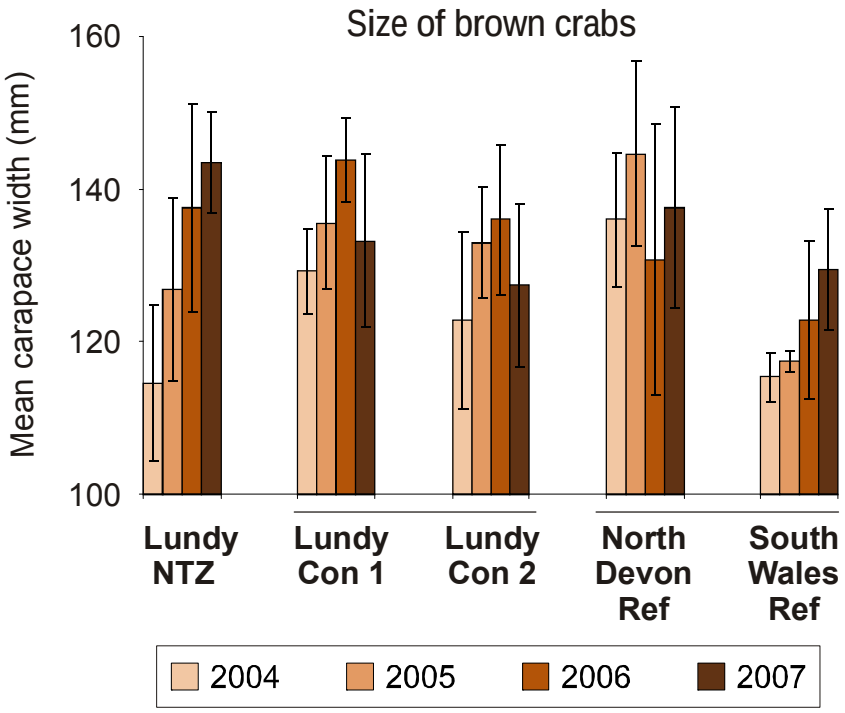

Figure 16. Size of brown crabs: Variation in the mean size of brown crabs among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents mean size over 5 days of sampling per year. Plotted means were calculated from sample sizes of *n* = 5 for all locations.

- Size of spider crabs

In analyses of data on the sizes of spider crabs (carapace width (CW) in mm) neither of the critical factors for testing potential effects of the NTZ (*i.e.* YE x LO: NTZ *v* CON and YE x LO: NTZ *v* REF) were significant (Tables 20-*i.* and 20-*ii.*).

Analyses of size-data for spider crabs revealed only one notable result for a factor for which there was no *a priori* hypothesis; this was a significant result for the factor YEAR in the analysis of data from the NTZ and Near Control locations (Table 20-*i.*). SNK tests revealed that this was attributable to the mean size of spider crabs in Near Control locations in 2005 (111.5 ± 2.0mm CW) being significantly greater than that for 2004 (100.1 ± 3.2mm CW) and 2007 (101.1 ± 2.4mm CW).

Table 20. Size of spider crabs: ANOVA of spider crab sizes for *(i)* NTZ *versus* Near Control locations (*n*=12) and *(ii)* NTZ *versus* Reference locations (*n*=12). The symbol '❶' denotes the pooled factors used as the denominator for Lo: NTZ *vs* Con. The symbol '❷' denotes the pooled factors used as the denominator for Ye x Lo: NTZ *vs* Con/Ref. ns - $P > 0.05$.

i. NTZ *versus* Control locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**268.76**	134.382					
LO: NTZ *v* CON	1	266.42	266.420	LO: CON	113.67	ns	1.41	ns
LO: CON ❶	1	2.34	2.344	RES: CON	0.01	**ns**		
YEAR	**3**	**3173.25**	1057.750	**YE x LO: CON**	**69.82**	$P < 0.01$		
YEAR x LOCATION	6	398.13	66.354					
YE x LO: NTZ *v* CON	3	352.68	117.559	YE x LO: CON	7.76	ns	0.61	ns
YE x LO: CON ❶❷	3	45.45	15.149	RES: CON	0.08	ns		
RESIDUAL	**132**	**30214.17**	229.100					
RES: NTZ	37	11535.75	311.777					
RES: CON ❶❷	95	18705.42	196.899					
TOTAL	**143**	**34081.31**						

Cochran's Test C = 0.2073 (P < 0.05) Largest variance = 570.0227, this occurred in NTZ 2004

ii. NTZ *versus* Reference locations

				Pre-Pooling			Post-Pooling	
Source of variation	**df**	**SS**	**MS**	**Denominator**	***F***	***P***	***F***	***P***
LOCATION	**2**	**1983.85**	991.924					
LO: NTZ *v* REF	1	415.68	415.681	LO: REF	0.27	ns		NO TEST
LO: REF	1	1568.17	1568.167	RES: REF	3.90	**ns**		
YEAR	**3**	**3618.30**	1206.100	**YE x LO: REF**	**3.37**	ns		
YEAR x LOCATION	6	1436.26	239.377					
YE x LO: NTZ *v* REF	3	361.18	120.394	YE x LO: REF	0.34	ns	0.30	ns
YE x LO: REF ❷	3	1075.08	358.361	RES: REF	0.89	ns		
RESIDUAL	**132**	**49759.25**	376.964					
RES: NTZ	37	11535.75	311.777					
RES: REF ❷	95	38223.50	402.353					
TOTAL	**143**	**56797.66**						

Cochran's Test C = 0.1876 (Not Significant)

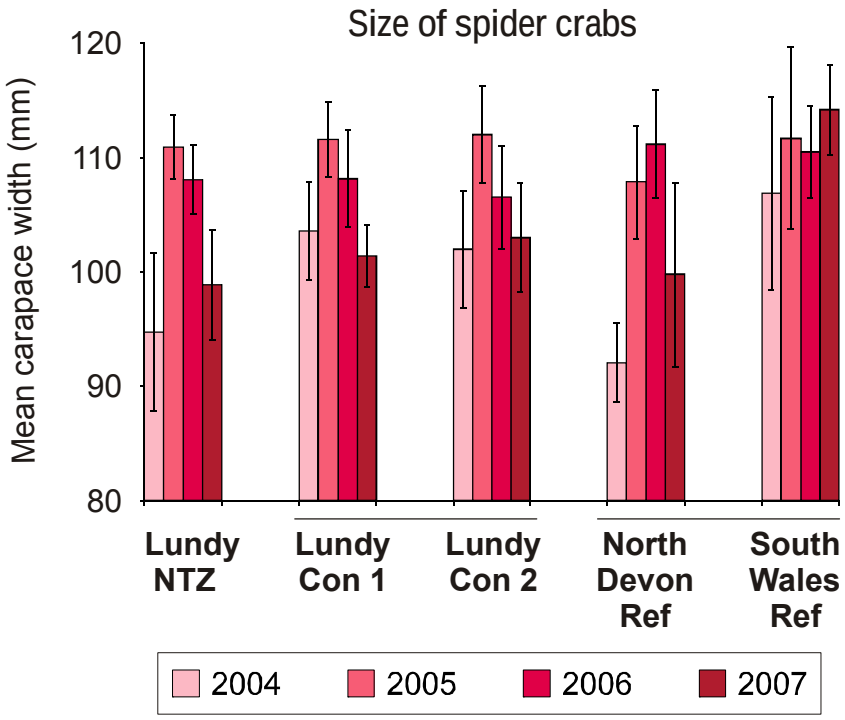

Figure 17. Sizes of spider crabs: Variation in the mean size spider crabs among NTZ, Near Control and Far Reference locations year from 2004 to 2007. Each bar represents mean size over 5 days of sampling per year. Plotted means were calculated from sample sizes of *n* = 12 for all locations.

3.2 Scallops

3.2.1 The abundances of scallops (Hypothesis-4)

As discussed in Section 2.2.2, the fact that scallop abundance data was available for only four plots per site in 2004, *versus* six plots per site in subsequent years, meant that there was a problem of how best to analyse these data to test for an effect of the NTZ. It was decided that retaining the 2004-baseline was the greatest priority, but that the more-powerful analysis with six plots per site would be used in preference if there were no significant difference in mean abundance between 2004 and 2005.

The ANOVA with data for all four years (Table 21-*i.*) revealed a significant effect of the factor YEAR. Critically, there was no significant change in abundance from 2004 to 2005 (as revealed by SNK tests), so this analysis was superseded by the analysis with a 2005-baseline and six plots per site (Table 21-*ii.*). Henceforth, all results described or presented graphically correspond to this latter analysis.

Analyses of data on the abundance of scallops in the period 2005 to 2007 showed a significant interaction of YE x LO (Table 21-*ii.*). SNK tests revealed that this was due to a significant increase in the abundance of scallops in Control locations from 2005 to 2006 (Figure 18). In 2005, the abundance of scallops in the NTZ (0.33 ± 0.07 per $10m^2$) was significantly greater than in the Control location (0.08 ± 0.02 per $10m^2$); a difference of 312%. The subsequent increase in the relative abundance of scallops in the Control location from 2005 to 2007 negated this initial significant difference. Mean abundances of scallops in the NTZ and Control locations in 2007 were 0.47 ± 0.10 per $10m^2$ and 0.56 ± 0.08 per $10m^2$, respectively.

Analysis of data on the abundance of scallops revealed two notable results for factors for which there was no *a priori* hypothesis. The first of these was a significant result for the factor SI(LO) (Table 21-*ii.*). SNK tests showed that this was attributable to NTZ site-2 having a consistently greater density of scallops than NTZ site-1 (Figure 18). When averaged across years, the mean abundance of scallops in NTZ site-2 (0.54 ± 0.08 per $10m^2$) was 200% greater than the mean

for NTZ site-1 (0.18 ± 0.04 per $10m^2$). The second unpredicted result of note was the significant outcome for the factor PLOTS(LO X YE X SI) (Table 21-*ii.*). SNK tests showed that there were significant differences among plots within six of the 12 possible combinations of location, year and site. The occurrences of these significant plot-to-plot differences had no obvious relationship with any of these different factors in the sampling design. With respect to location, there were three such differences in the NTZ and three in the control location. With respect to years, there was one in 2005, three in 2006 and two in 2007.

Table 21. Scallops: Two alternate analyses of L*n*(*X*+0.1)-transformed abundances of scallops per $10m^2$ in the NTZ and control locations (see previous text for explanation): *(i)* an analysis of 2004-2007 data with 4 plots per site and *(ii)* an analysis of 2005-2007 data with 6 plots per site. ns – *P* > 0.05.

***i.* Years 2004 to 2007, 4 plots per site**

Source	SS	df	MS	*F*	*P*	Denominator in *F*-ratio
LOCATION	0.02	1	0.015	0.00	ns	SITES(LO)
YEAR	27.93	3	9.310	6.03	*P* < 0.01⌘	❶-POOLED MS
SITES(LO)	8.60	2	4.299	2.78	ns	❶-POOLED MS
PLOTS(LO X YE X SI) ❶	80.05	48	1.668	2.84	*P* < 0.001	RESIDUAL
LO X YE	7.61	3	2.535	1.64	ns	❶-POOLED MS
YE X SI(LO) ❶	3.38	6	0.563	0.34	ns	PLOTS(LO X YE X SI)
RESIDUAL	112.63	192	0.587			
TOTAL	240.21	255				
❶-POOLED MS	83.43	54	1.545	2.63		RESIDUAL

Cochran's Test C = 0.0442 (Not Significant)

⌘ SNK test for YEAR: 2004 = 2005 < 2006 = 2007

***ii.* Years 2005 to 2007, 6 plots per site**

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	0.05	1	0.053	0.01	ns	SITES(LO)
YEAR	24.05	2	12.026	6.78	*P* < 0.01	❶-POOLED MS
SITES(LO)	18.63	2	9.317	5.26	*P* < 0.01 ⌘2	❶-POOLED MS
PLOTS(LO X YE X SI) ❶	110.78	60	1.846	3.01	*P* < 0.001	RESIDUAL
LO X YE	11.30	2	5.651	3.19	*P* < 0.05⌘2	❶-POOLED MS
YE X SI(LO) ❶	2.66	4	0.666	0.36	ns	PLOTS(LO X YE X SI)
RESIDUAL	132.34	216	0.613			
TOTAL	299.82	287				
❶-POOLED MS	113.44	64	1.773	2.90		RESIDUAL

Cochran's Test C = 0.0482 (Not Significant)

⌘1 SNK test for LO X YE. *(i)* LO(YE): 2005; NTZ > CON / 2006; NTZ = CON / 2007; NTZ = CON

(ii) YE(LO): NTZ; 2005 = 2006 = 2007 / CON; 2005 < 2006 = 2007

⌘2 SNK test for SI(LO): NTZ 1 < NTZ 2 / Con 1 = Con 2

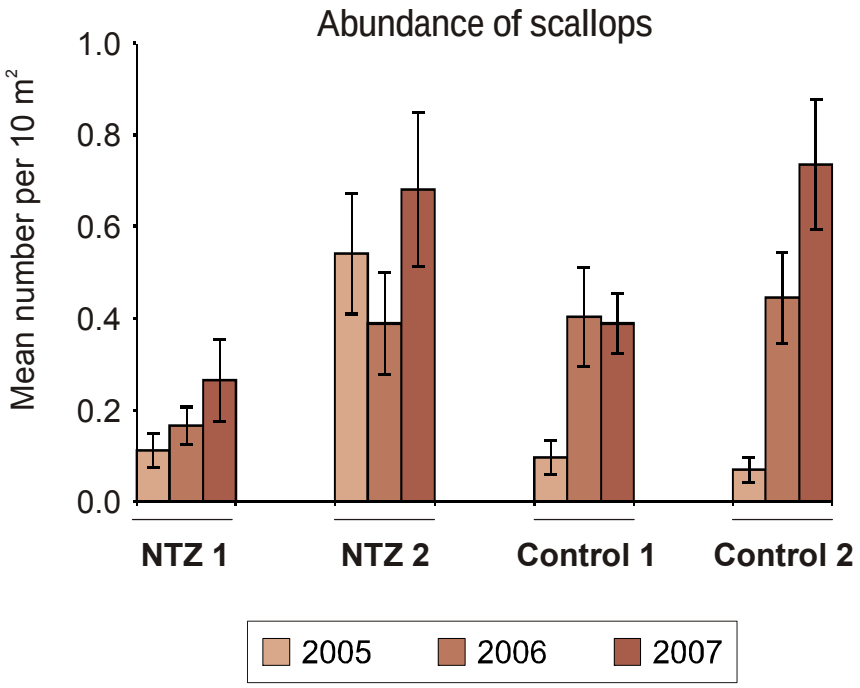

Figure 18. Abundance of scallops: Mean abundance of scallops per 10m^2 in NTZ *versus* control locations in the period 2005 to 2007. Each bar represents the mean of 6 replicate plots per site.

3.2.2 *The size of scallops (Hypothesis-5)*

Analyses of data on the size (shell width) of scallops showed a significant interaction of YE x LO (Table 22). SNK tests showed that this was attributable to a trend of progressively increasing mean size in the Control location whilst mean size in the NTZ remained relatively constant (Figure 19). From 2004 to 2007 the mean size of scallops in the Control location increased 55% from 7.8 ± 1.0cm to 12.1 ± 0.4cm. Until 2006 the mean size of scallops in the NTZ (13.0 ± 0.2cm) was significantly greater than that in the Control location. From 2006 onwards, the difference in mean size between the NTZ and the Control location was no longer significant.

Table 22. Size of scallops: ANOVA of scallop sizes (shell width in cm) for NTZ *versus* control locations in the period 2004 to 2007 (*n*=8).

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	116.91	1	116.910	23.33	$P < 0.001$	RESIDUAL
YEAR	42.29	3	14.098	2.81	$P < 0.05$	RESIDUAL
LO x YE	49.57	3	16.525	3.3	$P < 0.05^{\text{⌘}}$	RESIDUAL
RESIDUAL	280.59	56	5.011			
TOTAL	489.37	63				

Cochran's Test C = 0.4277 ($P < 0.01$) Largest variance = 17.1429, this occurred in Control 2005

⌘ SNK test for LO x YE

(i) LO(YE): 2004; NTZ > CON / 2005; NTZ > CON / 2006; NTZ = CON / 2007; NTZ = CON

(ii) YE(LO): NTZ; 2004 = 2005 = 2006 = 2007 / CON; 2004 = 2005 = 2006 = 2007

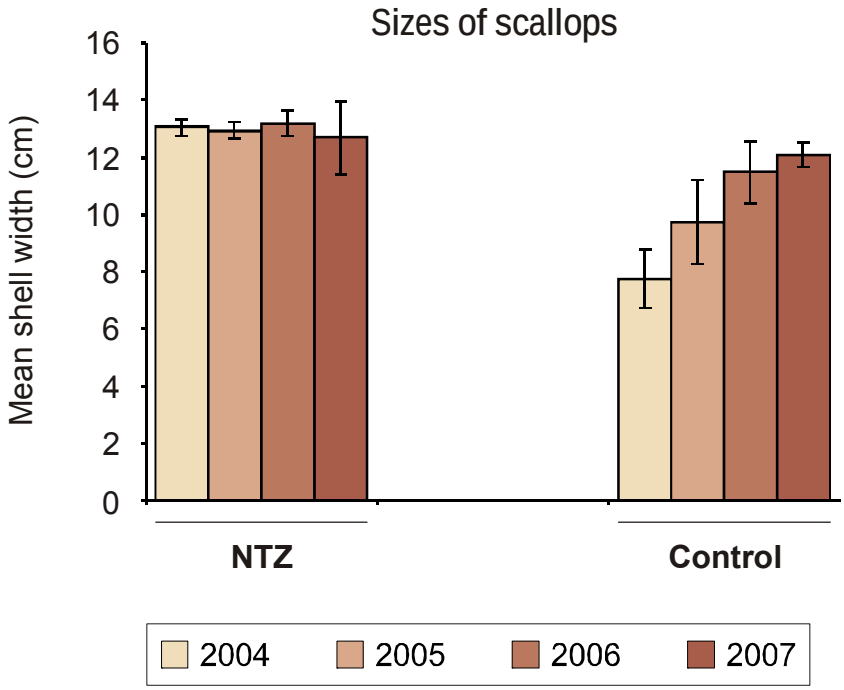

Figure 19. Size of scallops: Mean sizes of scallops in NTZ *versus* control locations in the period 2004 to 2007. Bars show mean shell width (cm) for each site (*n*=8).

3.2.3 *The size-structure of scallop populations (Hypothesis-6)*

Kolmogorov-Smirnov tests comparing the size-structure of scallop populations in NTZ *versus* Control locations revealed no changes in size-structure that indicated a potential effect of the NTZ.

Kolmogorov-Smirnov tests revealed significant differences between NTZ and Control locations in 2004 and 2006, but not in 2005 and 2007 (Table 23). The difference between NTZ and Control populations in 2004 appeared to be due to the presence of small scallops (4.5 to 6.0cm) in the Control location only and the greater abundance of large scallops (10.0 to 14.0cm) in the NTZ (Figure 20).

In 2006, the significant difference between NTZ and Control populations appears to have arisen from the fact that scallops <10cm in size were relatively abundant in the Control location (even more so than in 2004), but absent from the NTZ (Figure 20). In the course of the study, scallops <10cm in size were not found in the NTZ until 2007.

Table 23. Scallops: Results of two-sample Kolmogorov-Smirnov tests to compare the size-frequency distribution of scallop populations in NTZ *vs* Control locations in each year.

Year of NTZ *vs* Control comparison	n_1	n_2	Type of K-S test depends on n_1 & n_2: $n_1 + n_2 \leq 25$, test statistic = D_{n1n2}	Type of K-S test depends on n_1 & n_2: n_1 or $n_2 > 25$, test statistic = D	*P*
2004	17	8	103	-	$P < 0.01$
2005	47	12	-	0.417	ns
2006	40	61	-	0.320	$P < 0.05$
2007	68	81	-	0.165	ns

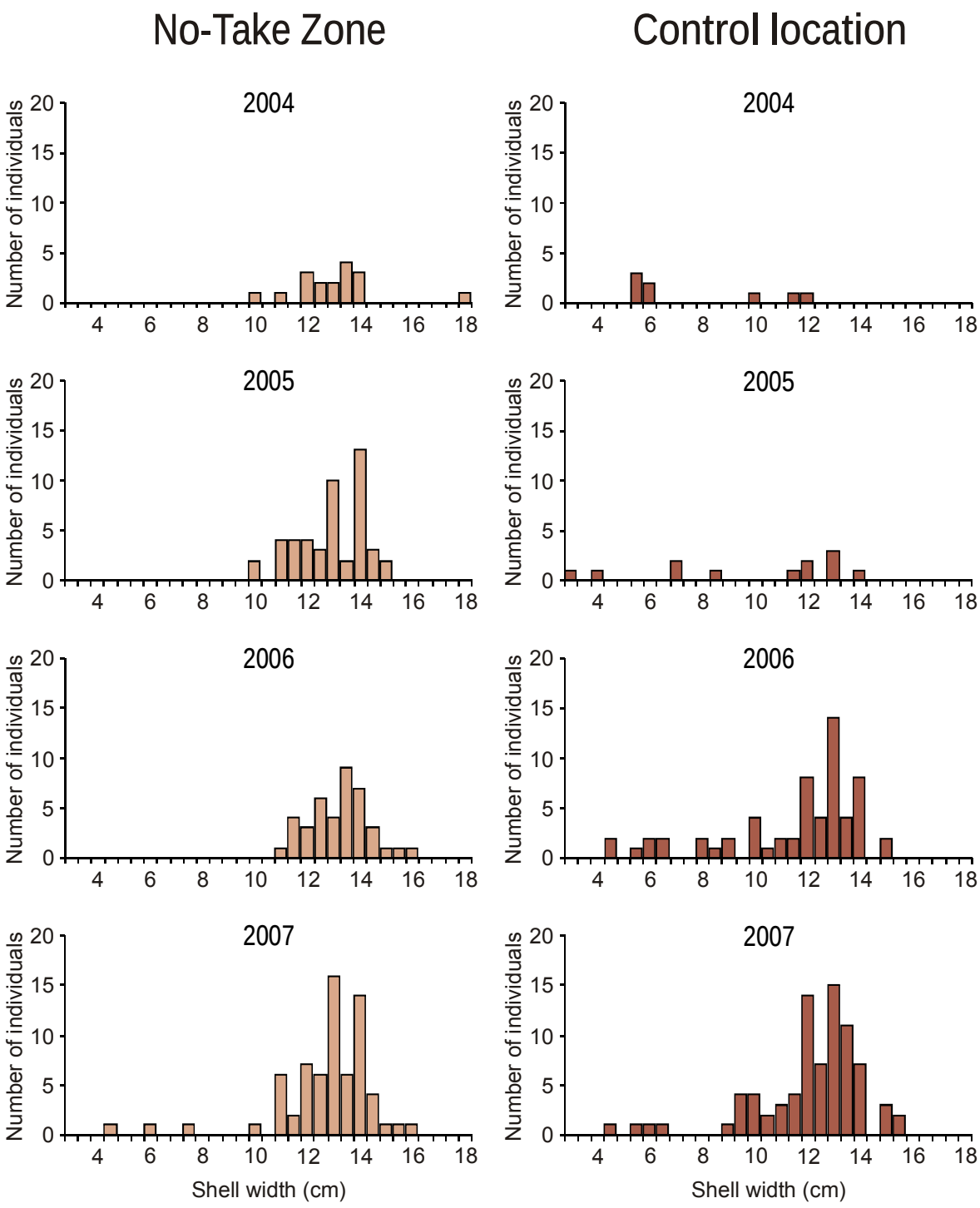

Figure 20. Sizes of scallops: Size-frequencies of scallops within NTZ and Control locations in each year of sampling from 2004 to 2007.

3.3 Sessile epifauna in circalittoral rocky habitats

3.3.1 The composition of epifaunal assemblages (Hypothesis-7)

- Temporal changes in assemblage composition

From 2004 to 2007, assemblages of sessile epifauna showed no changes in composition that would indicate a potential effect of the NTZ. In fact, with only one exception, there was no significant change in assemblage composition at any sampling site throughout the entire four-year period of the study (Table 24).

Table 24. Sessile epifauna: Bray-Curtis dissimilarities and results of ANOSIM tests between years for each site (using 4th root transformed-data). ns – $P > 0.05$

Year comparison (no. of years interval)	Multivariate comparisons between years for each site			
	Site	**Bray- Curtis Dissimilarity**	**R-value**	**Significance**
2004 *vs* 2005 (1-year interval)	**NTZ 1**	25.2	0.150	ns
	NTZ 2	34.8	-0.131	ns
	Control 1	22.1	-0.356	ns
	Control 2	36.5	0.069	ns
2005 *vs* 2006 (1-year interval)	**NTZ 1**	27.6	0.148	ns
	NTZ 2	33.8	-0.067	ns
	Control 1	38.1	0.152	ns
	Control 2	29.3	0.022	ns
2006 *vs* 2007 (1-year interval)	**NTZ 1**	27.0	0.046	ns
	NTZ 2	28.1	0.011	ns
	Control 1	33.8	0.252	$P < 0.05$
	Control 2	25.5	0.002	ns
2004 *vs* 2006 (2-year interval)	**NTZ 1**	25.1	-0.046	ns
	NTZ 2	35.4	-0.019	ns
	Control 1	35.0	-0.222	ns
	Control 2	33.8	0.075	ns
2005 *vs* 2007 (2-year interval)	**NTZ 1**	22.8	-0.137	ns
	NTZ 2	29.8	-0.052	ns
	Control 1	25.2	0.065	ns
	Control 2	28.0	0.043	ns
2004 *vs* 2007 (3-year interval)	**NTZ 1**	23.7	-0.017	ns
	NTZ 2	31.0	-0.009	ns
	Control 1	18.2	-0.067	ns
	Control 2	32.1	0.091	ns

Bray Curtis dissimilarity values for comparisons between consecutive years for each site of sampling ranged from 22.1 to 38.1, with a mean (±SE) of 30.2 (±1.5). Of the twelve such comparisons, only one, the 2006 *vs* 2007 comparison for Control site-1, was significant via ANOSIM (Table 24). The Bray-Curtis dissimilarity value for this comparison was 33.8. SIMPER analysis showed that this significant difference was mainly due to differences in the abundance of *Alcyonium digitatum*, which contributed 27.4% to the overall difference, and total axinellid sponges, which contributed 16.3%.

Progressively increasing the length of interval for comparison from one to two to three years revealed no increase in the magnitude of temporal change in assemblage composition within sites. None of the comparisons for two and three year intervals were statistically significant by ANOSIM (Table 24) and there was no tendency for increase in the magnitude of Bray-Curtis dissimilarity values; in fact, they tended to become smaller. Among within-site comparisons over a 2-year interval, Bray-Curtis dissimilarities ranged from 22.8 to 35.4, with a mean of 29.4 (±1.7). For the same comparisons over a three year interval Bray-Curtis dissimilarities ranged from 18.2 to 32.1, with a mean of 26.3 (±3.3).

- Spatial differences in assemblage composition

Throughout the four years of the monitoring study to date, there was a consistent pattern of spatial variation in assemblage composition among sampling sites (Figure 21). These spatial differences in assemblages were generally larger than temporal changes within sites and, in most cases, were also statistically significant in ANOSIM tests (Table 25).

The pattern of spatial variation in assemblage composition observed among sites around Lundy has two main components, both of which are clearly visible in the nMDS plot in Figure 21. The first point to note is that there are large, consistent differences in assemblage composition between Control sites on the west coast of Lundy and sites within the NTZ on the east coast of the island. This is evidenced by the fact that symbols representing samples from west coast Control sites and east coast NTZ sites cluster separately in the nMDS plot and there is relatively little overlap between these clusters. The second point to note is that there was

roughly the same amount of difference between assemblages in the two replicate NTZ sites as there was between NTZ and Control sites. Simultaneously, assemblages in the two replicate Control sites were almost indistinguishable from each other, as evidenced by the fact that symbols representing samples from replicate Control sites are clustered tightly together in the nMDS-plot.

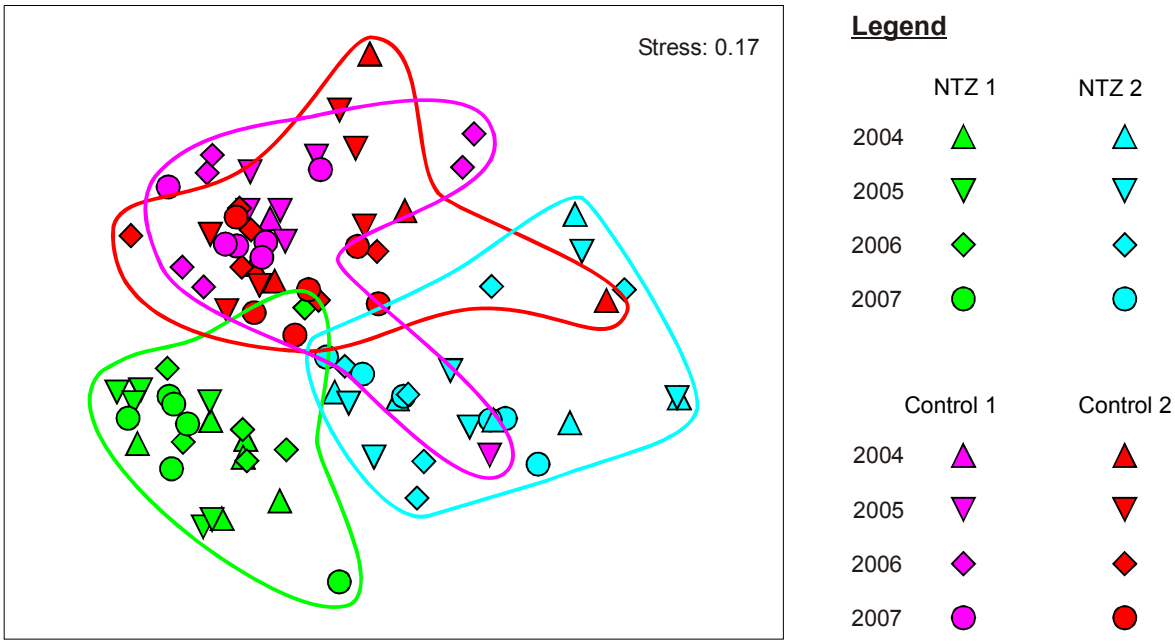

Figure 21. Sessile epifauna of circalittoral rocky habitats: nMDS-plot summarising multivariate differences in the composition of assemblages of sessile epifauna among sites within locations in each year.

Bray-Curtis dissimilarity values calculated for pairwise comparisons of the different types of sites in each year (Table 25) show that the difference between assemblages in the two replicate NTZ sites was, on average, slightly greater than the difference between NTZ and Control sites (49.7 *versus* 46.4, respectively). For comparison, the average Bray-Curtis dissimilarity between assemblages in the replicate Control sites, which appeared very similar in the nMDS-plot, was 33.5. This is roughly the same order of magnitude of dissimilarity as year-to-year variability within individual sites.

Table 25. Sessile epifauna: Dissimilarities and results of ANOSIM tests between pairwise combinations of different sites in each year. Data are 4th root transformed. ns - *P* > 0.05.

Epifauna: multivariate comparisons between sites												
	2004			2005			2006			2007		
Comparison of sites	**B-C dissim**	**R**	***P***	**B-C dissim**	**R**	***P***	**B-C dissim**	**R**	***P***	**B-C dissim**	**R**	***P***
NTZ 1 *vs* NTZ 2	52.3	0.702	*P* < 0.01	54.3	0.743	*P* < 0.01	43.9	0.663	*P* < 0.01	48.3	0.872	*P* < 0.01
Control 1 *vs* Control 2	36.9	-.08	ns	36.2	0.233	*P* < 0.05	31.9	-.013	ns	29.0	0.494	*P* < 0.01
NTZ 1 *vs* Control 1	43.3	0.956	ns	49.3	0.843	*P* < 0.01	46.6	0.622	*P* < 0.01	46.6	0.937	*P* < 0.01
NTZ 1 *vs* Control 2	51.3	0.755	*P* < 0.01	47.0	0.809	*P* < 0.01	39.2	0.754	*P* < 0.01	41.6	0.791	*P* < 0.01
NTZ 2 *vs* Control 1	51.4	0.511	ns	48.1	0.470	*P* < 0.05	50.9	0.643	*P* < 0.01	45.8	0.894	*P* < 0.01
NTZ 2 *vs* Control 2	47.2	0.307	*P* < 0.05	50.8	0.607	*P* < 0.01	46.5	0.709	*P* < 0.01	36.4	0.526	*P* < 0.01

Results of ANOSIM tests reflected the interpretation of patterns of variation in epifaunal assemblages based the nMDS plot and Bray-Curtis dissimilarity values. The difference between replicate NTZ sites was statistically significant in all four ANOSIM comparisons (one per year) (Table 25). The two Control sites were significantly different in two out of the four ANOSIM tests (in 2005 and 2007). Of the 16 possible ANOSIM contrasts between NTZ and Control sites (4 per year x 4 years), only two were non-significant, both in 2004.

SIMPER analysis of each of the different multivariate comparisons between pairs of sites revealed that only 6 of the 12 epifaunal variables had contributed ≥15% to one or more of the 22 statistically significant Bray-Curtis dissimilarity values (Table 26). Ranked in order of the number of significant spatial comparisons in which they contributed 15% or more, these variables were: *(i) Aiptasia mutablis* (11 comparisons); *(ii* and *iii) Alcyonium digitatum* and *Pentapora fascialis* (6 comparisons each); *(iv)* total axinellid sponges (5 comparisons); *(v) Cliona celata* (3 comparisons); and *(vi) Raspalia ramosa* (2 comparisons).

Some of these variables were more consistently associated with particular types of spatial comparison than others (Table 26). All 11 of significant Bray-Curtis dissimilarity values to which *Aiptasia mutablis* contributed ≥15% were for comparisons involving NTZ site-1 (with SIMPER percentages ranging from 22.1 to 36.4%). Similarly, Control site-1 featured in every one of the 6 comparisons in which *Alcyonium digitatum* contributed ≥15% to significant Bray-Curtis dissimilarity values (with SIMPER percentages ranging from 16.3 to 38.1%).

Contributions of ≥15% due to other epifaunal variables were less-consistently associated with contrasts involving specific sites and/or much less-frequent (Table 26). *Pentapora fascialis* contributed ≥15% to significant Bray-Curtis dissimilarities for 5 comparisons between NTZ and Control sites (Simper percentages ranging from 18.8% to 29.3%) and 1 comparison (in 2005) between replicate Control sites (contributing 18.8%). The 5 significant Bray-Curtis dissimilarities to which total axinellid sponges contributed ≥15% were all for NTZ *versus* Control comparisons (with SIMPER percentages ranging from 15.3 to 21.0%). All 3 of the significant Bray-Curtis dissimilarities for which *Cliona celata* contributed ≥15% were for NTZ

versus Control comparisons (with SIMPER percentages ranging from 16.1% to 21.7%). *Raspalia ramosa* contributed ≥15% to significant Bray-Curtis dissimilarities for only two comparisons, both of which were comparisons between replicate NTZ sites (contributing 19.8% in 2005 and 16.9% in 2007).

Table 26. Sessile epifauna: taxa that contributed ≥15% to Bray-Curtis dissimilarities in pairwise contrasts between NTZ and Control sites in each year of sampling (2004 to 2007). Data are 4th root transformed. ns - $P > 0.05$.

	Epifauna: SIMPER analysis of multivariate comparisons between sites in each year							
	2004		2005		2006		2007	
Site comparison	**Taxa**	**SIMPER %**	**Taxa**	**SIMPER %**	**Taxa**	**SIMPER %**	**Taxa**	**SIMPER %**
NTZ 1 vs NTZ 2	*Aiptasia mutablis*	36.1	*Aiptasia mutablis*	29.1	*Aiptasia mutablis*	29.3	*Aiptasia mutablis*	36.4
	Total axinellid sponges	16.9	*Raspalia ramosa*	19.8	-	-	*Raspalia ramosa*	16.9
	-	-	Total axinellid sponges	16.4	-	-	-	-
	ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$	
NTZ 1 vs Control 1	ANOSIM ns		*Aiptasia mutablis*	25.5	*Aiptasia mutablis*	22.1	*Aiptasia mutablis*	27.0
			Alcyonium digitatum	16.3	-	-	*Alcyonium digitatum*	25.5
			ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$	
NTZ 1 vs Control 2	*Aiptasia mutablis*	30.5	*Aiptasia mutablis*	24.6	*Aiptasia mutablis*	25.4	*Aiptasia mutablis*	33.6
	ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$	
NTZ 2 vs Control 1	ANOSIM ns		*Alcyonium digitatum*	27.3	*Pentapora fascialis*	19.3	*Alcyonium digitatum*	37.1
			Cliona celata	16.9	Total axinellid sponges	15.7	-	-
			Total axinellid sponges	15.3	-	-	-	-
			ANOSIM $P < 0.05$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$	

Table 26. Continued.

Epifauna: SIMPER analysis of multivariate comparisons between sites in each year								
	2004		2005		2006		2007	
Site comparison	**Taxa**	**SIMPER %**	**Taxa**	**SIMPER %**	**Taxa**	**SIMPER %**	**Taxa**	**SIMPER %**
NTZ 2 vs Control 2	*Pentapora fascialis*	23.9	*Pentapora fascialis*	24.6	*Pentapora fascialis*	22.3	*Pentapora fascialis*	29.3
	Cliona celata	21.7	-	-	-	-	*Cliona celata*	16.1
	Total axinellid sponges	21.0	-	-	-	-	-	-
	ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.01$		ANOSIM $P < 0.05$	
Control 1 vs Control 2	ANOSIM ns		*Pentapora fascialis*	18.8	ANOSIM ns		*Alcyonium digitatum*	38.1
			Alcyonium digitatum	18.5			-	-
			-	-			-	-
			ANOSIM $P < 0.05$				ANOSIM $P < 0.01$	

3.3.2 *The abundances of individuals species of epifauna (Hypothesis-8)*

ANOVA was only applied to the six variables that contributed ≥15% to Bray-Curtis dissimilarity values for significant ANOSIM-contrasts between years for each site (Table 24), and/or between sites in each year (Table 25): these were *(i) Aiptasia mutablis*; *(ii) Alcyonium digitatum*; *(iii) Pentapora fascialis*; *(iv)* total axinellid sponges; *(v) Cliona celata* and *(vi) Raspalia ramosa*. There was no significant interaction of LO x YE for any of these variables (Table 27). There was, however, at least one notable result that was unpredicted for each of these variables.

For *Cliona celata* there was a significant result for the factor LOCATION (Table 27-*v.*). This was due to *C. celata* being 600% more abundant on average in the Control location (1.4 ± 0.1 per m^2) compared to the NTZ (0.2 ± 0.0 per m^2) (Figure 22-*v.*).

The factor SITE(LO) was significant for each of the other five taxa (Table 27). For *Aiptasia mutablis*, total axinellid sponges and *Raspalia ramosa* this was attributable to greater mean abundance in NTZ site-1 compared to NTZ site-2 (Figure 22-*i., ii., iii., iv.* & *vi.*). *Aiptasia mutablis* was present in NTZ site-1 at a mean density of 11.4 ± 1.3 per m^2, but was entirely absent from NTZ site-2. Axinellid sponges were 174% more abundant on average in NTZ site-1 (8.5 ± 0.6 per m^2) compared to NTZ site-2 (3.1 ± 0.3 per m^2). *Raspalia ramosa* was 2,700% more abundant on average in NTZ site-1 (2.8 ± per 0.3 per m^2) compared to NTZ site-2 (0.1 ± 0.1 per m^2).

For *Alcyonium digitatum* and *Pentapora fascialis*, significant results for SITE(LO) attributable to differences between replicate Control sites (Figure 22). *A. digitatum* was 492% more abundant on average in Control site-1 (7.7 per m^2 ± 0.8) than in Control site-2 (1.3 per m^2 ± 0.3). In *P. fascialis*, the situation was reversed with greater mean abundance (by 116%) in Control site-2 (2.6 per m^2 ± 0.2) compared to Control site-1 (1.2 per m^2 ± 0.2).

The only instance of significant temporal change was for *Raspalia ramosa*, which gave a significant result for the factor YE x SITE(LO) (Table 27-*vi.*). SNK tests showed that this was due to significant changes in mean abundance in NTZ site-1

throughout the study. The mean abundance of *Raspalia ramosa* in NTZ site-1 declined 80% from 2005 to 2006 (4.6 ± 0.6 per m^2 to 0.9 ± 0.2 per m^2) and then increased 211% from 2006 to 2007 (to 2.9 ± 0.5 per m^2) (Figure 22-*vi.*).

For information, mean abundances for the other six species of sessile epifauna that were monitored for this study (*i.e. Eunicella verrucosa*, *Anemonia viridis*, *Alcyonium glomeratum*, *Polymastia boletiformis*, *Polymastia mammilaris* and *Stolonica socialis*) are presented in Table 28.

Table 27. Sessile epifauna: ANOVA of L*n*(*X*+0.001)-transformed abundances per m^2 for the 7 species of sessile epifauna that contributed ≥15% to Bray-Curtis dissimilarities in pairwise SIMPER contrasts between locations (NTZ *vs* Control) and/or years (2005 to 2007). ns - *P* > 0.05.

i. Aiptasia mutablis

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	1722.67	1	1722.667	1.00	ns	SITE(LO)
SITE(LO)	3445.33	2	1722.667	106.60	*P* < 0.001⌘	❶-POOLED MS
YEAR	14.47	2	7.237	0.45	ns	❶-POOLED MS
PLOTS(LO x SI x YE) ❶	1005.22	60	16.754	3.73	*P* < 0.001	RESIDUAL
LO x YE	14.47	2	7.237	0.45	ns	❶-POOLED MS
YE x SI (LO) ❶	28.95	4	7.237	0.45	ns	❶-POOLED MS
RESIDUAL	3558.21	792	4.493			
TOTAL	9789.32	863				
❶-POOLED MS	1034.16	64	16.159			

Cochran's Test C = 0.0892 (*P* < 0.01) Largest variance = 28.8378, this occurred in NTZ Site-1, Plot 6, 2005

⌘ SNK test for SITE(LO): NTZ 1 > NTZ 2 / Control 1 = Control 2

ii. Alcyonium digitatum

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	1707.73	1	1707.733	2.92	ns	SITE(LO)
SITE(LO)	1168.80	2	584.398	14.10	*P* < 0.001⌘	PLOT(LO x SI x YE)
YEAR	81.30	2	40.651	0.52	ns	YE x SI (LO)
PLOTS(LO x SI x YE)	2487.20	60	41.453	8.44	*P* < 0.001	RESIDUAL
LO x YE	96.57	2	48.286	0.62	ns	YE x SI (LO)
YE x SI (LO)	311.87	4	77.967	1.88	ns	PLOT(LO x SI x YE)
RESIDUAL	3888.64	792	4.910			
TOTAL	9742.11	863				

Cochran's Test C = 0.0736 (*P* < 0.01) Largest variance = 26.0184, this occurred in Con Site-1, Plot 4, 2007

⌘ SNK test for SITE(LO): NTZ 1 = NTZ 2 / Control 1 > Control 2

Table 27. Sessile epifauna: Continued.

iii. Total* axinellid *sponges

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	514.84	1	514.839	1.15	ns	SITE(LO)
SITE(LO)	893.99	2	446.996	7.44	$P < 0.01$ ⌘	❶-POOLED MS
YEAR	10.46	2	5.228	0.09	ns	❶-POOLED MS
PLOTS(LO x SI x YE) ❶	3639.30	60	60.655	4.60	$P < 0.001$	RESIDUAL
LO x YE	344.97	2	172.483	2.87	ns	❶-POOLED MS
YE x SI (LO) ❶	208.40	4	52.101	0.87	ns	❶-POOLED MS
RESIDUAL	10434.64	792	13.175			
TOTAL	16046.60	863				
❶-POOLED MS	3847.71	64	60.120			

Cochran's Test C = 0.0238 (Not Significant)

⌘ SNK test for YE x SITE(LO): NTZ site-1: 2005 > 2007 = 2006 / NTZ site-2: 2005 = 2006 = 2007 / Control site-1: 2005 = 2006 = 2007 / Control site-2: 2005 = 2006 = 2007

iv. Pentapora fascialis

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	1913.44	1	1913.441	4.08	ns	SITE(LO)
SITE(LO)	939.06	2	469.529	16.73	$P < 0.001$ ⌘	PLOT(LO x SI x YE)
YEAR	15.31	2	7.655	0.12	ns	YE x SI (LO)
PLOTS(LO x SI x YE)	1684.22	60	28.070	3.97	$P < 0.001$	RESIDUAL
LO x YE	13.76	2	6.880	0.11	ns	YE x SI (LO)
YE x SI (LO)	252.02	4	63.004	2.24	ns	PLOT(LO x SI x YE)
RESIDUAL	5596.26	792	7.066			
TOTAL	10414.06	863				

Cochran's Test C = 0.0450 (Not Significant)

⌘ SNK test for SITE(LO): NTZ 1 = NTZ 2 / Control 1 < Control 2

v. Cliona celata

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	963.75	1	963.752	27.97	$P < 0.001$ ⌘	❶-POOLED MS
SITE(LO) ❶	7.25	2	3.626	0.11	ns	❶-POOLED MS
YEAR	107.07	2	53.5339	1.55	ns	❶-POOLED MS
PLOTS(LO x SI x YE) ❶	2236.90	60	37.2816	4.67	$P < 0.001$	RESIDUAL
LO x YE	32.21	2	16.1027	0.47	ns	❶-POOLED MS
YE x SI (LO) ❶	29.98	4	7.496	0.22	ns	❶-POOLED MS
RESIDUAL	6318.23	792	7.978			
TOTAL	9695.38	863				
❶-POOLED MS	2274.13	66	34.457			

Cochran's Test C = 0.0364 (Not Significant)

⌘ SNK test for LOCATION: NTZ < Control

Table 27. Sessile epifauna: Continued.

vi. Raspalia ramosa

Source	SS	df	MS	*F*	*P*	Denominator in F-ratio
LOCATION	80.15	1	80.155	0.11	ns	SITE(LO)
SITE(LO)	1417.99	2	708.996	30.50	$P < 0.001^{\text{⌘}}$	PLOT(LO x SI x YE)
YEAR	258.13	2	129.0662	2.02	ns	YE x SI (LO)
PLOTS(LO x SI x YE)	1394.66	60	23.2444	2.79	$P < 0.001$	RESIDUAL
LO x YE	73.54	2	36.7712	0.57	ns	YE x SI (LO)
YE x SI (LO)	255.89	4	63.973	2.75	$P < 0.05$	PLOT(LO x SI x YE)
RESIDUAL	6590.36	792	8.321			
TOTAL	10070.74	863				

Cochran's Test C = 0.0354 (Not Significant)

⌘ SNK test for SITE(LO): NTZ 1 > NTZ 2; Control 1 = Control 2

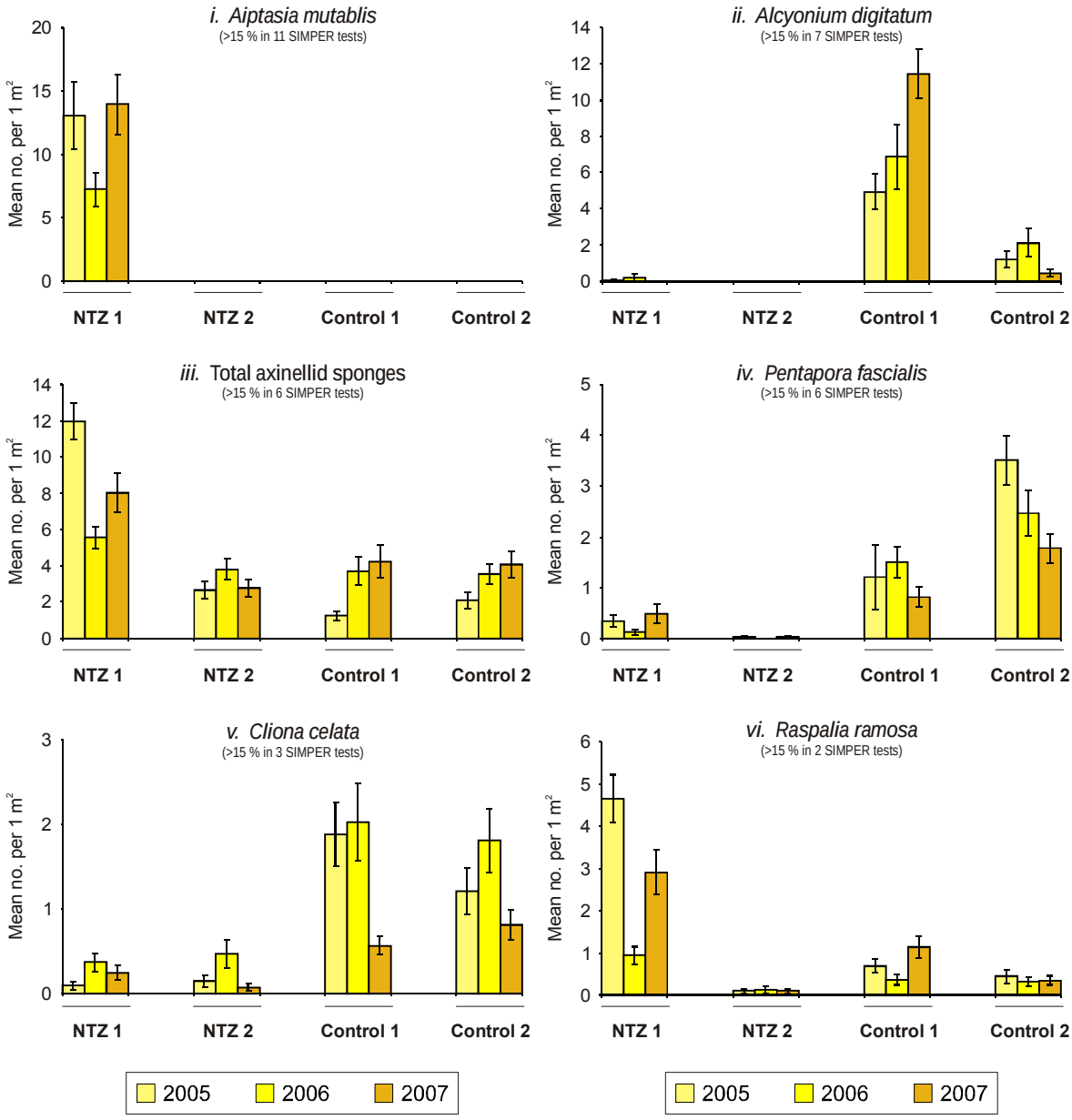

Figure 22. Sessile epifauna: Mean abundances per m^2 for the 6 epifaunal variables shown by SIMPER analysis to have contributed ≥15% to significant Bray-Curtis dissimilarities for pairwise contrasts between either sites (NTZ *vs* Control) or years (all combinations of 2004, 2005, 2006 and 2007). Each bar represents the mean of 6 plots (transects) per site.

Table 28. Sessile epifauna: Mean abundances per m^2 (±SE) of the six epifaunal species that exhibited no significant spatial differences or temporal changes in the course of NTZ monitoring from 2004 to 2007. Sample size (*n*) =144 in each case, except for the Control location in 2004 when *n* = 72 due to incomplete sampling owing to problems of weather and sea-state.

Mean abundances of species that showed no significant differences or changes									
		2004		2005		2006		2007	
Species	**location**	**Mean**	**±SE**	**Mean**	**±SE**	**Mean**	**±SE**	**Mean**	**±SE**
Eunicella verrucosa	NTZ	0.09	0.03	0.14	0.04	0.10	0.03	0.10	0.03
	CONTROL	0.00	0.00	0.05	0.03	0.02	0.02	0.05	0.02
Anemonia viridis	NTZ	0.01	0.01	0.02	0.02	0.09	0.04	0.00	0.00
	CONTROL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Alcyonium glomeratum	NTZ	0.02	0.02	0.00	0.00	0.07	0.06	0.01	0.01
	CONTROL	0.10	0.09	0.06	0.04	0.00	0.00	0.02	0.02
Polymastia boletiformis	NTZ	0.01	0.01	0.09	0.04	0.02	0.02	0.02	0.02
	CONTROL	0.07	0.06	0.17	0.08	0.21	0.13	0.02	0.02
Polymastia mammilaris	NTZ	0.06	0.04	0.48	0.12	0.02	0.02	0.27	0.10
	CONTROL	0.01	0.02	0.09	0.04	0.46	0.14	0.04	0.02
Stolonica socialis	NTZ	0.02	0.02	0.00	0.00	0.00	0.00	0.01	0.01
	CONTROL	0.00	0.00	0.06	0.04	0.21	0.08	0.25	0.13

4 DISCUSSION

4.1 General overview of monitoring results

In 2004, a programme of annual monitoring was established to test hypotheses about potential ecological effects of the Lundy NTZ, which was designated 18 months earlier in January 2003. Monitoring was targeted at three distinct components of Lundy's marine fauna:

i. populations of four species of commercially-fished crustacean; the lobster (*Homarus gammarus*), brown crab (*Cancer pagurus*), velvet crab (*Necora puber*) and spider crab (*Maja squinado*);

ii. populations of scallop (*Pecten maximus*) and

iii. an assemblage of sessile epifauna in circalittoral rocky habitats that are of interest for nature conservation, including, erect sponges, pink sea-fan (*Eunicella verrucosa*), dead men's fingers (*Alcyonium digitatum*) and ross coral (*Pentapora fascialis*).

Concern for this latter group of species was the main reason for the designation of the Lundy NTZ.

After four years of monitoring (to 2007), only lobster, brown crab and velvet crab had produced evidence of an effect of the NTZ. Monitoring yielded no evidence of a response to the NTZ in spider crabs, scallops or sessile epifauna (either as an assemblage or as individual species).

For lobster and brown crab, the apparent effects of the NTZ were positive, as hypothesised, and manifested as increased mean abundance and/or increased sizes of individuals within the NTZ relative to fished areas (Sections 3.1.1 & 3.1.2). Lobster provided the most compelling evidence for a positive effect of the NTZ, both in terms of the multiplicity of evidence and the magnitude of changes. Distinct forms of evidence for a positive effect of the NTZ were obtained for landable-sized lobsters (carapace length (CL) ≥90mm) and undersized lobsters (CL <90mm).

When monitoring began in 2004 (18 months post-designation) the mean abundance of landable-sized lobsters in the NTZ was already 205% greater than the average for control and reference locations. In the course of subsequent monitoring, the mean abundance in the NTZ increased by 127% whilst abundances in control and reference locations remained relatively constant. By 2007, landable-sized lobsters were 427% more abundant in the NTZ compared to control and reference locations. Landable-sized lobsters in the NTZ also showed a small (~5%), but statistically significant increase in average size relative to control and reference locations.

From 2004 to 2007, the mean abundance of undersized lobsters increased significantly in the NTZ (up 97%) and in adjacent control locations (up 124%), but showed no significant changes in the more-distant (20-90km) reference locations.

Abundances of velvet crabs exhibited a pattern of change that was almost the exact opposite of that seen in undersized lobsters; *i.e.* mean abundance declined significantly within the NTZ and adjacent control locations (by 65 to 75%), whilst remaining approximately static in reference locations (Section 3.1.1).

Whilst brown crabs did not increase in relative abundance within the NTZ, individuals within the NTZ did exhibit a significant 25% increase in size (carapace width) compared to individuals in control and reference locations (Section 3.1.2).

Spider crabs and scallops showed no significant differences in either abundance or size between the NTZ and fished control locations at any stage in the study (for results for spider crabs see Sections 3.1.1 & 3.1.2; for scallops see sections 3.2.1-3.2.3).

The assemblage of sessile epifauna showed a consistent significant difference in composition between the NTZ and the control location (Section 3.3.1), but this was expected *a priori* because the former is on the sheltered east coast of Lundy whilst the latter is on the more exposed west coast. This arrangement of sampling locations for sessile epifauna was an unavoidable necessity. With respect to potential effects of the NTZ, the critical finding for sessile epifauna was that the difference in assemblage composition between the NTZ (east coast) and the control location (west coast) showed no significant change during four years of

monitoring. Nor were there any significant changes in the relative abundance of individual epifaunal taxa in these locations (Section 3.3.2).

The remainder of this section interprets monitoring results in light of the biology and ecology of the study organisms, relevant local information and published findings from similar studies elsewhere. After drawing our conclusions, we make a series of recommendations for future research on the Lundy NTZ.

4.2 Abundance and size of landable-sized lobsters

Our findings for the lobster *Homarus gammarus* are consistent with findings from studies of the effects of NTZs on various species of clawed (astacid) and spiny (palinurid) lobsters elsewhere in the world (MacDiarmid & Breen 1993, Childress 1997, Edgar & Barret 1999, Rowe 2002, Goni *et al.* 2006). These studies demonstrate that lobsters can quickly increase in abundance and size following the establishment of a NTZ, even when it is only small or moderate in size (1-5km^2).

If the increase in the abundance of landable-sized lobsters within the Lundy NTZ is a response to the cessation of fishing, then this is mostly likely to have been caused by adult lobsters migrating into the NTZ and then progressively accumulating in vacant territories whose previous occupants had been removed by fishing. Given the apparent rapidity of response (evident only 18 months post-designation) and what is known of the growth-rate of *H. gammarus*, it is unlikely that recruitment of newly-settled juveniles made any substantial contribution to the proliferation of landable-sized lobsters in the NTZ. Nevertheless, information on the relationship between age and size in *H. gammarus* (Bannister & Howard 1991, Bannister *et al.* 1994, Sheehy *et al.* 1999) suggests that some individuals that recruited to the NTZ in its first year (2003) could have joined the local population of landable-sized lobsters towards the end of the study.

The proposal that the landable-sized lobsters increased in the NTZ mainly via the accumulation of adult immigrants presupposes *(i)* that population-size in fished areas is generally less than the local carrying capacity and *(ii)* that adult lobsters occasionally relocate from territory to territory (through choice or compulsion), but

are inclined to establish long-term occupancy in a favourable territory. This interpretation of the behaviour of *H. gammarus* is supported by the fact that the progressive increase in the abundance of landable-sized lobsters in the NTZ was accompanied by a progressive increase in their average size relative to fished locations. This would be difficult to explain if there was significant turnover of landable-sized lobsters within the NTZ.

Direct evidence of both high mobility and strict territoriality in adult *H. gammarus* is provided by a tag-recapture study of individuals caught in the vicinity of a small voluntary NTZ at St Agnes in Cornwall (Hoskin 2006). Out of 180 lobsters given individually-numbered 'streamer tags' during this study, ten were recaptured. Five were recaptured almost exactly where they were first captured, three after ~1 month at liberty, one after 9 months and one after 12 months. The other five lobsters moved distances ranging from 0.5km to 32km during their time at liberty. The individual that moved 32km did so in eleven months. The greatest rate of movement was exhibited by two individuals that moved more than 10km in two weeks.

The view that lobsters switch opportunistically between mobile and territorial modes is also shared by Pawson (1995). In a review of the structure and dynamics of lobster stocks in the English Channel he asserted that *"lobster do not undertake regular migrations, but simply make small random movements which could be prompted by local competition for food or by the need to change habitats as their size increases".*

It was remarked previously that evidence of an effect of the Lundy NTZ was seen only 18 months after its designation. At this time (May/June 2004), the mean abundance of landable-sized lobsters in the NTZ was 205% greater than in fished areas. It was recognised at the time that this initial difference might reflect naturally high abundance in this area rather than an effect of the NTZ. Whilst this could not be formally disproved because of the absence of 'before' data, it was considered highly unlikely because none of the local fishermen had claimed that lobsters were especially prolific in this area when they were consulted on the NTZ proposal (Chris Davis, Natural England, pers. comm.). If lobsters had been

especially prolific in this area, it seems likely that fishermen would have made this known when it was proposed for closure.

Lobsters increased in size and abundance within the Lundy NTZ despite it being subject to some illegal potting. In 2005, we observed a string of lobster pots that had been deployed in the far northern section of the NTZ. In 2006, a further string of pots were seized from the NTZ by Devon Sea Fisheries. In 2008, we observed a fishing boat hauling a string of pots in the NTZ, again in the far northern section. These instances of illegal fishing were all during the summer when the waters around Lundy are busy with private leisure craft and charter angling and diving boats. This is also when the Lundy Wardens patrol the NTZ and conduct wildlife surveys around the island by boat. We suspect that there is more illegal fishing in the NTZ in the spring and autumn when fishermen are typically less observed by others. The section of the NTZ north of Gull Rock (approximately half-way up Lundy's east coast) is especially vulnerable to illegal lobster potting as it cannot be seen from the south-east corner of Lundy, which is where the island's permanent inhabitants live and where most of their activities are concentrated (around the jetty and the road linking it to the village).

Scientifically, the problem with illegal fishing in the Lundy NTZ is that it may confound efforts to evaluate its effectiveness for achieving conservation goals. If carried out with sufficient frequency it would make the area appear less effective than would otherwise be the case if it were a complete no-take zone.

4.3 Potential spillover of undersized lobsters

The significant increase in the relative abundance of undersized lobsters inside and adjacent to the NTZ is consistent with some form of spillover effect. It is not immediately obvious, however, how this could have occurred. The conventional mechanism of spillover is that reproductive biomass increases within a no-take reserve (due to increased abundance and/or size of individuals), which results in greater net export of offspring from the reserve compared to similar fished areas (Dugan & Davis 1993, Roberts & Polunin 1993, Guénette *et al.* 1998). Whilst it is easy to envisage increased reproductive output from the NTZ (see Tully *et al.* 2001 for an analysis of the positive relationship between size and fecundity in *H.*

gammarus), explaining how this could have led to increased abundance of small lobsters in adjacent areas is not straightforward given that *H. gammarus* has a planktonic larval stage.

The duration of the planktonic larval phase in *H. gammarus* is given as 18-35 days by Richards & Wickins (1979) and three weeks by Pawson (1995). For the Lundy lobster population to have gained from enhanced fecundity in the NTZ, larvae spawned in the NTZ would have had to have remained in the area throughout their planktonic phase. It seems unlikely that lobster larvae could have restricted their dispersal to this extent, particularly around Lundy where there are very strong tidal currents (up to 2.5ms^{-1}) (DTI 2004).

The late larval stages of Homarid lobsters are strong forward swimmers (Cobb 1997, Katz *et al.* 1994), but information for *H. gammarus* suggests that they do not use this ability in any systematic way to influence passive dispersal. Planktonic larvae that behave in this way are usually trying to avoid or minimise dispersal in adverse directions or facilitate dispersal in favourable directions. They accomplish this by swimming up or down in the water column in response to vertical differences in the strength and/or direction of currents. This allows them to avoid or exploit flows in certain directions and thus influence their direction and distance of dispersal (Burton & Feldman 1982). Whilst larval *H. gammarus* do make daily vertical migrations, these follow the day-night cycle rather than the ebb and flow of tides and as such are probably trophic in nature, rather than dispersal-related (Nichols & Lovewell 1987, Tully & Ceidigh 1987).

The most powerful evidence against highly-restricted dispersal in larval *H. gammarus* comes from large-scale studies of its genetic population structure using selectively-neutral genetic markers (Jørstad *et al.* 2004, 2005, Triantafyllidis *et al.* 2005). These studies show relatively little fine-scale (<100km) genetic differentiation amongst local populations of *H. gammarus* throughout most of the north-east Atlantic. There are some distinct subgroups of *H. gammarus* at the regional scale, such as in northern Norway and the Netherlands, but within the major Atlantic group it seems that there is no correlation between geographic and genetic distance. According to population genetic theory (Wright 1943, Kimura &

Weiss 1964, Slatkin 1985 & 1987), this genetic evidence would tend to indicate moderate to high levels of gene low (genetically-effective migration) amongst local populations.

Genetic evidence that larval dispersal in *H. gammarus* is not highly restricted supports the view that elevated abundance of undersized lobsters in and adjacent to the Lundy NTZ was not the product of enhanced fecundity within the NTZ. Nevertheless, other aspects of lobster ecology and certain monitoring results present the possibility that one or more less-conventional mechanisms of spillover may have operated. Here we consider two such mechanisms. The first relies on enhancement of the NTZ's attractiveness as a place for lobster post-larvae to settle; the second relies on reduction in predation and/or interspecific competition pressures that impact upon juvenile lobsters.

The possibility that the NTZ might have become a more attractive place for lobster post-larvae to settle arises from a laboratory study by Boudreau *et al.* (1993) that showed that they are attracted to adult odours. In a series of choice-chamber experiments with the American lobster *H. americanus*, Boudreau *et al.* (1993) found that post-larvae exhibited a significant tendency (≥73%) to swim upstream towards a flow of seawater containing adult metabolites in preference to an alternate flow of untreated seawater. This and similar findings with the odours of algae from the habitat of adult lobsters led Boudreau *et al.* (1993) to concluded that *"distance chemoreception may play a role in habitat selection by lobster post-larvae at settlement".* Childress & Jury (2006) went further in interpreting the results of Boudreau *et al.* (1993), proposing that they *"suggest an initial guide-effect benefit for clawed lobsters since conspecific attraction could reduce the search time for a suitable benthic substrate at the time of settlement".* Conspecific attraction may explain how the enhanced population of adult lobsters in the NTZ could have boosted local recruitment. This type of reserve effect was hypothesised by Dugan & Davis (1993) in light of evidence for gregarious settlement of abalone larvae with conspecific adults (Shepherd 1990) and polychaetes (Jensen & Morse 1984).

If the enhanced population of adult lobsters in the NTZ had increased local recruitment by attracting more settlers, it would still be necessary to explain how this could have given rise to increased abundance of undersized lobsters in adjacent areas. This could be readily explained by intraspecific competition among juveniles. Juvenile homarid lobsters are solitary and aggressive towards each other (potentially cannibalistic), hence they require increasing amounts of space as they grow (Wahle & Fogarty 2006). In laboratory growth-trials with *H. americanus,* Aiken & Waddy (1978) observed that growth of communally-reared juveniles was adversely affected if the area available to each individual was less than 18-times the square of carapace length. In wild populations, an effective way for juvenile lobsters to avoid intra-specific competition would be to move to areas of progressively lower density as they grow. Other possible explanations for the increase in undersized lobsters in areas adjacent to the NTZ are that these areas also had elevated concentrations of attractive adult odours due to proximity to the NTZ, and/or that some post-larvae were stimulated to settle within the NTZ, but drifted out of the NTZ before reaching the seabed.

The suggestion that juvenile *H. gammarus* might preferentially settle in areas of high adult density is contrary to the commonly held view that juvenile homarid lobsters suffer significant predation by adults. Significantly, however, this view is mainly based on studies of lobsters in laboratory and field enclosures, often without the provision of shelters for individuals to hide in (Wahle & Fogarty 2006). There is no compelling evidence from natural homarid populations that predation by adults has a significant impact on the abundance of conspecific juveniles. The opposite view, that adult lobsters are not important predators of juveniles in wild populations, is supported here by the fact that juveniles increased in abundance in the Lundy NTZ despite simultaneous increases in the abundance and size of adults in the same area. Whilst there is clearly potential for agonistic interactions within homarid populations, these findings tend to indicate that juvenile *H. gammarus* are effective at avoiding encounters with adults (*e.g.* by using different microhabitats), and/or that adults typically do not seek juveniles to predate or intimidate.

Our second suggestion for the increase in undersized lobsters within and adjacent to the Lundy NTZ involves the possibility that large lobsters relieve new recruits and juveniles from predation and/or competition from other species. The recognition of this possibility arose from the fact that, simultaneous to the general enhancement of lobsters within and adjacent to the NTZ, there was a significant decline in the abundance of velvet crabs in the same areas. This and other information about potential interactions between these species (reviewed below) led us to speculate that the increase in large lobsters caused the decline in velvet crabs (via predation and/or competition), which in turn reduced the impact of velvet crabs on small lobsters.

Published information on interactions between homarid lobsters and portunid crabs (including *Necora puber*) and their respective diets provides some support for this model. Both taxa include other smaller, hard-shelled crustaceans in their diet (Choy 1986, Cobb & Wahle 1994, Cobb & Castro 2006, Childress & Jury 2006, Freire *et al.* 1996) and, if there is no great disparity in body-size, they are also likely to compete for food (Williams *et al.* 2006). That *H. gammarus* may eat *N. puber* is also demonstrated by the fact that fishermen in the north-east of England use freshly-killed velvet crabs as pot-bait for lobsters (Giles Bartlett, ex-officer of North Eastern Sea Fisheries, pers. comm.).

If the proposed model of interactions between *H. gammarus* and *Necora puber* is accurate, an explanation is still required for how an increase in landable-sized lobsters in the NTZ could have caused a decline in velvet crabs in adjacent areas (to a distance of ~5km, which is the greatest distance from the NTZ boundary to the furthest control site on Lundy's west coast). One possibility is that the decline in velvet crabs began in the NTZ with the increase in large lobsters and then spread to surrounding areas as new recruits 'spilled over' and grew to a size at which they could also outcompete and predate velvet crabs. Another possibility is that adult lobsters residing in the NTZ impacted velvet crabs in surrounding areas during occasional excursions to these areas. Various tagging studies of *H. gammarus* (*e.g.* Bannister *et al.* 1994, Jensen *et al.* 1994, Smith *et al.* 1998, Hoskin 2006) have shown that adult lobsters are quite capable of moving the required distance (up to 5km), but it is unclear whether they are capable of homing

from such a distance. The only study of homing in *H. gammarus* that we know of used acoustic telemetry to track three individuals that were translocated different distances from their locations of capture (van der Meeren 1997). One individual was translocated 1km and homed successfully within a few hours; the other two were translocated 5km and did not home during 2-3 weeks of tracking. Unfortunately, these results are inconclusive for present purposes, partly because of small sample size, but mainly because translocation may have caused disorientation.

Finally, it must be reiterated that whilst increased abundance of undersized lobsters within and adjacent to the NTZ is consistent with a form of spillover, it does not prove that spillover has occurred. A critical requisite of the spillover model is that populations in reserves exhibit greater net export of migrants than populations in fished areas. Until this has been tested and verified for undersized lobsters at Lundy, it cannot be concluded that spillover has occurred. Goñi *et al.* (2006) emphasised the importance of this test and cautioned that researchers evaluating MPAs should not claim to have detected spillover without having first done this test. Their review of the small number of studies that have measured immigration and emigration for reserve *versus* non-reserve populations (*e.g.* Davis & Dodrill 1989, Rowe 2001, Zeller *et al.* 2003, Kelly & MacDiarmid 2003, Tremain *et al.* 2004, Goñi *et al.* 2006) show that spillover is often not proved. Until it is certain that the net export of undersized lobsters from the Lundy NTZ is significantly greater than that from adjacent fished areas, spillover cannot be concluded and it would be premature to investigate potential mechanisms linking the general increase in undersized lobsters around Lundy to effects of the NTZ. At this stage, it remains a possibility that what looks like enhancement and spillover of undersized lobsters from the NTZ may simply have been a highly localised natural increase that just happened to coincide with the establishment of the NTZ.

4.4 Interpretation of results for velvet crab

In the preceding section, we proposed that the decline in velvet crab numbers in the NTZ and adjacent control locations might have been caused by increased predation and competition from lobsters. An alternative or contributory explanation

that must be acknowledged is that the decline in velvet crabs was an artefact of sampling them with baited pots that also caught lobsters. Thus, in locations where pots were catching increasing numbers of lobsters, fear of predation may have made velvet crabs increasingly unwilling to enter pots and/or keen to escape if already inside. Being relatively small and able to swim, it is much easier for velvet crabs to escape from pots than lobsters, brown crab or spider crab. Either response by velvet crabs would result in fewer being sampled and a false appearance of declining abundance.

Whilst this alternate explanation seems plausible, it is somewhat at odds with our observation that individual pots frequently contained several large lobsters and several velvet crabs, with all alive and intact when the pot was retrieved. Evidence of lobsters killing velvet crabs inside of pots was rare. Predation or fighting amongst trapped crustaceans typically only occurs when pots are lost (*i.e.* 'ghost-fishing') or left to soak for a week or longer. For shorter soak-times (24-48 hours), trapped crustaceans generally seem to co-exist without predating or fighting each other (M. Hoskin, personal observation). Hence, we suggest that the decline in velvet crabs in areas with enhanced numbers of lobsters was a real ecological change and not an artefact of the sampling method. We would recommend, however, that the relationship between catch-rates of lobsters and velvet crabs in baited pots should be investigated experimentally.

4.5 Interpretation of results for brown crab

Brown crab (*Cancer pagurus*), like lobster, showed a significant increase in average size within the NTZ compared to control and reference locations. This suggests that they were able to live longer and grow larger in the NTZ than in fished areas. If that were the case, however, brown crab might also have been expected to have shown enhanced abundance in the NTZ, but they did not (unlike lobster). Brown crabs were in fact less abundant on average within the NTZ than in any of the fished areas that were sampled for comparison. A possible explanation is that increasing body-size within the NTZ may have suppressed positive effects on abundance by increasing the average size of territory required per individual. Alternately (or additionally), brown crab might have failed to

increase in abundance within the NTZ due to competition and/or predation from large lobsters, as was implicated in the decline of velvet crab. If that were the case, the fact that brown crab did not also decline in abundance in the NTZ may have been because they are typically much larger than velvet crab (up to 250mm CL *versus* 65mm CL in *Necora puber*; Hayward & Ryland 2000). Hence, brown crabs may have had a refuge in body-size from agonistic interactions with lobsters that was unattainable by velvet crabs.

On a final note of caution, it is important to recognise that the conclusion of a significant increase in the size of brown crab within the NTZ derived from an ANOVA test with a sample size (*n*) of only five individuals. This small sample size was attributable to the low abundance of brown crabs within the NTZ (on average, only one individual per 40 pots) and the requirement of ANOVA for equal replication for all factor levels. Given the small sample size for this test, it is quite likely that what appears to be evidence of an effect of the NTZ on the size of brown crab was actually a statistical artefact attributable to sampling error.

4.6 Interpretation of results for spider crab

Spider crabs did not exhibit any changes in abundance or size that indicated an effect of the Lundy NTZ. This is almost certainly because of the small size of the Lundy NTZ (~4km^2) and the fact that spider crabs are highly migratory throughout their lives, moving between inshore and offshore areas on a seasonal basis (Pawson 1995). The scale of migration is such that individual spider crabs are unlikely to have spent sufficient time in the Lundy NTZ to have gained any lasting benefit that was detectable at the population-level. It is the commonly-held view that fished species only benefit from NTZs when reserve size is large relative to the scale of migration (*e.g.* Hilborn 2003, Roberts *et al.* 2003b).

4.7 Considerations for future research on lobster and crabs

The abundance and size of lobsters in the Lundy NTZ increased progressively throughout the monitoring programme, so further monitoring could well show a continuation of these trends. For spiny lobster (*Jasus edwarsii*) in New Zealand marine reserves there is evidence that abundance and size may continue

increasing for up to 21 years (Kelly 1999, Kelly *et al.* 2000). Given the commercial importance of lobster and the fact that Lundy currently provides the best opportunity to observe the effects of a NTZ on this species, the continuation of this monitoring programme should be a priority for fisheries research. From the perspective of Natural England's main interest in the Lundy NTZ, *i.e.* the conservation of sessile reef epifauna, further lobster research might not be an obvious funding priority. It could be argued, however, that further evidence of benefits for lobsters from the Lundy NTZ might strengthen the case for NTZs in other sites where lobsters co-occur with species of interest for nature conservation.

Continued monitoring of lobsters would provide an opportunity to assess the maximal population density and body-size attainable by *H. gammarus* within a NTZ and the opportunity to assess the long-term stability of population enhancement within the NTZ. Continued monitoring would also permit further investigation of potential spillover of undersized lobsters from the NTZ into adjacent areas.

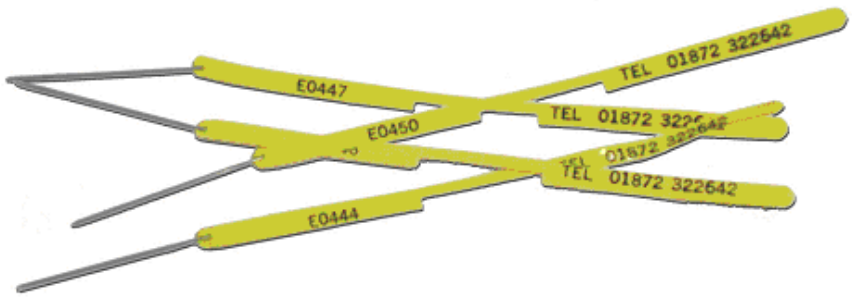

Figure 23. Streamer-tags. Each tag is individually numbered and gives a telephone number for fishermen to report recaptures.

As discussed previously, demonstrating a spillover benefit from a NTZ requires proof of enhanced production within the NTZ and evidence that the NTZ is a greater net exporter of migrants than comparable fished areas. For undersized lobsters, enhanced production within the NTZ is evidenced by increased abundance. Hence, proof of spillover only requires proof of enhanced emigration from the NTZ. If monitoring were continued, migration into and out of the NTZ,

control and reference locations could be measured at little additional cost via an ancillary programme of 'streamer tagging'.

A streamer tag (Figure 23) is attached to a lobster by inserting it into the dorsal muscle tissue between the carapace and the first abdominal segment. The advantage of fixing the tag intramuscularly is that it is retained during ecdysis, which allows information on the long-term growth and migration of individuals to be obtained. Streamer-tagging does not guarantee permanent tagging, however, and it has been estimated that tag loss in *H. americanus* may be as high as 40% for moulted individuals and 11% for non-moulted individuals (Rowe & Haedrich 2001). Nevertheless, streamer-tagging studies of *H. gammarus* have achieved recapture rates as high as 48%, with periods at liberty of 1-2 years being relatively common for tagged individuals (Jensen *at al*. 1994, Hoskin 2006).

If undersized lobsters from the NTZ, control and reference locations were streamer-tagged, recaptures of tagged individuals would generate data on rates of migration to and from these locations (providing only that the location of each recapture was recorded). For reliable assessment of migration to and from each location, the method, level and timing of sampling to recapture tagged lobsters would need to be the same in all locations. Confounding methodological influences and random natural variations would otherwise combine to produce inaccurate estimates of migration and an unreliable test of spillover. It would be optimal, therefore, if the tagging and recapturing of lobsters for the assessment of spillover was done via continuation of the present monitoring scheme.

The alternative would be to sample lobsters for tagging and recapture via commercial fishing, but this would present a number of difficulties in addition to issues to do with unbalanced, non-standardised sampling. The first difficulty is that fishermen could not sample lobsters from the NTZ for tagging or recapture without special dispensation. Any scientific fishing within the NTZ by commercial fishermen would need to be properly supervised to prevent abuse, either by the fishermen involved or by others who might exploit the opportunity to fish illegally in the NTZ. Nevertheless, if tagging and recapture of lobsters was done principally via fisheries-independent sampling (as advised), it would still be sensible to

encourage commercial fishermen to report any tagged lobsters that they might catch. Whilst information obtained in this way would be less useful overall for assessing spillover, it would still add to knowledge on the growth, longevity and movements of lobsters. As such, any streamer-tagging programme should be advertised and there should be a reward available to fishermen for each complete recapture report that they provide (*i.e.* tag number plus the precise location and date of recapture).

If spillover was proved via streamer tagging and this eventually resulted in an increase in the population of landable-sized lobsters outside the NTZ, this would constitute the first UK demonstration of a NTZ directly benefiting a commercial fishery.

Proof that the Lundy NTZ is benefiting lobster populations in surrounding areas would conceivably argue for the development of a network of such reserves to support the sustainability of lobster fisheries. From 1980 to 1999, total annual lobster landings for England and Wales climbed steadily from ~300 to ~900 tonnes (Bannister 1999). This increase prompted Bannister (1999) to express the concern that lobster fishing was becoming unsustainable and that stocks might be close to the point of collapse. Collapses in stocks of *H. gammarus* that were apparently due to over-fishing have occurred in a number of Scandinavian and Mediterranean countries (Cobb & Castro 2006). Since 1999, total lobster landings for England and Wales have continued increasing, exceeding 1,500 tonnes in 2006 (Marine & Fisheries Agency 2007).

In south-west England, recent concern about the sustainability of local lobster stocks has led to a scheme for artificial stock enhancement involving the release of hatchery-reared juvenile lobsters (The National Lobster Hatchery at Padstow, Cornwall: www.nationallobsterhatchery.co.uk/). The cost-effectiveness of such schemes has long been doubted and there are potential concerns about the quality of hatchery-reared juveniles, both in terms of individual fitness and potential for genetic impacts on natural populations (Blankenship & Leber 1997, Bannister & Addison 1998, Cobb & Castro 2006). Currently there is no reliable evidence that the release of hatchery-reared lobsters from the National Lobster Hatchery has

benefited either lobster stocks or lobster fishing in south-west England. Evidence that even small NTZs provide natural stock enhancement for lobster further undermines the justification for such complex, costly and risky schemes. We recommend that the Lundy NTZ should be used as the basis for an economic and biological cost-benefit analysis of artificial (hatchery-based) stock enhancement *versus* natural (NTZ-based) stock enhancement. It is our belief that this analysis would conclude substantially in favour of the NTZ approach.

As well as providing the opportunity for further investigation of the apparent effects of the Lundy NTZ on lobsters, continuation of the potting survey would also allow for further investigations of brown crab, velvet crab, spider crab at no extra cost. Of particular interest are potential future changes in the size of brown crabs within the NTZ and potential interactions between lobsters and velvet crabs, both in natural habitats and in pots during sampling.

As reported earlier, lobsters and velvet crabs exhibited opposite trends in abundance in the NTZ and adjacent control locations, with the former increasing and the latter decreasing. The increase in lobsters is presumed to be real, but it uncertain whether the decline in velvet crab is real (potentially due to increased predation and competition from lobsters), or an artefact of their being sampled in baited pots that also catch lobsters (*i.e.* because increased catch-rate of lobsters reduces the 'catchability' of velvet crabs). An effective test to discriminate between these alternate explanations for the decline in velvet crab would be to compare catch-rates in conventional pots *versus* pots that were modified to exclude all but the smallest lobsters. This could be simply achieved by fixing a narrow-necked restrictor device of ~8cm aperture into the funnel of a standard parlour pot.

Continued monitoring of spider crab is unlikely to reveal direct effects on the NTZ, but it entails no extra expense and requires little extra effort, so there is no compelling reason why it should stop as long as monitoring of lobster, brown crab and velvet crab continues. Continuation of the *status quo* for spider crab will, if nothing else, further substantiate the common view that wide-ranging species do not benefit from small NTZs.

It would be helpful for interpreting the results of any future monitoring of lobster and crabs if there was information available on the seasonal patterns and levels of commercial potting effort in the different control and reference locations, or at the very least in the control locations within the Lundy MNR. The most efficient and potentially the most reliable way of obtaining this information would be from the fishermen concerned. The risk with this approach is that fishermen might perceive various reasons for overstating or understating their levels of fishing effort. Employing others to survey numbers of boats and dahn buoys would be more expensive and almost certainly less reliable as potting effort depends on the number of pots per string and the frequency with which each string is fished and re-deployed, neither of which can be readily observed by outsiders.

If it were possible to establish a constructive relationship with the relevant fishermen, it would also be worth exploring the possibility of obtaining information on their landings from different locations around Lundy and their estimates of the numbers of undersized lobsters in their catches. It would also be valuable to census the opinions of local fishermen on the wider ecological effects of the Lundy NTZ. As well as being useful for the interpretation of monitoring data, such information would also constitute an independent assessment of scientific conclusions about the Lundy NTZ. It might also highlight interesting new subjects for investigation in relation to the NTZ that had not been envisaged previously. More-contentiously, we also recommend that there should be increased surveillance for illegal fishing in the Lundy NTZ, particularly in the autumn, spring and winter (when there are fewer non-fishermen on the water) and especially in the less-visible northern section of the NTZ. As well as being important for assessing compliance with the NTZ, the information gained would be helpful for interpreting the results of future monitoring. As stated previously, illegal fishing in the NTZ may confound scientific efforts to assess the effectiveness of the NTZ for achieving conservation goals.

4.8 Interpretation of results for scallops

Scallop populations exhibited no changes in abundance, mean size or overall size-frequency distribution that indicated potential effects of the Lundy NTZ. What

significant variations there were for these attributes were mainly confined to the control location. Scallops in the control location were initially significantly smaller and less abundant than those in the NTZ, but by 2007, both size and abundance had increased in the control location and differences relative to the NTZ were non-significant. The size-frequency distributions of scallops in the NTZ and control location varied from year to year, but there were no consistent trends. In 2004 and 2006, the scallop population in the NTZ had a significantly different size-distribution to that in the control location, but in 2005 and 2007 there were no significant differences. Differences in size-frequency distribution in 2004 and 2006 were mainly attributable to there being more small scallops (≤10cm shell width) in the control location. During the study there were either no or very few small scallops in the NTZ.

The low abundance of small scallops in the NTZ compared to the control location may be attributable to the fact that the scallop beds in the NTZ were much closer to reef habitat than those in the control location (<200m *versus* ~2km). The potential significance of this is that there are several common animals capable of predating scallops that are primarily associated with reef habitats, these include lobster, brown crab, velvet crab and ballan wrasse (*Labrus bergylta*) (Elner & Jamieson 1979, Jamieson *et al.* 1982, Lake *et al.* 1987, Strohmeier *et al.* 2005). In each case, the capacity to predate scallops is greatest for 'small' scallops, which means <70-90mm shell width for lobster and brown crab; <50mm shell width for velvet crab and <30mm shell width for ballan wrasse.

If the low abundance of small scallops in the NTZ is due to their greater accessibility to reef-dwelling predators, then this influence is likely to have increased following the establishment of the NTZ. Clearly the enhancement of lobster size and abundance in the NTZ is potentially significant in this context, as is evidence that the NTZ may have caused an increase in the size of brown crabs. There is no information available on potential effects of the Lundy NTZ on ballan wrasse, but it is conceivable that they may have also benefited. As well as being relatively territorial (Sjölander *et al.* 1972, Darwall *et al.* 1992) ballan wrasse are likely to have experienced an appreciable reduction in mortality in the NTZ due to the cessation of angling and lobster fishing, which commonly entails a substantial

by-catch of ballan wrasse. By-catch of ballan wrasse in lobster pots often results in mortality, either via injuries incurred within the pot or by being retained by fishermen for use as pot bait (M. Hoskin, personal observation).

As well as indicating that protection from fishing has not benefited scallops within the NTZ, monitoring results also show that diver-harvesting has caused no perceptible decline in scallops in the control location. Unfortunately the level of diver-harvesting in this area is unknown, so it is not possible to interpret this result more-objectively. Diver-harvesting of scallops within the control location is ostensibly wholly recreational. There is a popular wreck-diving site (the MV *Robert*) in the centre of the control location and it is a common practice for divers to swim away from this wreck towards the end of their dive to gather scallops in the surrounding area. A smaller number of recreational divers also do longer 'drift dives' in the area for the sole purpose of scallop gathering. Whilst there is no legitimate commercial scallop diving around Lundy, it is believed that some recreational divers may sell scallops illegitimately to local pubs and restaurants (Chris Davis, Natural England and Keith Hiscock, Marine Biological Association of the UK; pers. comms.).

On the subject of illegal fishing: on two occasions in 2005, commercial fishing boats towing either scallop dredges or trawl-nets were seen from the shore to be fishing either within the MNR or extremely close to its eastern boundary. During subsequent scallop surveys in the control location adjacent to the boundary, evidence of the passage of some form of towed bottom-gear was apparent in the form of unnatural linear features on the seabed and a marked absence of epifauna (*e.g.* sabellid tube worms) and the burrows of large infauna. In the assessment of the NTZ on scallops, undetected scallop dredging in the control location would tend to exaggerate the impact of recreational scallop-harvesting by divers, which is presumed to be the only form of scallop fishing in this area (Natural England 2008). Bottom-trawling also catches scallops, but less effectively than dredging, so it is less of a concern in this context.

4.9 Considerations for future research on scallops

Whilst scallops do not appear to have benefited from the Lundy NTZ thus far, it is possible that they may still benefit from it in the future. In a similar investigation of an area closed area to scallop fishing off Port Erin on the Isle of Man (Beukers-Stewart *et al.* 2005), it took ~10 years before scallops showed any significant benefit of the closure. In 2003, 14 years post-designation and four years after the first sign of a response, the abundance of landable-sized scallops (≥110mm shell width) in the closed area was more than seven times greater than that in a nearby control area that was still fished (mainly via dredging). The explanation for the lag between the cessation of fishing (in 1989) and the occurrence of a significant response is that prior to increased recruitment during the mid to late-1990's there was no opportunity for differentiation between closed and open areas. After this recruitment 'pulse', scallop fishing in the open areas revealed the benefit of closed area protection. At present, the situation with scallops in the closed and open areas at Lundy (*i.e.* low density and very few recruits) resembles that in the Isle of Man closed area prior to the mid-1990s.

If the abundance of scallops in the Lundy NTZ increased 700%, as occurred in the Isle of Man closed area, the Lundy monitoring programme for scallops should have more than adequate statistical power to detect an effect of this size. That said, however, it would now seem that the actual power of the present monitoring programme is somewhat less than was predicted in the 2004 pilot study (Hoskin *et al.* 2004). Power analyses using pilot data indicated that with the significance level (α) set at 0.05, the present monitoring scheme for scallops should have 80% probability of distinguishing at least a 50% increase in scallop abundance due to the NTZ. The conclusion that actual power is less than was planned is based on our finding greater small-scale spatial variation in scallop abundances (variation among replicate plots within sites) during actual monitoring than we found in the pilot study. For a given level of sampling replication, increasing background variability always reduces the size of effect that can be detected (Cohen 1977).

If there were a strong scallop recruitment event at Lundy this might lead to an increase in recreational diver-harvesting and possibly the commencement of

legitimate commercial scallop diving. It might also encourage illegal scallop dredging, particularly in the control area. Increased recruitment plus one or more of these changed fishing scenarios would increase the likelihood of detecting a positive effect of the NTZ on scallops.

Having invested in baseline monitoring, it would be unfortunate if these changes occurred, but the opportunity to obtain useful knowledge from them was missed. As discussed previously, the Isle of Man experiment (Beukers-Stewart *et al.* 2005) indicates that scallop populations in the Lundy NTZ and control location are unlikely to differentiate until there has been a significant recruitment event. Until this occurs, further monitoring is likely to continue recording low densities of mostly large (>10cm shell width) scallops in both locations. This would not be very informative or an effective use of resources. So rather than continue monitoring in anticipation of a recruitment event, we recommend suspending monitoring and replacing it with less expensive 'surveillance' sampling targeted specifically at scallop spat. The aim of this surveillance would be to detect when a significant recruitment event has occurred (if one occurs) and hence anticipate when diver-monitoring might be usefully resumed to assess potential effects of the NTZ. If this surveillance were implemented, we would recommend the resumption of monitoring two years after a significant recruitment event. This would give individuals sufficient time to attain a shell width of ~5cm (Hoskin *et al.* 2004), at which point they would be readily detectable by divers.

Surveillance for scallop recruitment could be done by via the deployment of spat collector devices at various sites in the Lundy NTZ and the control location. Such devices are widely used in the collection of wild scallop spat for on-growing in various types of aquaculture operation (Parsons & Robinson 2006). A common device is an artificial substrate consisting of an 'onion' sack containing monofilament 'gillnetting', as used by commercial fishermen. This type of spat-collector is most effectively deployed in mid-water, usually attached to a rope that is anchored to the seabed and buoyed at the surface. Surveillance of spatfall would simply involve annual deployment of spat-collectors at the start of the settlement season and retrieval at the end of the season in order to count their catches of spat. The timing and frequency of spawning is quite variable in *Pecten*

maximus, but it generally occurs in the period from mid-summer to mid-autumn (Brand 2006). The planktonic larval stage of *P maximus* lasts 3-8 weeks (Brand 2006), so spatfall would be expected to take place during late summer to early winter.

If it is decided to resume monitoring to assess potential effects of the NTZ on scallops, we recommend a re-assessment of the number of plots of sampling required within each site. This is because monitoring revealed much greater small-scale variation in scallop abundance than was detected in the pilot study (Hoskin *et al.* 2004) from which the present sampling programme was designed (as was discussed previously). Re-assessment of the number of plots per site for future monitoring should be done via power analyses (as per Hoskin *et al.* 2004) using the present monitoring data.

We would also recommend surveys to record levels of scallop harvesting by divers and improved surveillance for illegal scallop dredging and trawling within the control location. Both would be would be helpful for interpreting the results of future monitoring of scallops. Information on levels of recreational scallop diving activity and the numbers of scallops typically taken by individual divers could be sought from local dive clubs and dive charter boats.

4.10 Interpretation of results for sessile epifauna

During four years of monitoring in circalittoral reef habitats around Lundy there were no NTZ-related changes in the assemblage of sessile epifauna. There were no changes indicating recovery from potential fisheries impacts in the NTZ, nor were there signs of ongoing impacts of fishing in the control location. There was also very little evidence of significant natural changes. The only notable findings were consistent, large-scale (2-10km) spatial differences in abundance between certain areas for certain species. The most notable of these spatial differences were:

i. differences between the NTZ on the east coast of Lundy and the control location on the west coast for species such as dead men's fingers

(*Alcyonium digitatum*), ross coral (*Pentapora fascialis*) and the boring sponge *Cliona celata*; and

ii. differences between replicate sites within the NTZ for species such as the trumpet anemone (*Aiptasia mutablis*), the sponge *Raspalia ramosa* and axinellid sponges.

The magnitude of these spatial differences varied little during the monitoring programme, which indicates the influence of consistent environmental differences among the different areas concerned (*e.g.* differences in wave energy, depth, bedrock *versus* boulder reef, etc.)

The fact that no epifaunal species increased in abundance within the NTZ or declined in abundance in the fished control location indicates that these taxa are generally insensitive or resilient to the types and levels of fishing that they were once exposed to within the NTZ and which they are still exposed to outside. In relation to potential impacts, the main type of fishing of relevance to Lundy's sessile reef epifauna is commercial potting for lobster and crabs. The absence of any evident impact of potting on the abundances of sessile epifauna is consistent with the findings of Eno *et al.* (2001), who did a more explicit study of the physical impacts of lobster pots on these fauna.

Although the Lundy NTZ does not appear to have enhanced populations of sessile epifauna, it is nevertheless significant for the management of the Lundy MNR that several species that are important for nature conservation have their greatest local abundances within NTZ. Important epifauna that were most abundant within the NTZ included *Eunicella verrucosa*, *Aiptasia mutablis*, *Raspalia ramosa* and axinellid sponges. If increased fishing and/or new forms of fishing within the Lundy MNR ever threatened these taxa, Natural England could derive some reassurance from the fact that they had significant strongholds within NTZ.

Whilst the cessation of fishing does not appear to have relieved long-lived sessile epifauna within the NTZ from significant physical disturbance, it may be having more-subtle, indirect effects on this assemblage that are still developing. If that is the case, the data gathered thus far provide a robust baseline against which potential future changes could be assessed.

If long-lived sessile epifauna in the Lundy NTZ continue showing no changes indicating recovery from potential impacts of previous fishing, this could be interpreted as a failure of the NTZ in terms of its original nature conservation justification. This could weaken the case for NTZs in other areas where there is a similar combination of fisheries and nature conservation interests.

4.11 Considerations for future research on sessile epifauna

Whilst it was concluded that sessile epifauna on circalittoral rocky reefs at Lundy have thus far been generally insensitive or resilient to physical interactions with commercial potting gear, it should not be assumed that this would remain the case were there a substantial increase in potting effort. If potting effort were likely to increase greatly around Lundy, we would recommend continued monitoring of epifauna to maintain capacity to assess potential impacts outside the NTZ. We believe, however, that there is little scope for the Lundy MNR to accommodate any significant increase in potting effort, so this is not a strong justification for continued monitoring of epifauna.

To provide for a further assessment the physical effects of potting gear on epifauna, in 2007 we replicated epifauna monitoring in two additional sites in the Lundy NTZ where we have consistently deployed pots for experimental sampling of lobsters and crabs. The usual epifauna monitoring sites in the NTZ were kept free of experimental potting to prevent it confounding attempts to assess effects of the NTZ on epifauna. These additional data were collected to provide for a test of the hypothesis that sessile epifauna were not physically impacted by experimental potting in the NTZ (which was a cause for concern at the start of this study). This additional sampling was done opportunistically and, unfortunately, it was not possible to analyse and interpret the resultant data (see Appendix 2) for this report. Having dived in the parts of the NTZ where experimental potting was done and observed the epifauna there, we would predict that the result of this analysis would support our previous conclusion that potting gear does not directly affect sessile epifauna to any significant degree. We recommend that at some point in the future, the additional data should be analysed to test this prediction formally.

Whilst it seems unlikely that Lundy's sessile epifauna will show future changes that are directly related to fishing, or its cessation within the NTZ, interactions with fished species such as lobster might yet produce indirect effects on this assemblage. The best-known example of such effects comes from two marine reserves in northern New Zealand – the Cape Rodney to Okakari Point Marine Reserve and the Tawharanui Marine Park. When these reserves were first designated, rocky habitats in many shallow subtidal areas were dominated by encrusting corraline red algae due to high levels of grazing by sea urchins (*Evechinus chloroticus*) – so-called 'urchin barrens'. During the next 20 years, urchin barrens in many parts of these reserves underwent a visibly and ecologically dramatic transformation to habitats dominated by brown macroalgae (mixed fucoid habitat or kelp forest depending on depth). The cause of this transformation was increased predation of urchins by spiny lobster (*Jasus edwardsii*) and red snapper (*Pagrus auratus*), which had both increased in abundance and size under protection from fishing (Cole *et al.* 1990, MacDiarmid & Breen 1993, Babcock *et al.* 1999).

In the context of Lundy, it is worth noting that when spiny lobster and red snapper were first seen to increase in these New Zealand reserves, there was no expectation that their proliferation would have such profound ecological consequences. Nevertheless, analogous changes of a similarly dramatic nature are unlikely at Lundy because there is no conspicuously dominant grazer that is also eaten by *Homarus gammarus*, nor is there any obviously grazer-dominated habitat equivalent to the New Zealand urchin barrens.

Returning to Lundy's circalittoral sessile epifauna, which is the main interest here, one mechanism by which they might be indirectly affected by the NTZ involves the velvet crab *Necora puber*. Recall that the abundance of velvet crabs appears to have declined significantly around Lundy since establishment of the NTZ and that this is potentially due to increased predation and/or competition from lobsters. At Lundy, circalittoral sponges, bryozoans, ascidians and cnidarians frequently co-occur with a variety of turf-forming brown and red algae, which in turn form an important part of the diet of velvet crabs (Choy 1986). Whilst it seems doubtful that velvet crabs could be as potent a grazing force as the urchin *Evechinus*

chloroticus in New Zealand, it is plausible that their decline might increase algal cover and leave less space available for recruitment of epifauna. If this occurred, we would predict only subtle changes in the abundances of some epifauna, rather than anything akin to the 'urchin barren to kelp forest' transformation seen in New Zealand marine reserves.

Sponges, bryozoans, ascidians and cnidarians are unlikely to be directly affected by the proliferation of lobsters within the Lundy NTZ as homarid lobsters typically do not eat such taxa (Cobb & Wahle 1994, Childress & Jury 2006, Cobb & Castro 2006). Lobsters might affect these taxa indirectly via interactions with other species that do eat them, but we know of no obvious candidates. Sponges, bryozoans, ascidians and cnidarians are typically well-defended chemically and/or physically and often have low nutritional content, so they are generally less affected by predation than many other sessile fauna (Paul 1992, Butler 1995). Nevertheless, they are not immune from predation and there is evidence of changes in such taxa due to specialist predators, such as certain types of fish (*e.g.* Ayling 1981) and generalists, such as sea urchins (*e.g.* Watanabe & Harrold 1991).

Given evidence of the kind of dramatic indirect effects of marine reserves seen in New Zealand, it is inevitable that those studying marine reserves elsewhere in the World will attempt to identify critical habitat-structuring species (so-called 'keystone' species) and trophic cascades that might give rise to analogous indirect effects in their systems. According to Hall (1999), however, attempts to predict the indirect ecological effects of changes in fishing effort are likely to fail for all but the most well-studied ecosystems in which key ecological interactions have been carefully elucidated via rigorous experimentation. In support of this view, Hall (1999) cites an account by Elner & Vadas (1990) of attempts over 15 years to elucidate the relations between lobster (*Homarus americanus)* and sea urchins off the north-west coast of Canada. It was initially assumed that *H. americanus* was a keystone predator of urchins and that urchin numbers and the prevalence of urchin barrens increased when lobsters were overfished and decreased when fishing pressure was reduced. After much study and experimentation it was eventually discovered that the main factor affecting urchin numbers was a long-term (15-20

year) cycle in seawater temperature and that predator control was much less important than had been assumed.

Whilst we may not be able to predict the likely mechanism, we believe there is still potential for indirect effects of the Lundy NTZ on sessile epifauna and therefore a good case for further monitoring of this assemblage. There is no compelling reason, however, why future monitoring of sessile epifauna need be consecutive with monitoring thus far. As reported previously, sessile epifauna at Lundy have so far shown no significant temporal changes. As such, we have precise knowledge of the baseline composition of this assemblage in each sampling location. Hence, if monitoring was suspended for a few years and then resumed later, it is unlikely that this would compromise any future attempt to assess potential changes in epifauna due to the NTZ.

The question of how long to suspend monitoring for before resuming is a difficult one. We believe that indirect effects of the NTZ are more likely than direct effects for sessile epifauna, but if we cannot reliably predict likely mechanisms of indirect effects, as Hall (1999) argues, then nor can we predict how long it might take such effects to emerge. The literature on effects of marine reserves provides few useful guides either. In the three studies we know of where marine reserves are believed to have indirectly affected sessile, sublittoral benthos these effects were first detected 3 years post-designation (in a Tasmanian study reported by Edgar & Barret 1999), 11 years post-designation (in an Italian study reported by Micheli *et al.* 2005) and 19 years post-designation (the above-mentioned New Zealand example reported by Babcock *et al.* 1999). In the latter two studies, indirect effects may have emerged several years prior to their first detection because there had been either no previous monitoring (*e.g.* Micheli *et al.* 2005), or a long interval since previous monitoring (16 years previously in the case of Babcock *et al.* 1999). In the absence of any other relevant information, we therefore recommend that if monitoring to assess effects of the Lundy NTZ on sessile epifauna is suspended, it should be resumed after 5-10 years.

To better assess potential mechanisms for future changes in sessile epifauna at Lundy, and the likely time-scale of such changes, it would be instructive to know

why epifaunal populations are currently relatively static. There are two possible explanations: *(i)* either there is negligible recruitment and mortality (*i.e.* static equilibrium), or, *(ii)* there is regular mortality and recruitment in equal measure (*i.e.* dynamic equilibrium). The potential significance of these different scenarios can be seen with reference to the earlier suggestion that sessile epifauna might be impacted by increased cover of turf-forming algae due to reduced numbers of velvet crabs. If new recruitment to epifaunal populations is low and/or infrequent such that most individuals are several years old, it is unlikely that increased cover of turf-forming algae would cause a rapid epifaunal response, particularly in tall epifauna (*e.g.* pink sea fan, branching sponges, etc.) as these should be sufficiently well-established to have escaped from competition with turf-forming algae. If there is regular turnover of epifaunal populations, however, then increased cover of turf-forming algae could cause more rapid changes in epifaunal populations. In this scenario, new recruits would find it much harder to settle and grow to a size where competition for space with algae ceased being a problem.

Existing data cannot provide information on turnover within epifaunal populations because monitoring to assess potential effects of the NTZ requires randomised spatial sampling (because ANOVA requires data that are independent from time-to-time). Information on turnover could only be obtained via repeated monitoring of fixed quadrats to observe the recruitment, growth and mortality of individual animals (*e.g.* see the work of Cocito *et al.* 1998 on *Pentapora fascialis*). As well as being useful for predicting potential changes in epifauna due to protection from fishing, information on turnover within epifaunal populations would be useful for assessing their likely recoverability in the event of an anthropogenic impact.

4.12 Summary of conclusions

Of 20 taxa that were monitored only one, the lobster *Homarus gammarus*, appears to have derived an unambiguous benefit from the Lundy NTZ. This was evidenced by the increased abundance and size of landable-sized lobsters inside the NTZ and the increased abundance of undersized lobsters within and adjacent to the NTZ. The latter finding is potential evidence that the Lundy NTZ has produced a spillover benefit to the surrounding lobster fishery. Brown crab increased

significantly in size within the NTZ, but sample size was very small so this may have been a statistical artefact rather than an effect of the NTZ. Velvet crab declined significantly in abundance in the NTZ and it is believed that this is most likely the result of increased predation and/or competition from lobsters.

There is a range of likely explanations for why the remaining taxa showed no apparent effects of the Lundy NTZ. The lack of response in spider crabs is almost certainly because they are too itinerant to benefit from a NTZ as small as that at Lundy. We cannot envisage any realistic change in circumstances in which spider crabs could show an effect of the Lundy NTZ in the future. Scallops and sessile epifauna also showed no effects of the Lundy NTZ, but there are reasons to expect that they might show effects in the future.

We believe that scallops showed no apparent effects of the Lundy NTZ because densities and levels of fishing (by divers) in the control location were both too low to permit scope for significant differentiation. At present, scallop populations in both locations mostly comprise only a few large, old individuals – there appears to have been no significant recruitment in either location for several years. If a significant recruitment did occur, increased abundance of scallops might lead to increased scallop gathering in the control location and eventually a detectable difference in size and density relative to the NTZ.

There were no significant changes in sessile epifauna in the NTZ throughout the four-year study, so it was concluded that they were generally insensitive or resilient to the forms of fishing that were excluded from the NTZ. This view was strengthened by the fact that there were also no significant changes in sessile epifauna in nearby areas where the same fishing activities have continued. Despite the unresponsiveness of this assemblage thus far, we believe there is still potential for the NTZ to cause indirect effects, most likely via trophic cascades involving fished species such as lobster and crabs. Indirect effects of marine reserves on sessile benthos have been observed elsewhere in the World, but they typically take much longer to emerge than direct effects on fished species and their mechanisms are very hard to predict.

4.13 Summary of recommendations for future work

	1. Recommendations in relation to lobsters and crabs (from Section 4.7)	Priority
1.1	Continued experimental potting to test for potential effects of the Lundy NTZ on the abundance and size of lobster, brown crab and velvet crab (spider crab not a priority, but can continue being monitored at no extra cost).	**High**
1.2	A tag-recapture programme for lobsters (using streamer tags) to measure migration into and out of monitoring locations and so assess 'spillover' from the Lundy NTZ. Undersized lobsters are the main priority for streamer tagging. For reliable (unbiased) assessment of spillover, tagging and recapture should be done in the course of continued monitoring.	**High**
1.3	New surveys to record levels of commercial potting effort in the control and reference locations used for monitoring lobster and crabs (to help interpret future variations in their abundance and size).	**Medium**
1.4	Improved surveillance of illegal potting in the Lundy NTZ.	**Medium**
1.5	New surveys to compare estimates of velvet crab abundance obtained via sampling with standard parlour pots *versus* pots modified to exclude lobsters (to assess whether the catch rate of lobsters affects the 'catchability' of velvet crabs).	**Medium**
1.6	Measures to promote reports of streamer-tagged lobsters caught by commercial fishermen (to obtain information on the growth and movements of lobsters in addition to that obtained via the fisheries-independent tag-recapture programme recommended above (1.2)).	**Medium**
1.7	Results for lobsters in the Lundy NTZ to be used as the basis for an economic and biological cost-benefit analysis of artificial (hatchery-based) stock enhancement *versus* natural (NTZ-based) stock enhancement.	**Low**
	2. Recommendations in relation to scallops (from Section 4.9)	
2.1	Suspend monitoring to test for potential effects of the Lundy NTZ on scallops.	**High**
2.2	Implement 'surveillance' sampling of scallop spatfall (using 'onion' sack spat-collection devices) to detect a significant recruitment event, if one occurs.	**Medium**

2.3	Contingency to resume monitoring to test for potential effects of the Lundy NTZ on scallops no sooner than two years after a significant recruitment event.	**Medium**
2.4	New surveys to record scallop-harvesting effort by divers in the control location within the Lundy MNR (in the event of further monitoring to assess effects of the Lundy NTZ on scallops).	**Low**
3. Recommendations in relation to sessile epifauna (from Section 4.11)		
3.1	Suspension of monitoring to test for potential effects of the Lundy NTZ on sessile epifauna.	**High**
3.2	Contingency to resume monitoring to test for potential effects of the Lundy NTZ on sessile epifauna in 5-10 years (or when new information indicates it would be appropriate to do so; *e.g.* see recommendation 3.3, below).	**High**
3.3	New monitoring of epifauna in fixed quadrats to assess rates of growth of individual animals and turnover within populations (to inform prediction of the time-scale of potential future effects of the NTZ on epifauna).	**Medium**

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APPENDIX 1 – INTERPRETATION OF ANOVA MODELS

Table A1.1. Abundances of lobster and crabs: interpretation of terms in the ANOVA model used to test hypotheses on the abundances of lobster and crabs in NTZ *versus* Near Control locations (CON). This ANOVA is based on an experimental design with 4-factors; LOCATION, SITE, YEAR and TIME. Note that in some instances it was necessary to pool data across TIMES (YEAR) and/or SITES (LOCATION) prior to analysis, in which case terms for these factors do not appear in the ANOVA.

Variance factor	Summarises:
1. LOCATION	**Not tested, but decomposed into two component factors that were tested (1.1.& 1.2, below)**
1.1 LO: NTZ *v* CON	Difference in mean abundance between the NTZ and Near Control locations, averaged across years.
1.2 LO: CON	Difference in mean abundance between Near Control locations, averaged across years.
2. SITES (LOCATIONS)	**Not tested, but decomposed into two component factors that were tested (2.1.& 2.2, below)**
2.1 SITES (NTZ)	Difference in mean abundance between replicate sites within the NTZ, averaged across years
2.2 SITES (CON)	Difference in mean abundance between the replicate sites within Near Control locations, averaged across years
3. YEAR	**Difference in mean abundance between years, averaged across all locations**
4. TIME (YE)	**Differences in mean abundance among times of sampling within each year, averaged across locations.**
5. YEAR x LOCATION	**Not tested, but decomposed into two component factors that were tested (5.1.& 5.2, below)**
5.1 YE x LO: NTZ *v* CON	Year-to-year variation in the pattern of mean abundances between NTZ and Near Control locations.
5.2 YE x LO: CON	Year-to-year variation in the pattern of mean abundances between Near Control locations.
6. LOCATION x TIME (YEAR)	**Not tested, but decomposed into two component factors that were tested (6.1.& 6.2, below)**
6.1 TI (YE) x LO: NTZ *v* CON	Variation in mean abundances for NTZ *versus* Near Control locations from time-to-time within years.
6.2 TI (YE) x LO: CON	Variation in mean abundances between Near Control locations from time-to-time within years.
7. YEAR x SITE (LOCATION)	**Not tested, but decomposed into two component factors that were tested (7.1.& 7.2, below)**
7.1 YE x SI (NTZ)	Year-to-year variation in mean abundances between sites within the NTZ location.
7.2 YE x SI (CON)	Year-to-year variation in mean abundances between sites within Near Control locations.
8. TIME (YEAR) x SITE (LOCATION)	**Not tested, but decomposed into two component factors that were tested (8.1.& 8.2, below)**
8.1 TI (YE) x SI (NTZ)	Variation in mean abundances between sites in the NTZ location from time-to-time within years.
8.2 TI (YE) x SI (CON)	Variation in mean abundances between sites in Near Control locations from time-to-time within years.
9. RESIDUAL	**Not tested, but decomposed into two component factors that were tested (9.1.& 9.2, below)**
9.1 RES: NTZ	Variation in mean abundances among replicate strings of pots in each time and site within the NTZ location.
9.2 RES: CON	Variation in mean abundances among replicate strings of pots in each time and site within Near Control locations.

Table A1.2. Abundances of lobster and crabs: interpretation of terms in the ANOVA model used to test hypotheses on the abundances of lobster and crabs in NTZ *versus* Far Reference locations (REF). This ANOVA is based on an experimental design with 4-factors; LOCATION, SITE, YEAR and TIME. Note that in some instances it was necessary to pool data across TIMES (YEAR) and/or SITES (LOCATION) prior to analysis, in which case terms for these factors do not appear in the ANOVA.

Variance factor	Summarises:
1. LOCATION	**Not tested, but decomposed into two component factors that were tested (1.1.& 1.2, below)**
1.1 LO: NTZ *v* REF	Difference in mean abundance between the NTZ and Far Reference locations, averaged across years.
1.2 LO: REF	Difference in mean abundance between Far Reference locations, averaged across years.
2. SITES (LOCATIONS)	**Not tested, but decomposed into two component factors that were tested (2.1.& 2.2, below)**
2.1 SITES (NTZ)	Difference in mean abundance between replicate sites within the NTZ, averaged across years
2.2 SITES (REF)	Difference in mean abundance between the replicate sites within Far Reference locations, averaged across years
3. YEAR	**Difference in mean abundance between years, averaged across all locations**
4. TIME (YE)	**Differences in mean abundance among times of sampling within each year, averaged across locations.**
5. YEAR x LOCATION	**Not tested, but decomposed into two component factors that were tested (5.1.& 5.2, below)**
5.1 YE x LO: NTZ *v* REF	Year-to-year variation in the pattern of mean abundances between NTZ and Far Reference locations.
5.2 YE x LO: REF	Year-to-year variation in the pattern of mean abundances between Far Reference locations.
6. LOCATION x TIME (YEAR)	**Not tested, but decomposed into two component factors that were tested (6.1.& 6.2, below)**
6.1 TI (YE) x LO: NTZ *v* REF	Variation in mean abundances for NTZ *versus* Far Reference locations from time-to-time within years.
6.2 TI (YE) x LO: REF	Variation in mean abundances between Far Reference locations from time-to-time within years.
7. YEAR x SITE (LOCATION)	**Not tested, but decomposed into two component factors that were tested (7.1.& 7.2, below)**
7.1 YE x SI (NTZ)	Year-to-year variation in mean abundances between sites within the NTZ location.
7.2 YE x SI (REF)	Year-to-year variation in mean abundances between sites within Far Reference locations.
8. TIME (YEAR) x SITE (LOCATION)	**Not tested, but decomposed into two component factors that were tested (8.1.& 8.2, below)**
8.1 TI (YE) x SI (NTZ)	Variation in mean abundances between sites in the NTZ location from time-to-time within years.
8.2 TI (YE) x SI (REF)	Variation in mean abundances between sites in Far Reference locations from time-to-time within years.
9. RESIDUAL	**Not tested, but decomposed into two component factors that were tested (9.1.& 9.2, below)**
9.1 RES: NTZ	Variation in mean abundances among replicate strings of pots in each time and site within the NTZ location.
9.2 RES: REF	Variation in mean abundances among replicate strings of pots in each time and site within Far Reference locations.

Table A1.3. Abundances of lobster and crabs - ancillary analysis for testing the spillover hypothesis: interpretation of terms in the ANOVA model used to test hypotheses on the abundances of lobster and crabs in Near Control (Con) *versus* Far Reference (Ref) locations. This ANOVA is based on an experimental design with 4-factors; DISTANCE, SITE, YEAR and TIME.

Variance factor	Summarises:
1. DISTANCE: CON V REF	Difference in mean abundance between Near Control locations *versus* Far Reference locations in South Wales and North Devon with data averaged across years.
2. LOCATION (DISTANCE)	Difference in mean abundances between replicate Near Control locations and Far Reference locations with data averaged across years.
3. SITES (DISTANCE X LOCATION)	Difference in mean abundances between replicate sites within each Near Control and Far Reference with data averaged across years.
4. YEAR	Difference in mean abundance from year-to-year with data averaged across distances and locations
5. TIME (YEAR)	Variation from time-to-time within years with data averaged across all locations
6. DISTANCE X YEAR	Year-to-year variation in the pattern of difference between Near Control *versus* Far Reference locations.
7. DISTANCE X TIME (YEAR)	Variation from time-to-time within years in the pattern of difference between Near Control *versus* Far Reference locations.
8. YEAR X LOCATION (DISTANCE)	Year-to-year variation in the pattern of difference between replicate Near Control locations *versus* Far Reference locations.
9. TIME (YEAR) X LOCATION (DISTANCE)	Variation from time-to-time within years in the pattern of difference between replicate locations at each distance.
10. YEAR X SITE (DISTANCE X LOCATION)	Year-to-year variation in the pattern of difference between replicate sites within locations.
11. TI ME(YE) X SITE (DI X LO)	Variation from time-to-time within years in the pattern of difference between replicate sites within locations.
12. RESIDUAL	Variation in mean abundances among replicate strings of pots within the different combinations of time, site and year.

Table A1.4. Sizes of lobster and crabs: interpretation of terms in the ANOVA model used to test hypotheses on the mean sizes of lobster and crabs in NTZ *versus* Near Control locations. This ANOVA is based on a design with 2-factors; LOCATION and YEAR.

Variance term	Summarises
LOCATION	Difference in mean abundance between the NTZ and control location, averaged across years.
YEAR	Changes in mean abundance between years, averaged across locations
LOCATION X YEAR	Change in the difference in mean abundance between locations from year-to-year.
RESIDUAL	Difference in mean abundance among transects within plots

Table A1.5. Abundance of scallops: interpretation of terms in the ANOVA model used to test hypotheses on the mean abundances of scallops in NTZ *versus* control locations. This ANOVA is based on an experimental design with 4-factors; LOCATION, YEAR, SITE and PLOT.

Variance term	Summarises
LOCATION	Difference in mean abundance between the NTZ and control location, averaged across years.
SITE(LOCATION)	Difference in mean abundance between sites within NTZ and control locations, averaged across years.
YEAR	Changes in mean abundance between years, averaged across locations
PLOTS(LOCATION x SITE)	Difference in mean abundance among plots in different combinations of location and site.
LOCATION x YEAR	Change in the difference in mean abundance between locations from year-to-year.
YEAR x SITE(LOCATION)	Change in the difference in mean abundance between sites within locations from year-to-year.
YEAR x PLOTS(LO x SI)	Change in the difference in mean abundance among plots within sites from year-to-year.
RESIDUAL	Difference in mean abundance among transects within plots

Table A1.6. Size of scallops: interpretation of terms in the ANOVA model used to test hypotheses on the mean size of scallops in NTZ *versus* control locations. This ANOVA is based on a design with 2-factors; LOCATION and YEAR.

Variance term	Summarises
LOCATION	Difference in mean abundance between the NTZ and control location, averaged across years.
YEAR	Changes in mean abundance between years, averaged across locations
LOCATION x YEAR	Change in the difference in mean abundance between locations from year-to-year.
RESIDUAL	Difference in mean abundance among transects within plots

Table A1.7. Abundances of epifauna: interpretation of terms in the ANOVA model used to test hypotheses on the mean abundances of epifauna in NTZ *versus* control locations. This ANOVA is based on an experimental design with 3-factors; LOCATION, SITE and PLOT.

Variance term	Summarises
LOCATION	Difference in mean abundance between the NTZ and control location with data averaged across years.
SITE(LOCATION)	Difference in mean abundance between sites within NTZ and control locations with data averaged across years.
YEAR	Changes in mean abundance between years, with data averaged across locations.
PLOTS(LO x SI x YE)	Difference in mean abundance among plots in different combinations of location, site and year
LOCATION x YEAR	Change in the difference in mean abundance between locations from year-to-year.
YEAR x SITE (LOCATION)	Change in the difference in mean abundance between sites within locations from year-to-year.
RESIDUAL	Difference in mean abundance among quadrats within plots

APPENDIX 2 – ADDITIONAL DATA ON SESSILE EPIFAUNA

Table A2.1. Abundances of sessile epifauna: data collected in 2007 on the abundances of sessile epifauna (per 75 cm x 75 cm quadrat) at two sites in the Lundy NTZ where annual experimental potting for lobsters and crabs was carried out and two further NTZ sites in that were not subject to experimental potting. These data could be used to test the hypothesis that sessile epifauna were not physically impacted by experimental potting in the NTZ.

Treatment	Site	Plot	Quadrat	Axinella dissimilis	Axinella infundibuliformis	Axinella damicornis	Homaxinella subdola	Raspalia ramosa	Polymastia boletiformis	Polymastia mammilaris	Cliona celata	Alcyonium digitatum	Alcyonium glomeratum	Eunicella verrucosa	Anemonia viridis	Aiptasia mutablis	Pentapora fascialis	Stolonica socialis
NTZ + potting	1	1	1	7	0	0	0	2	0	1	0	0	0	0	0	7	0	0
NTZ + potting	1	1	2	7	1	3	0	0	0	0	0	0	0	0	0	9	0	0
NTZ + potting	1	1	3	3	0	0	2	0	0	1	0	0	0	1	0	30	0	0
NTZ + potting	1	1	4	2	0	0	0	2	0	1	0	0	0	0	0	17	0	0
NTZ + potting	1	1	5	4	0	0	2	2	0	1	0	0	0	0	0	23	0	0
NTZ + potting	1	1	6	3	0	0	0	4	0	0	0	0	0	0	0	6	0	0
NTZ + potting	1	1	7	0	0	1	5	2	0	0	0	0	0	0	0	24	0	0
NTZ + potting	1	1	8	3	0	0	1	2	0	0	0	0	0	0	0	30	0	0
NTZ + potting	1	1	9	14	0	0	5	5	0	0	0	0	0	0	0	46	0	0
NTZ + potting	1	1	10	1	0	0	0	0	0	0	0	0	0	0	2	5	0	0
NTZ + potting	1	1	11	0	0	0	5	2	0	3	0	0	0	0	0	29	0	0
NTZ + potting	1	1	12	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
NTZ + potting	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	2	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NTZ + potting	1	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	2	8	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0
NTZ + potting	1	2	9	1	0	0	0	0	0	0	0	0	0	0	0	5	0	0
NTZ + potting	1	2	10	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0
NTZ + potting	1	2	11	5	0	0	0	0	0	0	0	0	0	0	0	7	0	0
NTZ + potting	1	2	12	1	0	0	0	0	0	0	0	0	0	0	0	12	0	0
NTZ + potting	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	2	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0
NTZ + potting	1	3	3	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0
NTZ + potting	1	3	4	2	0	0	1	2	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	5	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	6	6	0	0	0	2	0	0	0	0	0	0	0	0	1	0
NTZ + potting	1	3	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	8	5	0	0	0	2	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	9	4	0	0	2	4	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	10	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	11	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	3	12	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	4	1	0	0	0	1	0	0	0	0	0	0	3	0	0	1	0
NTZ + potting	1	4	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	4	3	2	1	0	1	0	0	1	1	0	0	0	0	0	0	0
NTZ + potting	1	4	4	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0
NTZ + potting	1	4	5	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0
NTZ + potting	1	4	6	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0
NTZ + potting	1	4	7	6	0	0	1	1	0	5	0	0	0	1	0	0	0	0
NTZ + potting	1	4	8	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0
NTZ + potting	1	4	9	1	0	0	5	0	0	0	0	0	0	0	0	0	2	0
NTZ + potting	1	4	10	2	0	0	3	0	0	1	0	0	0	0	0	3	0	0
NTZ + potting	1	4	11	0	0	0	6	0	0	1	0	0	0	0	0	1	0	0
NTZ + potting	1	4	12	0	0	0	4	2	0	2	0	0	0	0	0	1	0	0
NTZ + potting	1	5	1	1	0	0	8	4	0	5	0	0	0	0	0	0	0	0
NTZ + potting	1	5	2	4	0	0	9	0	0	7	0	0	0	1	0	0	0	0
NTZ + potting	1	5	3	3	0	0	3	0	0	2	0	0	1	0	0	1	0	0
NTZ + potting	1	5	4	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0
NTZ + potting	1	5	5	0	0	0	1	1	0	0	0	0	0	0	0	8	0	0
NTZ + potting	1	5	6	1	0	0	0	2	0	0	0	0	0	0	0	14	0	0
NTZ + potting	1	5	7	0	0	3	0	0	0	0	1	0	0	0	0	3	1	0
NTZ + potting	1	5	8	0	0	1	9	2	0	4	0	0	0	0	0	8	0	0

Treatment	Site	Plot	Quadrat	Axinella dissimilis	Axinella infundibuliformis	Axinella damicornis	Homaxinella subdola	Raspalia ramosa	Polymastia boletiformis	Polymastia mammillaris	Ciona celata	Alcyonium digitatum	Alcyonium glomeratum	Eunicella verrucosa	Anemonia viridis	Aiptasia mutabilis	Pentapora fascialis	Stolonica socialis
NTZ + potting	1	5	9	0	0	0	6	0	0	1	0	0	0	0	0	29	0	0
NTZ + potting	1	5	10	0	0	0	12	2	0	4	0	0	0	0	0	27	0	0
NTZ + potting	1	5	11	0	0	0	4	2	0	3	0	0	0	0	0	12	0	0
NTZ + potting	1	5	12	0	0	0	6	2	0	2	0	0	0	0	0	14	0	0
NTZ + potting	1	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	6	4	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NTZ + potting	1	6	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	6	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	1	6	7	3	0	0	0	1	0	1	0	0	0	1	0	0	0	0
NTZ + potting	1	6	8	3	1	1	0	1	0	1	0	0	0	0	0	0	0	0
NTZ + potting	1	6	9	0	0	0	0	2	0	0	0	0	2	0	0	0	1	0
NTZ + potting	1	6	10	2	0	0	3	3	0	1	0	0	0	0	0	0	0	0
NTZ + potting	1	6	11	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
NTZ + potting	1	6	12	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0
NTZ + potting	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NTZ + potting	2	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
NTZ + potting	2	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	8	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
NTZ + potting	2	1	11	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
NTZ + potting	2	1	12	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
NTZ + potting	2	2	1	0	0	5	1	0	0	0	0	0	0	0	0	2	0	0
NTZ + potting	2	2	2	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0
NTZ + potting	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	2	4	0	0	6	0	0	0	0	0	0	0	0	0	22	0	0
NTZ + potting	2	2	5	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	2	6	0	0	3	0	0	0	0	0	0	0	0	0	12	0	0
NTZ + potting	2	2	7	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0
NTZ + potting	2	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	2	9	9	0	7	3	0	0	0	0	0	0	0	0	53	0	0
NTZ + potting	2	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	2	11	2	0	0	0	0	0	0	0	0	0	0	0	24	0	0
NTZ + potting	2	2	12	3	0	0	0	0	0	0	0	0	0	0	0	8	0	0
NTZ + potting	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
NTZ + potting	2	3	2	2	0	0	3	3	0	0	0	0	0	0	0	20	0	0
NTZ + potting	2	3	3	2	0	0	1	3	0	0	1	0	0	0	0	25	0	0
NTZ + potting	2	3	4	2	0	0	0	2	0	0	0	0	0	0	0	20	0	0
NTZ + potting	2	3	5	5	0	0	8	3	0	0	0	0	0	0	0	12	0	0
NTZ + potting	2	3	6	3	0	0	3	1	0	1	0	0	0	0	0	10	0	0
NTZ + potting	2	3	7	3	0	0	12	4	0	1	0	0	0	0	0	10	0	0
NTZ + potting	2	3	8	3	0	0	6	2	0	0	0	0	0	0	3	30	0	0
NTZ + potting	2	3	9	1	0	0	3	5	0	0	0	0	0	0	0	40	0	0
NTZ + potting	2	3	10	2	0	0	5	6	1	1	0	0	0	0	1	50	0	0
NTZ + potting	2	3	11	2	0	0	7	4	0	3	1	0	0	0	0	40	0	0
NTZ + potting	2	3	12	0	0	0	4	8	0	1	0	0	0	0	0	20	1	0
NTZ + potting	2	4	1	1	0	0	0	0	0	0	0	0	0	0	0	23	2	0
NTZ + potting	2	4	2	2	0	0	1	3	0	0	1	0	0	0	0	33	0	0
NTZ + potting	2	4	3	0	0	0	0	0	0	0	1	0	0	0	0	7	0	0
NTZ + potting	2	4	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ + potting	2	4	5	9	0	0	3	3	0	0	0	0	0	0	0	19	0	0
NTZ + potting	2	4	6	10	0	1	4	0	0	2	0	0	0	0	0	10	0	0
NTZ + potting	2	4	7	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NTZ + potting	2	4	8	0	0	0	0	0	0	0	0	0	0	0	0	20	2	0
NTZ + potting	2	4	9	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
NTZ + potting	2	4	10	0	0	0	0	0	0	0	0	0	0	0	0	24	4	0
NTZ + potting	2	4	11	2	0	0	0	0	0	0	0	0	0	0	0	27	0	0
NTZ + potting	2	4	12	2	0	0	3	0	0	0	0	0	0	0	0	11	1	0
NTZ + potting	2	5	1	1	0	3	10	0	0	1	0	0	0	0	0	0	0	0
NTZ + potting	2	5	2	2	0	0	0	2	0	0	0	0	0	0	0	1	0	0
NTZ + potting	2	5	3	0	0	3	9	2	0	0	0	0	0	0	0	2	0	0
NTZ + potting	2	5	4	2	0	0	0	3	0	0	0	0	0	0	0	1	0	0

Treatment	Site	Plot	Quadrat	Axinella dissimilis	Axinella infundibuliformis	Axinella damicornis	Homaxinella subdola	Raspalia ramosa	Polymastia boletiformis	Polymastia mammillaris	Ciona celata	Alcyonium digitatum	Alcyonium glomeratum	Eunicella verrucosa	Anemonia viridis	Aiptasia mutabilis	Pentapora fascialis	Stolonica socialis
NTZ + potting	2	5	5	0	0	2	4	0	0	0	0	0	0	0	0	3	0	0
NTZ + potting	2	5	6	0	0	2	1	2	0	0	0	0	0	1	0	0	0	0
NTZ + potting	2	5	7	0	2	0	1	0	0	0	0	0	0	0	0	3	0	0
NTZ + potting	2	5	8	0	0	0	5	2	0	0	0	0	0	0	0	6	0	0
NTZ + potting	2	5	9	0	0	0	2	0	0	0	0	0	0	1	0	4	0	0
NTZ + potting	2	5	10	0	0	2	5	0	0	0	0	0	0	0	0	6	1	0
NTZ + potting	2	5	11	0	0	0	2	0	0	0	0	0	0	0	0	17	0	0
NTZ + potting	2	5	12	0	0	2	3	1	0	0	0	0	0	0	0	9	1	0
NTZ + potting	2	6	1	0	0	0	0	0	0	0	0	0	0	0	0	15	1	0
NTZ + potting	2	6	2	0	0	0	1	0	0	0	0	0	0	0	0	10	0	0
NTZ + potting	2	6	3	0	0	1	0	1	0	0	0	0	0	1	0	12	0	0
NTZ + potting	2	6	4	0	0	1	2	2	0	0	0	0	0	1	0	6	0	0
NTZ + potting	2	6	5	1	0	0	3	0	0	0	0	0	0	0	0	5	0	0
NTZ + potting	2	6	6	0	0	0	4	3	0	0	0	0	0	0	0	20	0	0
NTZ + potting	2	6	7	3	0	2	6	1	0	0	0	0	0	0	0	10	0	0
NTZ + potting	2	6	8	0	0	0	8	4	0	1	0	0	0	1	0	8	0	0
NTZ + potting	2	6	9	6	0	0	8	1	0	0	0	0	0	0	0	15	0	0
NTZ + potting	2	6	10	0	0	0	4	3	0	0	0	0	0	1	0	15	0	0
NTZ + potting	2	6	11	1	0	0	1	0	0	0	0	0	0	0	0	5	1	0
NTZ + potting	2	6	12	0	1	0	3	0	0	0	0	0	0	0	0	12	1	0
NTZ - potting	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	6	5	0
NTZ - potting	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0
NTZ - potting	1	1	3	0	0	0	2	0	0	0	0	0	0	0	0	7	0	0
NTZ - potting	1	1	4	0	0	0	4	6	0	0	0	0	0	0	0	0	2	0
NTZ - potting	1	1	5	0	0	0	10	11	0	0	0	0	0	0	0	56	0	0
NTZ - potting	1	1	6	0	0	0	2	2	0	0	0	0	0	0	0	31	1	0
NTZ - potting	1	1	7	0	0	0	1	0	0	0	0	0	0	0	0	0	5	0
NTZ - potting	1	1	8	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	1	9	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	1	10	0	0	0	16	5	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	1	11	1	0	0	2	1	0	1	0	0	0	0	0	0	0	0
NTZ - potting	1	1	12	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
NTZ - potting	1	2	1	1	0	0	21	7	0	0	0	0	0	0	0	2	0	0
NTZ - potting	1	2	2	1	0	0	12	2	0	0	0	0	0	0	0	4	0	0
NTZ - potting	1	2	3	7	0	0	1	7	0	0	1	0	0	1	0	0	0	0
NTZ - potting	1	2	4	3	0	0	8	5	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	2	5	0	1	0	14	5	0	0	0	0	0	0	0	2	0	0
NTZ - potting	1	2	6	0	1	0	5	0	0	0	0	0	0	0	0	3	0	0
NTZ - potting	1	2	7	0	0	0	5	3	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	2	8	1	0	0	5	3	0	0	0	0	0	1	0	1	1	0
NTZ - potting	1	2	9	0	0	0	4	4	0	0	0	0	0	0	0	6	0	0
NTZ - potting	1	2	10	0	0	0	2	0	0	1	0	0	0	0	0	7	0	0
NTZ - potting	1	2	11	1	0	0	3	0	0	0	0	0	0	0	0	16	0	0
NTZ - potting	1	2	12	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	3	1	0	0	0	3	0	0	0	2	0	0	0	0	7	0	0
NTZ - potting	1	3	2	0	0	0	1	0	0	0	1	0	0	0	0	18	0	0
NTZ - potting	1	3	3	2	0	0	9	0	0	0	0	0	0	0	0	8	2	0
NTZ - potting	1	3	4	0	0	0	1	0	0	0	1	0	0	0	0	5	0	0
NTZ - potting	1	3	5	0	0	0	0	0	0	0	2	0	0	0	0	17	0	0
NTZ - potting	1	3	6	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
NTZ - potting	1	3	7	0	0	0	16	1	0	0	0	0	0	0	0	2	0	0
NTZ - potting	1	3	8	0	0	0	8	7	0	4	0	0	0	0	0	0	0	0
NTZ - potting	1	3	9	0	0	2	13	0	0	0	0	0	0	0	0	4	0	0
NTZ - potting	1	3	10	0	0	1	8	0	0	0	0	0	0	1	0	14	0	0
NTZ - potting	1	3	11	4	0	0	3	3	0	2	0	0	1	0	0	21	0	0
NTZ - potting	1	3	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NTZ - potting	1	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	4	3	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	4	4	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
NTZ - potting	1	4	5	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0
NTZ - potting	1	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	4	7	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
NTZ - potting	1	4	8	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NTZ - potting	1	4	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	4	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	4	11	0	0	0	0	0	0	0	0	0	0	0	0	51	0	0
NTZ - potting	1	4	12	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0

Treatment	Site	Plot	Quadrat	Axinella dissimilis	Axinella infundibuliformis	Axinella damicornis	Homaxinella subdola	Raspalia ramosa	Polymastia boletiformis	Polymastia mammillaris	Ciona celata	Alcyonium digitatum	Alcyonium glomeratum	Eunicella verrucosa	Anemonia viridis	Aiptasia mutabilis	Pentapora fascialis	Stolonica socialis
NTZ - potting	1	5	1	0	0	0	2	1	0	0	1	0	0	0	0	0	1	0
NTZ - potting	1	5	2	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0
NTZ - potting	1	5	3	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
NTZ - potting	1	5	4	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
NTZ - potting	1	5	5	0	0	0	4	5	0	3	0	0	0	0	0	1	0	0
NTZ - potting	1	5	6	1	0	0	0	2	1	4	0	0	0	0	0	0	0	0
NTZ - potting	1	5	7	1	0	0	2	1	0	0	0	0	0	0	0	2	0	0
NTZ - potting	1	5	8	2	0	0	0	1	0	0	0	0	0	0	0	6	0	0
NTZ - potting	1	5	9	3	0	0	2	1	0	0	0	0	0	1	0	2	0	0
NTZ - potting	1	5	10	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
NTZ - potting	1	5	11	0	0	0	0	0	0	1	0	0	0	0	0	24	0	0
NTZ - potting	1	5	12	0	0	0	0	0	1	0	0	0	0	0	0	10	0	0
NTZ - potting	1	6	1	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0
NTZ - potting	1	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	6	3	0	0	0	8	2	0	0	0	0	0	0	0	8	0	0
NTZ - potting	1	6	4	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0
NTZ - potting	1	6	5	0	0	0	8	3	0	0	0	0	0	0	0	0	0	0
NTZ - potting	1	6	6	0	0	0	16	8	0	0	0	0	0	0	0	15	0	0
NTZ - potting	1	6	7	0	0	0	4	3	0	0	0	0	0	0	0	25	0	0
NTZ - potting	1	6	8	0	0	0	6	0	0	1	0	0	0	0	0	18	0	0
NTZ - potting	1	6	9	0	0	0	12	4	0	1	0	0	0	0	0	12	0	0
NTZ - potting	1	6	10	0	0	0	5	5	0	0	0	0	0	0	0	30	0	0
NTZ - potting	1	6	11	2	0	0	9	3	0	0	1	0	0	0	0	15	0	0
NTZ - potting	1	6	12	0	0	0	9	4	0	0	0	0	0	0	0	8	0	0
NTZ - potting	2	1	1	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NTZ - potting	2	1	3	3	0	0	0	0	0	0	1	0	0	1	0	0	0	0
NTZ - potting	2	1	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	9	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	10	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
NTZ - potting	2	1	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	1	12	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	7	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	8	6	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NTZ - potting	2	2	9	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	10	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	2	11	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
NTZ - potting	2	2	12	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	3	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	8	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Treatment	Site	Plot	Quadrat	Axinella dissimilis	Axinella infundibuliformis	Axinella damicornis	Homaxinella subdola	Raspalia ramosa	Polymastia boletiformis	Polymastia mammillaris	Ciona celata	Alcyonium digitatum	Alcyonium glomeratum	Eunicella verrucosa	Anemonia viridis	Aiptasia mutablis	Pentapora fascialis	Stolonica socialis
NTZ - potting	2	4	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	10	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	4	12	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	2	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	4	5	0	1	0	1	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	6	9	0	0	0	1	0	0	1	0	0	0	0	0	0	0
NTZ - potting	2	5	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	5	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTZ - potting	2	6	12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0